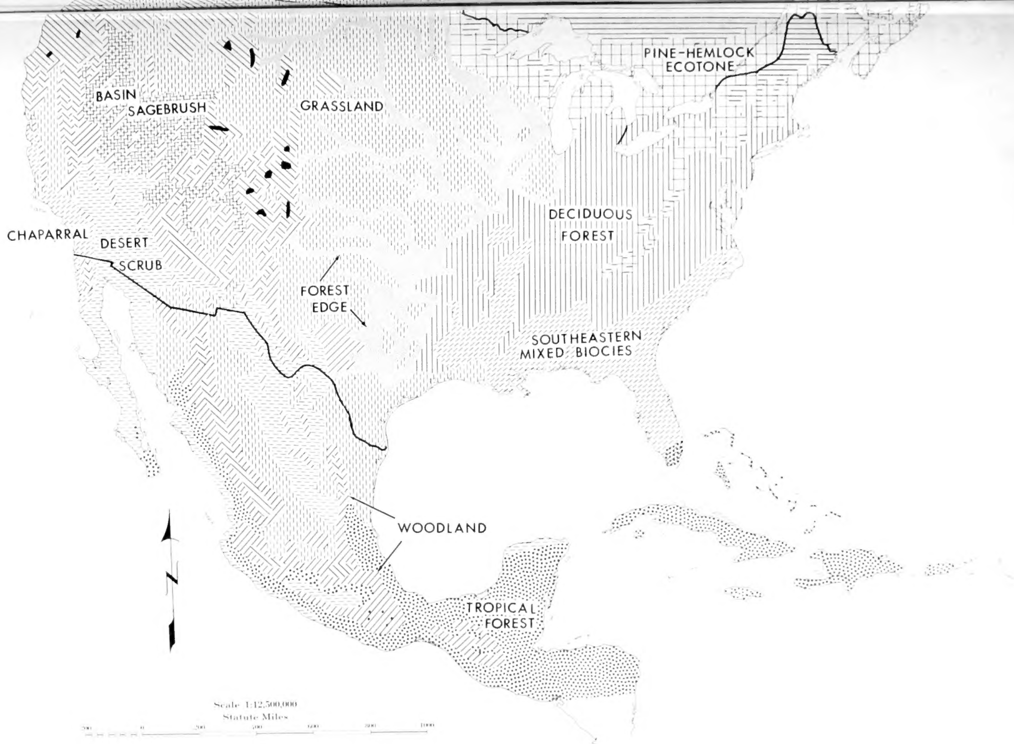
ANIMAL ECOLOGY

S. CHARLES KENDEIGH

Occurrence and Distribution of Biociations in North America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ANIMAL ECOLOGY

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ECOLOGY

S. CHARLES KENDEIGH

Zoology Department
University of Illinois

ANIMAL ECOLOGY

S. Charles Kendeigh

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To my teachers of ecology

LYNDS JONES, OBERLIN COLLEGE

JOHN E. WEAVER, UNIVERSITY OF NEBRASKA

VICTOR E. SHELFORD, UNIVERSITY OF ILLINOIS

Preface

The science of ecology, born at the beginning of the present century after a gestation period of several hundreds of years, has now matured into an honored and respected scholarly discipline and field of research. This book is an effort to summarize the basic concepts and principles of the subject and present the elementary factual information with which a person to be competent in this field should be familiar, especially as these things apply to animals.

After a Background section for orientation, local communities and habitats are discussed in some detail. It is my firm belief that one beginning the study of ecology should first of all become thoroughly acquainted with the places where animals 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. The reader well founded in this knowledge is ready to understand the ecological processes and community dynamics which are presented in the third section. In the fourth and final section, the reader is introduced to the broad field of geographic ecology, which will give him some knowledge of how animals are distributed over the world, and why they occur where they do.

Physiological ecology, the study of the manner in which organisms respond and adjust to environmental factors, is dealt with sparingly. The proper development of this subject takes one extensively into laboratory experimentation, which is best left to the advanced student. Our emphasis is kept on the study of the free-living organism in its natural environment. Although the quantitative aspect of ecology is emphasized, I do not believe that in an introductory book it is desirable to approach the subject from a statistical point-of-view. Too few readers will have an adequate statistical background, and the introduction to the subject matter of ecology should not be delayed until an adequate background of statistics is obtained—as necessary as that is to advanced work in the field.

I have not thought it desirable to devote a special chapter to applied ecology or, more particularly, to wildlife management. The fundamental principles of wildlife management are the same as the fundamental principles of ecology, since wildlife biology is the ecology of game species. Throughout the book, however, I have tried to show the relation of basic concepts to problems in wildlife management. The special obligation of the wildlife manager is to make practical use of these principles for the promotion of wildlife populations.

This book is designed for a course given at the junior-senior-graduate level, to students who have at least a year's background in zoology. I give such a course during the autumn semester. If I were to give it during the spring, I would probably change the order of study of the four sections to I–IV–III–II. Section IV would here substitute for Section II in providing the student with some knowledge of communities before undertaking section III. This would permit field studies late in the spring to be more closely correlated with the discussion of local habitats and communities.

During the first semester at the University of Illinois I have a half-day or a full-day trip every Saturday until winter weather sets in, and there are two half-day winter trips. Also included in the field work is one weekend camping trip to study communities not found locally. The students get to see at first hand a large variety of animals, and to measure population sizes by quantitative methods that may be crude but are 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 is also done in the field to analyze the manner in which both aquatic and terrestrial species respond to environmental factors. There is a small amount of laboratory work for learning quantitative methods of counting plankton, examining different kinds of respiratory systems in aquatic organisms, searching and identifying microorganisms in the soil, experiments in choice of habitats, and map-making. Methods for measuring productivity are discussed but actual practice with these methods is left for an advanced class.

Enough material is given on plants in this book, it is hoped, to bring out their essential place in the ecosystem and to emphasize the bioecological point-of-view. I believe it would be possible for an instructor to use this textbook in a course in general ecology by supplementing in lectures the material and concepts presented in the book with additional material on plants.

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. Checklist 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.

Pertinent references to literature are cited in the text in connection with each major topic. These references serve only as an introduction to the very extensive literature in ecology.

Finally, I wish to acknowledge the help of many persons in the preparation of this text, particularly, Stanley A. Cain, Edward S. Deevey, Ralph W. Dexter, Paul L. Errington, F. E. J. Fry, Clarence J. Goodnight, F. T. Ide, Bostwick Ketchum, Ernst Mayr, Howard T. Odum, Orlando Park, Frank Pitelka, W. E. Ricker, Gordon A. Riley, M. D. F. Udvardy, and R. H. Whittaker. In addition, several of my colleagues at the University of Illinois read and commented on early drafts of chapters. John Riina, of Prentice-

Hall, Inc., was very cooperative in having two or three and occasionally four people read various chapters, and two persons read the entire manuscript. The final manuscript was expertly edited by Oren Hunt, whose help was invaluable.

Illustrations come from several sources. I am most grateful to Dr. Victor E. Shelford for supplying 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 who 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 a number of individuals for supplying photographs or other illustrative material for which acknowledgement is made in the legends of the figures, and to Colleen Nelson, Katherine Little, and Nan Brown for preparing special drawings.

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Champaign, Illinois
S.C.K.

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1

Background:

The 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 of organisms;
2. Regional variations in the abundance of organisms;
3. Temporal changes in the occurrence, abundance, and activities or organisms;
4. The interrelations between organisms in populations and communities;
5. The structural adaptations and functional adjustments of organisms to their physical environment;
6. The behavior of organisms under natural conditions;
7. The evolutionary development of all these interrelations; and
8. The biological productivity of nature and how this may best serve mankind.

METHODS

To the achievement of these objectives the following methods or points of attack are fundamental:

Observation in detail of how organisms live under natural conditions.

PROMINENT LEADERS IN THE DEVELOPMENT OF ECOLOGY IN AMERICA


C.C. Adams, animal ecologist (courtesy Dorothy Kehaya).


F.E. Clements, plant ecologist.


Aldo Leopold, wildlife manager.

Concentration of studies not on the rare but on the most abundant and influential organisms in the community.

Measurement and evaluation of physical factors in the actual microhabitat occupied by organisms.

Correlation of findings of experimental studies of organisms in the laboratory with observations of those organisms in the field.

Use of quantitative—not just qualitative—**techniques** in field studies as well as laboratory studies.

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 in 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 become familiar with and employ good statistical procedures (Williams 1954).

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 compre-

hending the beauty of its organization is perhaps better in proportion (Macfadyen 1957: 246).

RELATION TO OTHER SCIENCES

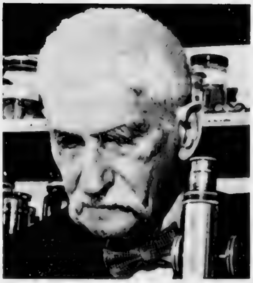
Ecology is one of the three main divisions of biology; the other two being morphology and physiology. The emphasis in morphology is on understanding the structure of organisms; in physiology, on how they function; and in ecology, on their adjustments to the environment. These divisions overlap broadly. 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. The evolution of adaptation and of species is of mutual interest to the ecologist and to the geneticist; bioclimatology is a connecting link between ecology and physiology. 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.

In this book we shall survey the fundamentals and basic facts of animal ecology. We will study *community ecology,* the local distribution of animals in various habitats, the recognition of community units, and succession; *ecological dynamics,* the processes of dispersal, ecesis, reaction, coaction, productivity, competition, speciation, and regulation of abundance; and *geographic ecology,* geographic distribution, palaeoecology, and biomes. We will also be interested throughout the text with how species and individuals respond and adjust to the physical factors of their environment, but a full study of *physiological ecology* must be left to another time and place.

When special consideration of their ecology is given to one or another taxonomic group, we speak



E.A. Birge, limnologist.

Henry C. Cowles, plant ecologist (courtesy R.J. Pool).

Victor E. Shelford, animal ecologist.

of *mammalian ecology, avian ecology, insect ecology, parasitology,* and so on. 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. *Animal 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,* 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 BC, 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 Danish 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 of the fact 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 (eg., 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.

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 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 world-wide distribution of animals made by the French naturalist, Georges L. L. Buffon (lived 1707–1788), and the explorations of the German botanist, Alexander von Humboldt (lived 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 (1890–1898) 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 effect 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, 1926, 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 in Europe 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 Howard and Eugene 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 AD. 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 three-fold 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 1897–1899 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 to 1918, 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 1913–1935, and Naumann 1918–1932; 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. Doubtless the most comprehensive treatment of the subject in all its aspects 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 1960 had a membership of over two thousand. The British Ecological Society, organized in 1913, has a membership of about one thousand. The society in America has given birth to several offspring during its 45 years of existence: The Wildlife Society, Society of Limnologists and Oceanographers, The Nature Conservancy, and a Section on Animal Behavior and Sociobiology. Several of these organizations have their own journals. The Ecological Society of America publishes two periodicals: *Ecology* for short papers and *Ecological Monographs* for long ones. The British Ecological Society also publishes two: *Journal of Ecology* for plant papers and *Journal of Animal Ecology* for animal papers. *Oikos* began publication in 1949 to represent ecologists in Denmark, Finland, Iceland, Norway, and Sweden. Announcement was made in 1960 of the organization of the International Society for Tropical Ecology to include India and adjacent countries. There will be a *Bulletin*. The Ecological Society of Australia was organized in 1960. The New Zealand Ecological Society came into existence in 1952 and regularly publishes *Proceedings* of its annual conferences. The *Japanese Journal of Ecology*, begun in 1954, is the official publication of the Ecological Society of Japan. Most of its articles are in Japanese, but they have summaries in a European language. Finally, many papers of interest to ecologists appear in zoological journals of various sorts that do not carry the word ecology in their titles.

2

The 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, in an unspecific way, 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,* the marine and fresh-water; of the lithosphere there is one, land (Hesse *et al.* 1951).

A *habitat* is a specific set of physical conditions (e.g., 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 topographic unit characterized by both uniform physical conditions and uniform 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 freshwater 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, 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 (Taning 1952); 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 over the substratum (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 is 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.* If the generation following is similar in growth-form to the parent generation, it is a similar morphological response to a similar environment (Schmaulhausen 1949). If the growth-form persists through many generations and appears to be an adaptation, even though not inherited, it is often called an *ecad.* 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 and mosses, but 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

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).**

plants, but for the animal ecologist the following simplified classification, based on Pound and Clements (1900), is sufficient for general purposes:

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, usually elongated leaves.
            - (b) **Broad-leaved**: leaves much as on deciduous trees but shed irregularly.

Life-forms of animals

Systems to classify the life-forms of animals have been little developed (Remane 1943, 1952). 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 bryozoa *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 subdivided; for instance, 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
Arboreal (climbing): squirrel, opossum, monkey
Aerial (flying): bat

Adaptations

Plants and animals of specific life-forms are adaptations 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 form 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.

The manner in which reproduction occurs and the special structures concerned with reproduction vary with each type of animal and often with each individual species. These adaptations are universal and too numerous even to attempt to classify at this point but are certainly obvious to all. The primary objectives in the life of each species are to maintain the existence of the individual and to reproduce its own kind, and all adaptations to live in favorable habitats are designed toward these ends.

Natural selection

To be heritable, a variation must have been caused either by mutations in the genes or chromosomes of the individual or by new combination of genes. Mutations are produced at random, and mostly independent of natural environmental conditions, although there is some experimental evidence that they may be induced or increased in frequency by cosmic rays, ultraviolet rays, heat, and certain chemicals. There is no reason to believe, however, that environmental factors can ordinarily influence the kind of mutations that occur.

Heritable variations in the structure of organisms, and in their physiology and behavior as well, may be favorable, unfavorable, or of neutral value to the existence of the species. Variations that decrease the efficiency of a species in its struggle for existence against competitors and unfavorable environmental conditions usually disappear, but variations that increase this efficiency give those individuals that possess them a better chance for survival and for giving birth to similar offspring. Thus, there is natural selection of the fitter individuals, and a gradual improvement in the relations between the species and its environment. It is in this way that adaptations are established. A better understanding of the ecological relations between different species and between species and the environment will contribute to a better understanding of the process of evolution. At the same time a thorough understanding of the processes of evolution is necessary to understand how organisms become adapted to live in particular habitats (Simpson 1953).

A close study of differences between individuals shows that within many species convergent evolution occurs under similar environmental conditions. Many of these variations are genetic and apparently due to natural selection. The best established correlations are the following, although even they are subject to frequent exceptions (Mayr 1942, Dobzhansky 1951):

BERGMANN'S RULE: geographic races of a species possessing smaller body-size are found in the warmer parts of the range, races of large body-size in the cooler parts. This appears true for cold-blooded as well as warm-blooded animals (Ray 1960).

ALLEN'S RULE: tails, ears, bills, and other extremities of animals are relatively shorter in the cooler parts of a species' range than in the warmer parts.

GLOGER'S RULE: in warm-blooded species, black pigments increase in warm and humid habitats, reds and yellow-browns prevail in arid climates, and pigments become generally reduced in cold regions.

Races of birds in the cooler parts of a species' range lay more eggs per clutch than races in the warmer parts of the range. Likewise the number of young per litter of mammals averages higher in cooler climates.

The stomachs, intestines, and caeca of birds that live on a mixed diet are relatively smaller in the tropical- than in the temperate-zone races of a species.

The wings of birds that live in a cold climate or in high mountains are relatively longer than those of close relatives that live in lowlands or in a warm climate.

Races of birds in cool climates are more often and more strongly migratory than races in warm climates.

Races of mammals in warm climates have less under-fur and shorter contour hairs.

Fish of cool waters tend to have a larger number of vertebrae than those living in warm waters. Increase in salinity tends to induce the same result as low temperature.

Fish that inhabit swift waters tend to be larger and more streamlined than inhabitants of sluggish or stagnant waters.

Cyprinid fishes, isolated in desert springs, tend to lose their pelvic fins.

Land snails reach their greatest size in the area of optimum climate within the range of the species.

The relative weight of snail shells is highest in the forms exposed to the highest radiation of the sun or to the greatest aridity.

Land snails tend to have smooth, glassy, brown shells in cold climates, and to have white or strongly sculptured shells in hot dry climates.

It would appear at first glance that several of these rules have a physiological basis; for instance, large body size and short appendages give less surface area per volume of body and thus minimize heat loss from the body, in cold climates. It is doubtful, however, that the smaller surface area thus attained gives enough reduction of heat loss to be significant in warm-blooded animals and would not apply to cold-blooded ones. Rather the ability of warm-blooded animals to live in cold climates depends more importantly on the insulation of the body surface, its exposure, its vascularization, and its ability to tolerate a cold tissue temperature (Scholander 1955, Irving 1957). The older explanations of selective value of many of these rules are therefore doubtful.

PHYSIOLOGICAL ADJUSTMENTS

Nature of adjustments

Probably the first response of any organism to a change in the environment is physiological. A physiological response must certainly precede any change in form or structure which requires growth. Even a change in behavior must follow a change in some receptor or sense organ followed by nervous function; a fall in air temperature, for instance, brings a drop in the metabolic rate of cold-blooded organisms but a rise in the rate of warm-blooded organisms. Cold may stimulate nerve endings in the skin of birds or mammals and produce shivering and a search for protective cover. Transference from the dark to light may immediately initiate photosynthesis in resting chloroplastids within a plant cell, or a change in turgescence on opposite sides of a sessile zooid may result in a turning movement, an orientation to or away from the light source. Physiological responses are thus internal responses to factors of the environment. Often they are difficult to detect.

Types of response

Environmental factors influence organisms physiologically in various ways (Fry 1947). These effects may be classified as follows:

Lethal: causing death; for instance, extreme heat or cold, lack of moisture, and so forth.

Masking: modifying the effect of some other factor. Low relative humidity increases the rate of evaporation of moisture from body surfaces so that warm-blooded animals are able to survive at otherwise intolerably high air temperatures.

Directive: producing an orienting response in relation to some environmental response so that the organism gets itself into favorable conditions.

Controlling: influencing the rate at which some process functions, but not entering the reaction. Temperature, pressure, and viscosity, for instance, affect secretion, locomotion, and metabolism.

Deficient: curtailing an activity because some essential ingredient, such as a salt, oxygen, or the like is absent or at unfavorably low concentration.

The same environmental factor may produce different effects at different times and under different conditions. Temperature may be lethal, if extreme; masking, as when cold reduces the demand of cold-blooded organisms for food; directive, by inducing a search for more favorable locations; or controlling, as a modifier of the rate of metabolism. Often the distinction between controlling and deficient factors is not made, or they are considered as together constituting *limiting factors.*

Threshold and rate

Every environmental factor varies through a wider range of intensivity than any single organism could tolerate. Characteristically, there is for each individual organism a lower and an upper limit in the range of an environmental factor between which it functions efficiently. For any one factor, different organisms find optimal conditions for existence at different points along the range; hence their segregation into different habitats.

The *threshold* is the minimum quantity of any factor that produces a perceptible effect on the organism. It may be the lowest temperature at which an animal remains active, the least amount of moisture in the soil that permits growth of a plant, the minimum intensity of light at which a photoreceptor is stimulated, and so forth. Above the threshold, the rate of a function increases more or less rapidly as the quantity of heat, moisture, light, or other environmental factor is augmented, until a maximum rate is attained. Above the maximum, there is usually a decline in the rate of a process either because of some deleterious effect produced, the interference of some other factor, or exhaustion. The curve of decline at high temperatures is usually steeper than the curve of acceleration at low temperatures.

Law of toleration

For each species there is a range in an environmental factor within which the species functions at or near an optimum. There are extremes, both maximum and minimum, towards which the functions of

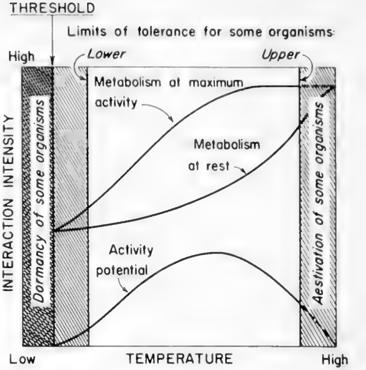


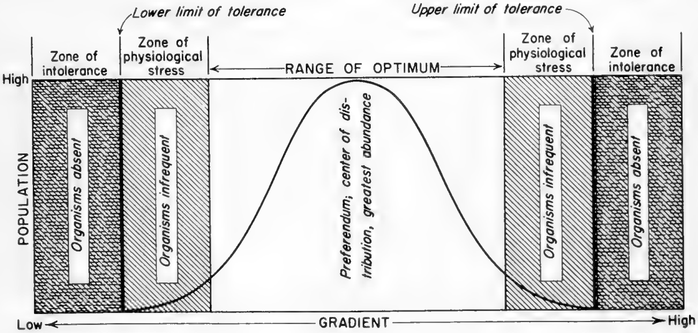
FIG. 2-2 **Interaction between environment and cold-blooded organisms: organism activity as a function of environmental temperature (modified from Fry 1947).**

a species are curtailed, then inhibited. In some organisms, such as fish, the *upper limit of tolerance* is reached before activity is reduced to zero. At low temperatures, the *lower limit of tolerance* may be reached while the animal is still capable, potentially, of considerable activity, and death is the result of other factors. On the other hand, some organisms may survive in an inactive or dormant state under environmental conditions that do not permit activity, only to become functional again when critical factors rise above the threshold. Before the limits of toleration are reached there are zones of increasing *physiological stress.*

The species as a whole is limited in its activities more by conditions that produce physiological discomforts or stresses than it is by the limits of toleration themselves. Death verges on the limits of toleration, and the existence of the species would be seriously jeopardized if it were frequently exposed to these extreme conditions. In retreat before conditions of stress there is a margin of safety, and the species adjusts its activities so that limits of toleration are avoided. There is variation in hardiness of individuals within a species, so that some hardy individuals find existence possible under conditions that disrupt other individuals. The population level of a species becomes reduced therefore before the limits of its range are actually reached. It is desirable to test by acclimation and breeding experiments whether these differences in physiological adaptiveness between individuals or populations are genetic or phenotypic (Prosser 1955).

Species vary in their limits of tolerance to the same factor. The Atlantic salmon, for instance, spends most of its adult life in the sea, but goes annually into fresh-water streams to breed. Most other marine fishes are killed quickly when placed in freshwater, as are fresh-water fish when placed in salt water. The following terms are used to indicate the relative extent to which organisms can tolerate variations in environmental factors. The prefix *steno-* means that the species, population, or individual has a narrow range of tolerance and the prefix *eury-* indicates that it has a wide range; thus *stenohaline*

FIG. 2-3 **Law of toleration in relation to distribution and population level—often a normal curve (modified from Shelford 1911).**



and *euryhaline* in respect to salinity, *stenohydric* and *euryhydric* in respect to water, *stenothermal* and *eurythermal* in respect to temperature, *stenophagic* and *euryphagic* in respect to food, *stenoecious* and *euryoecious* in respect to niche or habitat, and so on.

Law of the minimum

An organism is seldom, if ever, exposed solely to the effect of a single factor in its environment. On the contrary, an organism is subjected to the simultaneous action of all factors in its immediate surroundings. However, some factors exert more influence than do others, and the attempt to evaluate their relative roles has led to the development of the law of the minimum.

The first elaboration of this law was made by the German biochemist, Justus von Liebig, in 1840, who stated:

If one of the participating nutritive constituents of the soil or atmosphere be deficient or wanting or lacking in assimilability, either the plant does not grow or its organs develop only imperfectly. The deficient or lacking constituent makes those that are present inactive or lessens their activity. If the deficient or lacking constituent be added to the soil or if occurring in insoluble form it be made soluble, then the other nutrients become active (Browne 1942).

Blackman (1905) developed the more comprehensive concept of *limiting factors* when he listed five factors involved in controlling the rate of photosynthesis: amount of CO_2 available, amount of H_2O available, intensity of solar radiation, amount of chlorophyll present, and temperature of the chloroplast. Any one of these factors will control the rate of the process if the factor is present in least favorable amount, or may actually stop it when insufficient, even though all other factors occur in abundance. The same principle applies to animal functions.

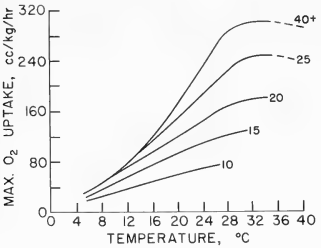


FIG. 2-4 **The relation between maximum respiration rate, temperature, and oxygen tension (mm Hg as shown by values in the graph) in young goldfish acclimated to each temperature before measurements were taken (Fry 1947).**

Since the rate of a process may be controlled by too great an amount of a substance, such as heat, as well as by too small an amount, and since the presence or abundance of an organism may be limited by a variety of environmental factors, biotic as well as chemical and physical, and since the limiting effect may be due to two or more interacting factors rather than a single isolated one (Shelford 1952), the *law of the minimum* may be restated in broad ecological terms, as follows: *the functioning of an organism is controlled or limited by that essential environmental factor or combination of factors present in the least favorable amount. The factors may not be continuously effective but only at some critical period during the year or perhaps only during some critical year in a climatic cycle* (Taylor 1934).

BEHAVIOR RESPONSES

Orientation

Behavior responses to changes in environmental factors can usually be detected immediately as turning or locomotor activities on the part of the organisms (Fraenkel and Gunn 1940). These movements tend to take the organism away from points of danger and into more favorable locations, or to perform some task essential to existence, or to reproduction. If the movement involves curvature or a turning movement either toward or away from the source of stimulus, the movement is called a *tropism*. Motile organisms frequently respond by actual locomotion toward or away from the stimulus rather than mere turning, and such guided or directed locomotor movements are called *taxes*. When the movements of the animal are random in direction, and there is no immediate orientation to the source of stimulus, but the frequency of turning or speed of the movements is dependent on the intensity of stimulation, such responses are termed *kineses*. As the result of kineses an animal may arrive by chance in a favorable environment, by which the intensity of the stimulus is reduced or entirely eliminated. To identify the stimulus to which the organism is responding, the following prefixes are employed: *thermo-*, temperature; *photo-*, light; *geo-*, gravity; *hydro-*, moisture; *chemo-*, chemicals; *thigmo-*, contact; *baro-*, pressure; *rheo*, current; and *galvano-*, electricity.

Jacques Loeb, during the period 1888–1918, vigorously maintained that all tropisms and taxes of organisms were mechanical, automatic, and explainable in simple concepts of physics and chemistry.

. . . the overwhelming majority of organisms have a bilaterally symmetrical structure. . . . Nor-

mally the processes inducing locomotion are equal in both halves of the central nervous system, and the tension of the symmetrical muscles being equal, the animal moves in as straight a line as the imperfections of its locomotor apparatus permit. If, however, the velocity of chemical reactions in one side of the body, e.g., in one eye of the insect, is increased, the physiological symmetry of both sides of the brain and as a consequence the equality of tension of the symmetrical muscles no longer exist. The muscles connected with the more strongly illuminated eye are thrown into a stronger tension, and if new impulses for locomotion originate in the central nervous system, they will no longer produce an equal response in the symmetrical muscles, but a stronger one in the muscles turning the head and body of the animal to the source of light. The animal will thus be compelled to change the direction of its motion and to turn to the source of light. . . (Loeb 1918).

The idea that all instinctive activities of organisms were forced and invariable responses to environmental factors met many objections. H. S. Jennings (1906) pointed out that many Protozoa are asymmetrical in body structure and hence could not lend support to the tonus theory. Furthermore, the movements and responses of many organisms to environmental stimuli were not stereotyped, but random in nature; of a *trial and error* sort. Although much of Loeb's theory has been disproven experimentally and appears untenable on the basis of observations of animal activities under natural conditions, it crystallized the need for objective analysis and interpretation of animal behavior, and the avoidance of teleological and anthropomorphic explanations. The study of orienting responses of organisms is of utmost ecological significance since it is largely by means of such responses that organisms find their proper and favorable habitats.

Preferendum

The behavior responses of animals and their orientation in respect to most environmental factors can be tested experimentally, and results thus obtained correlated with the animal's behavior under natural conditions. There is a variety of procedures and equipment suitable to these purposes (Shelford 1929, Warden, Jenkins, and Warner, I, 1935) and there is distinct value in verifying field observations with experimental analyses.

When the number of favorable responses at each unit intensity of an environmental factor is plotted against the entire range of that environmental factor, the usual result is a normal or Gaussian curve. The maximum number of responses normally occurs near the center of the range, with a progressive reduction in number toward each extreme. An extension in each direction from the peak of the responses to include 50, 25, or some smaller percentage of the total responses is called the *preferendum* for that animal or group of animals.

Innate behavior

Much of the behavior of organisms is determined by heredity and is characteristic of the species in its proper environment. This behavior may be evident at birth or it may not develop until the nervous system, including both the receptor and effector mechanisms, is fully matured. Such innate behavior is of various degrees of complexity. A *reflex* is a quick, automatic response of a single organ or organ system to a simple stimulus; for instance, the knee jerk in man. Tropisms, taxes, and kineses may involve a series of reflexes and represent a higher level of integration. An *instinct*, or *inherited behavior pattern*, is a complex fixed behavior that is activated, more or less automatically, when the animal is presented with the proper stimulus (Thorpe 1951).

The anatomical basis for these various grades of behavior lies in the structure of the nervous system and especially, in higher types of animals, in the interarrangement of neurones and synapses with each other and in the neural pathways that become established. Behavior patterns become elaborated through evolution, are as subject to mutation as any structural part of the body, and are a means whereby animals respond advantageously to the various factors in their normal environment.

Stimuli

Before an action will take place the nervous mechanism must be released by the reception of a *stimulus*. Stimuli may be either external or internal to the organism. Protoplasm is sensitive to any kind of stimulation, provided it is intense enough. In higher organisms, however, specialized tissues have become particularly sensitive to one kind of stimulus, and these tissues, or sense organs, are called *receptors*. There are several forms of receptors: *photoreceptors, phono-receptors, mechano-receptors, chemo-receptors, thermo-receptors,* and *stato-receptors*. Not all types of receptors are present in all organisms, and the structure and effectiveness of those present varies from one kind of animal to another. The efficiency of the receptor mechanisms is important, as they largely determine the environmental factors to which the animal will respond and the degree of sensitivity involved.

Stimuli may be internal, and derive either from

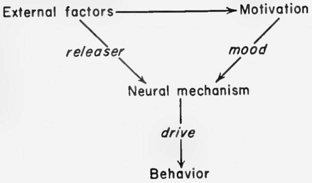


FIG. 2-5 **Factors involved in the activation of an instinct.**

hormones or as *kinesthesia* involving changes in the tension of muscles and tendons or changes in shape or form of muscle fibers. *Motivation* is established when there is an accumulation of internal stimuli potentials as the result of hormone action, kinesthetics, or changes of metabolism. A combination of motivation with proper external conditions and stimuli sets up a *drive,* such as the hunger drive, or reproductive drive (Richter 1927).

Once a major drive is initiated, satisfaction of it requires a series of events and stimuli at different levels of integration, so that a hierarchy of drives, actions, and stimuli is established. The significance of this hierarchy is that a major activity in the life cycle of an animal does not take place until the organism is in a proper *physiological state,* which depends, often in large part, on the environment, and then one action leads to another until *consummation* is completed. In the male stickleback, for instance, the reproductive drive is not initiated until hormone stimuli are released as the result of gonad enlargement and response to lengthening daily photoperiods. Once the reproductive stimulus is given, the first secondary drive is the establishment of nesting territories by fighting among male fishes. Then the nest is built. Only after this is completed is the male ready to receive the female.

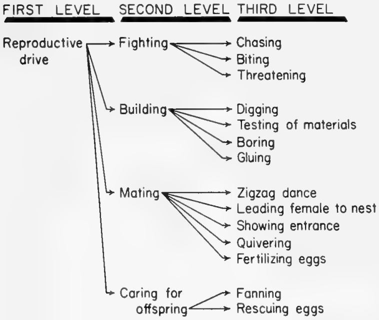


FIG. 2-6 **The hierarchy of drives and actions in the three-spined stickleback (after Tinbergen 1951).**

Even though an animal may have potential capacities in its sense organs with which to respond to the whole environment, a particular action is triggered by stimuli from only a very small part of the environment. This is a fundamental characteristic of innate behavior, and the discovery of these critical *sign stimuli* or *releasers* is necessary for an appreciation of the interrelation of animals in a community and how they respond to their environment (Lorenz 1935, Tinbergen 1951).

The complete enactment of mating behavior in the stickleback proceeds step by step in an orderly manner, each action a releaser for the next. If any one step is changed, or is interrupted, the behavior subsequent in the sequence does not take place. Releasers are of a variety of sorts in different species, but commonly involve particular colors or color patterns, call-notes or songs, shapes, chemicals, or contacts, as well as associated acts, positions, or movements on the part of another animal. If these triggers are not presented, the behavior does not become expressed even though a specific nervous mechanism is present. The analysis of behavior through observation and experimentation with the objective of understanding how an animal acts under natural conditions constitutes the science of *ethology,* an essential branch of ecology. Ethology differs from psychology in that it is concerned with understanding not only the causality of behavior but also the *survival value* of behavior patterns under natural conditions, and the *evolution* of these patterns. Psychology is concerned more with analyzing the nervous mechanisms that are involved.

Learning

All behavior is not, of course, automatic and inherited. Much of it represents the adjustment of fixed patterns to changes in and conditions of the animal's surroundings (Thorpe 1956). *Learning* may be defined as the adaptive change in individual behavior as a result of experience.

The simplest form of learning is *habituation,* that is, learning not to respond to stimuli which tend to be without significance in the life of the organism. Young animals, for instance, have an innate tendency to respond to a wide variety of danger stimuli, such as any sudden movement or noise. However, when such stimuli are presented repeatedly without association with further effects, the young animal learns to disregard them. There is some evidence, on the other hand, that instinctive recognition of a specialized predator of a species shows little or no habituation.

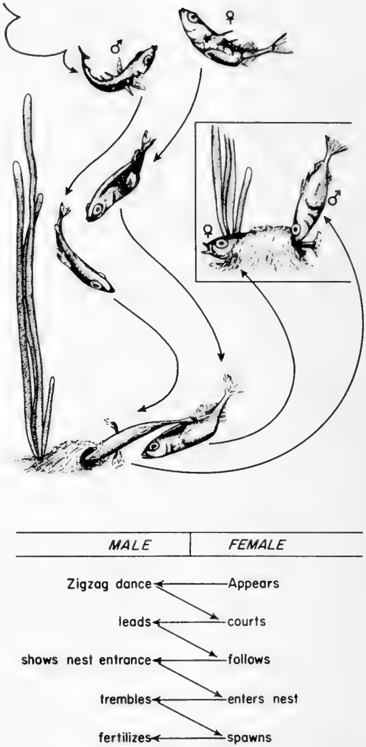
Conditioning is a form of learning and consists of the establishment of a connection between a normal reward or punishment and a new stimulus, that is, one that hitherto has had no meaning to the animal.

Imprinting is especially well shown in waterfowl and gallinaceous birds. Grey-lag geese reared from the egg in isolation react to their human keepers, or to the first relatively large moving object that they see, as they would the parents by following. This imprinting of the parent companion is confined to a very definite and usually very brief period following shortly on emergence from the egg. Once thoroughly established, the behavior is very stable, if not totally irreversible. Furthermore, this imprinting of a human being as a substitute for its own species will call forth, a year or more later, sexual reactions to man in the mature bird. There is no innate recognition by birds of parent, species, sex, or home locality, but there is evidence that these are learned through association and contact during the course of development. Imprinting doubtlessly also occurs in other animals than birds.

Imitation is another form of learning. An individual in a flock or herd may start to feed or run when it observes other individuals feeding or running. A young animal learns much that is traditional of the species by imitating its parents. Vocal imitation is conspicuous in the elaborate songs of some birds.

Trial and error learning involves trial responses to a variety of stimuli with gradual elimination of all responses and stimuli except the relevant ones. A chick pecks at random at all sorts of objects until it accidentally strikes one which is edible, whereafter the chick has a greater tendency to peck at objects that have a similar appearance. Repetition of the same act usually leads to the formation of a *habit*. Habits often appear stereotyped but differ from instincts in that they have to be learned and are not inherited.

Insight learning involves an apprehension of relations and the sudden adoption of an appropriate response without previous trial and error behavior. The mason wasp of India builds a cluster of clay cells. After depositing an egg in each cell, the female fills it with caterpillars and seals it with a lid. Eventually the whole cluster is covered with a layer of clay. While a wasp was away hunting for its prey, an experimenter made a large hole in the side of a cell. On its return, the wasp put in a caterpillar which fell out through the hole. A second caterpillar stuck in the hole with a large part hanging out through it. When the cell was completely provisioned, the wasp appeared to notice the hole for the first time and carefully examined it. With great and



MALE	FEMALE
Zigzag dance	Appears
leads	courts
shows nest entrance	follows
trembles	enters nest
fertilizes	spawns

FIG. 2-7 **Courtship and mating behavior of the three-spined stickleback (after Tinbergen 1951).**

prolonged effort she managed to stuff the caterpillar back into place. She then collected a pellet of clay and mended the hole. Such behavior as this involves an apprehension of relations and a sudden adaptive response not preceded by trial and error. Insight learning may be manifested in various ways as through homing ability, detouring around obstacles, tool-using, discrimination of forms and patterns, and so forth.

Ecological life histories

Developmental life histories trace the origin and growth of structures and functions of an animal from the egg stage until maturity is reached. Such studies are largely embryological in nature. *Behavior life histories* attempt to analyze the activities of animals in terms of innate and learned behavior, and the neural mechanisms involved. In order to do this, it is often necessary to trace the origin of each activity to the manner in which it first makes its appearance in the young animal. *Ecological life histories,* on the other hand, are concerned with the activities of a species throughout its life cycle, and in relation to its adjustments to natural conditions. Ecological life histories usually proceed with, first, analysis of the behavior adjustments needed for the survival of the mature animal; then of its reproductive behavior; and, lastly, of the development of behavior and physiological adjustments of the young animal. In general, the proper procedure is... *to discover and establish correlations between the behavior of the organism and the conditions in its environment, and then to test the significance of the correlations by appropriate experiments in nature or in the laboratory. The point should be emphasized that you start with nature, that is, with the organism in its environment. Also it should be noted that morphology and physiology of the organism are entirely subsidiary matters, although most important to the person interested in knowing how the organism behaves as it does...* (Huntsman 1948). The behavior of a species in relation to its environment is called its *mores* (Shelford 1913).

The following are important items that should be included in a complete ecological life history of a species:

1. Phylogenetic and geological history.
2. Geographic and habitat distribution with an analysis of adjustments to the physical environment and of biotic interrelations within the community.
3. Variations in population, through time and in space.
4. Changes in seasonal activities and physiological states: breeding, migration, hibernation.
5. Food, enemies.
6. Parasites, diseases.
7. Reproductive potential, mortality, rate of population turnover.
8. Requirements for reproduction: home range, territory, nest-site, nesting materials, etc.
9. Breeding behavior: mating, nesting, etc.
10. Development of offspring: rate, stages, generations per year, etc.

Useful outlines, methods, and bibliographies for ecological life history studies of different kinds of animals and plants have been published in the scientific periodical *Ecology* since October, 1949.

Ecological niche

The *ecological niche* is the particular position in a community and habitat occupied by an animal as the result of its peculiar structural adaptations, its physiological adjustments, and the special behavior patterns that have evolved to make best use of these potentialities. Important factors in the niches occupied by white-footed mice and deer mice are described in Table 2–1. Both mice are equipped with large eyes for nocturnal vision, large external ears for hearing, long vibrissae on the face for aid in running through dark underground burrows, and protective coloration. *P. l. noveboracensis* has a longer tail than *P. m. bairdii,* which appears to be an adaptation for climbing. It is possible that these two species are segregated into different niches because *bairdii* is more tolerant of extreme temperatures and low moisture conditions, and hence is more prevalent than *noveboracensis* in the exposed grassland habitat, but is unable to displace *noveboracensis* within the forest because of the latter's tree climbing ability.

Every species has its own peculiar niche. No two species can permanently occupy exactly the same niche in the same locality. The living together of many species in the same community is possible only because their various niche requirements are different. The analysis of the critical factors in these niche requirements is often very difficult but is one of the main objectives of ecology.

COMMUNITY INTERRELATIONS

The fact that species with similar tolerances and requirements aggregate into similar environments to form communities is a response of special interest. No organism occurs alone. Each must find its place in the community and establish relations with other members of it. The manner in which the response of species to each other is affected is shown in the structure and composition of the community

TABLE 2-1 Comparison of niches of the white-footed and deer mice, both species of the genus *Peromyscus*.

Factor	*P. leucopus noveboracensis*	*P. maniculatus bairdii*
Vegetation, substratum or space occupied	Deciduous forest; subterranean, terrestrial, arboreal; home range 0.12 hectare	Sparse grassland; subterranean and terrestrial only; home range 0.24 hectare
Microclimate	Shade, rich humus, moderate moisture, medium temperature	Sunlit habitat, low moisture, temperature often extreme
Food	Seeds, nuts, insects	Seeds, grass, insects
Enemies	Owls, foxes, weasels, shrews	Owls, foxes, weasels, shrews
stratum where food found	Surface of ground	Surface of ground
Reproductive site; nesting materials	Nests of leaves in burrows, logs, stumps, or tree cavities	Nests of dried grass in burrows, crannies, or clumps of grass
Diel activity	Nocturnal	Nocturnal
Seasonal activity	Active throughout year	Active throughout year

and in its internal dynamics, succession, and distribution. The analysis of the community responses and interrelations of organisms is a major objective of this book.

SUMMARY

The environment, or specifically the habitat, of an organism consists of the physical conditions that surround it. In order to live in a particular habitat, an organism must be *morphologically adapted* to it. This may be accomplished to a certain extent during growth, especially in sessile forms, but depends mainly on long evolutionary processes of variation and natural selection. Each organism must also be *physiologically adjusted* to the various factors of its environment. Species vary in their limits of tolerance, and those factors in their surroundings that are most immediately unfavorable limit their habitat distribution. In order for an organism to take advantage of its morphological and physiological adjustments, it must have the proper *behavior responses*. These inherited and acquired action patterns involve selective orientation in response to environmental stimuli. Occurrence of different species in the same habitat necessitates the establishment of compatible *community interrelations*.

3

Background:

The Biotic Community— Structure and Dynamics

The concept of the biotic community is basic to an understanding of ecology. We will here be concerned only with laying a foundation of general principles. Details will come in later chapters, but for proper orientation we must know something about how the community is organized, how it functions, and how it may be recognized.

INTERNAL STRUCTURE AND PROCESSES

Community and ecosystem

A *community,* or *biocenose,* is an aggregate of organisms which form a distinct ecological unit. Such a unit may be defined in terms of flora, of fauna, or both. Community units may be very large, like the continent-wide coniferous forest, or very small, like the community of invertebrates and fungi in a decaying log. The extent of a community is limited only by the requirement of a more or less uniform species composition.

A different community occurs in each different habitat and environmental unit of larger size, and in fact the composition and character of the community is an excellent indicator of the type of environment that is present. Since plant communities and animal communities occur together in the same habitat and have many interrelations, the one can scarcely be considered independently of the other. Together they make up the *biotic community,* and the biotic community along with its habitat is termed an *ecosystem* (Tansley 1935). The ecosystem is the best unit for the study of the circulation of matter and flow of energy between organisms and their environment.

Communities may be distinguished as major or minor. *Major communities* are those which, together with their habitats, form more or less complete and self-sustaining units or ecosystems, except for the indispensable input of solar energy. *Minor communities,* often called *societies,* are secondary aggregations within a major community and are not, therefore, completely independent units as far as circulation of energy is concerned. When in this book communities are spoken of the reference is to major communities unless otherwise indicated.

Dominance

When a number of species come together to form communities, each fits into a different niche and plays a different role in the internal dynamics of the community. *Dominance* is the relative control exerted by organisms over the species composition of the community. Species exerting this important control are called *dominants*. Plants are more frequently dominant in terrestrial communities than are animals. In aquatic communities, animals are relatively more important in this role, although dominance is often not developed.

Dominance is most commonly expressed in the *reactions* of an organism on its habitat (Clements and Shelford 1939). Dominants shoulder the full impact of the climate or the environment but modify this effect for other organisms within the community by tempering light, moisture, space, and other conditions. Only those other organisms that find these modified physical conditions tolerable can exist within the community. Furthermore, dominants are ordinarily the most prominent species in the community, make up its greatest mass of living material, and serve as the major source of food, substrate, and shelter for the animals that are present. In a forest community, trees are dominant. They decrease light intensity, increase the relative humidity, intercept precipitation, monopolize most of the moisture and nutrients in the soil, decrease wind velocity, and furnish shelter and food for animals. Grasses play a similar, though less conspicuous, role in prairie communities; sedges, rushes, and cattails in marsh communities; sagebrush in the arid habitat of the Great Basin; mussels and barnacles on a rocky seashore; and so forth.

Sometimes dominance is demonstrated in *coactions*, direct effects of organisms on each other. In some fresh-water ponds, carp and suckers may consume much, perhaps all, of the submerged vegetation. This coaction thus prevents the plant constituents from assuming their usual role in the community, and by so much prevents the occurrence of animal species that depend directly upon the plants. These fish also react upon the habitat by stirring up the bottom, from which they derive organic matter, thereby greatly increasing the turbidity of the water. Penetration of light into the water becomes poor, greatly handicapping sunfish, bass, and other species which locate food visually (Table 7–3).

In primeval days, bison on our western great plains fed on the luxuriant taller grasses more extensively than on the short grasses, with the consequence that, over extensive areas, short grass species replaced tall grasses almost entirely. Thus bison were coactant with and dominant over the composition and character of the community (Larson 1940). In a similar manner, when European meadow voles are numerous they reduce the vigor and prevalence of the grass dominants in consequence of their feeding and tunnelling in the ground, and angiosperms which are normally absent or scarce appear (Summerhayes 1941). Overpopulations of the European rabbit alter the character of the forest by frustrating reproduction of oak, beech, and hornbeam, upon the seedlings of which they feed to the exclusion of other species. When introduced into Australia, the European rabbit converted grassy areas into desert-like tracts (Bourliere 1956).

Although animals are more common coactors than plants, plants may occasionally exert dominance in this way. As a notable example, chestnut blight (a fungus) virtually eliminated the chestnut tree from the deciduous forest of eastern North America during the first few decades of the twentieth century. This fungus infects the cambium, forms pustules under the bark, and causes the bark to fall off and the leaves to wilt. The blight has eliminated the chestnut from the community, and the consequent opening up of the canopy has allowed the extensive invasion of new species of shrubs, herbs, and animal inhabitants.

Trees are the dominants in a forest community, but species in the lower stratum of shrubs modify the habitat still further and even the herbs exert some control over the physical conditions on the surface of the ground. A *subdominant* species must tolerate the conditions established for it by the dominants; but it in turn is a modifier of the community composition in a secondary manner.

Influence

By *influence* is meant effect upon the abundance, health, and activities of other organisms in the community but not to the extent of directly excluding species. Influence is conspicuously expressed through coactions, but it may be effected through reactions as well. Insects may partially or wholly defoliate a tree; a pack of wolves may diminish a population of deer over winter; squirrels may bury acorns and nuts and thereby aid germination of them; parasitic or poisonous plants may lower the vigor or destroy the life of some other plants or animals; animals may burrow into the soil and thereby increase percolation of water and air, a benefit to plants; and all organisms, upon death, add organic matter to the habitat. These and other actions influence the community, but unless these influences become extreme they do not absolutely determine whether or not other species will occur in the community. Influence, then, is of essentially the same nature as dominance but is less vigorous in the modifying role that it plays.

Evaluating and classifying animals ecologically

One of the most important, yet difficult, problems in ecology is evaluation of the roles the different kinds of animals play in community dynamics.

A basis for classifying species is exclusiveness, fidelity to the community. A species is *exclusive* when it occurs only in a single area, habitat, or community; *characteristic* (selective, preferential) when it is abundant in one area or community but also occurs in small numbers elsewhere; and *ubiquitous* (indifferent) when it is found more or less equably distributed in a wide variety of communities. The terms given in parentheses are synonyms used by plant ecologists (Braun-Blanquet 1932). Exclusive species are often rare and of little importance in the dynamics of a community, but when they are conspicuous they often make useful *indicator species* for identifying and recognizing community units.

The recognition of characteristic species presents special difficulties, since one must decide how much more abundant a species needs to be in one community to be sure a definite preference over another is indicated. In a distributional study of breeding bird populations in Ontario (Martin 1960), a species was considered characteristic of one type of vegetation if the species was at least three times more abundant in it than in any other type of vegetation. This was at population levels of from 1 to 9 pairs per 40 hectares (100 acres). For species reaching population densities of from 10 to 100 pairs per 40 hectares, preference was considered demonstrated if the species were twice as abundant in one type of vegetation as in any other. For populations greater than 100 pairs per 40 hectares, differences of 50 per cent are probably significant. It seems logical that a stricter test should be applied to small populations, for errors in measuring the size of populations and random population fluctuations attributable to factors other than choice produce a relatively greater disturbance in the data. An experimental study in measuring foliage insect populations also indicated that populations differing by a ratio of 3:1 could be accepted as statistically significant (Graves 1953). When the bottom fauna of two ponds were sampled, true differences could be detected at minimum ratios between their populations of 1.9 (Hayne and Ball 1956). A species, to be termed characteristic, should also be well distributed through a community, this to be indicated by its occurrence in at least 50 per cent of all samples taken (Thorson in Hedgpeth 1957).

Another criterion for evaluating species is by numbers of individuals present. Other things being equal, a species in time of high population affects other organisms to a much greater extent than it does at times of low population. A species that is permanently more abundant than another will consume more food, occupy more nest-sites, and demand more space; hence its influence will be greater. *Predominants* are the more numerous constituents of a community, in contrast to *members,* which are species of lesser importance. The dividing line between these two categories is an arbitrary one.

The time and duration of occurrence of a species in a community affects the amount of influence it exerts. Generally, the longer the yearly period during which a species is active, the more important its role becomes. Species may be classified on a temporal basis into *perennials,* those which are active in a community throughout the year, year after year; *seasonals,* which are present or active only part of the year; and *cyclics,* which may be very important some years but of negligible importance other years, as evidenced by their wide fluctuations in numbers. Even though present, a species is usually considered inactive when it is hibernating or dormant or when it is represented only by eggs, spores, or encysted stages of its life cycle.

The effect produced on the community by individuals and species may be modified by the way they form secondary groupings within the community. These minor aggregations of plants and animals are called *societies* and are of various sorts (Shelford 1932). *Layer societies* occupy different strata, such as the subterranean, ground, herb, shrub, and tree societies in a forest; *local societies* are usually parts of layer societies but are more confined in area, as groups of animals occupying an ant hill, a rotting log or stump, or a restricted but distinctive area of ground; and *seasonal societies* include all the organisms at particular times of the year.

Other factors that affect the influence of a species in the community are the size of individuals, their metabolism, food habits, and general behavior. A moose consumes more food than a mouse, and a warm-blooded mouse more than a cold-blooded salamander of the same size. A carnivore at the top of several food-chains affects the lives of more different species in the community web of life than a herbivore feeding on plants. Burrowing rodents react on the habitat more than do most birds. One factor may cancel another. An individual of a perennial species of carnivorous mammal certainly eats more than an individual cold-blooded herbivorous insect of small size and active only during the warm season. Yet there may be 1000 insects to one mammal, so that in the aggregate a single species of insect may actually produce more disturbance than a single species of mammal. The difficulty of evaluating the relative effects of species is partly alleviated by calculating their respective biomasses and energy requirements.

The *biomass* of a species is the average weight or volume of an average individual, multiplied by the total number of individuals present. The computation of the biomass of each species thus corrects for differences in size and number of individuals between species. Because of differences between species in body moisture and amount of inert substances such as endoskeleton, chitin, shell, and the like, biomass is expressed with greater accuracy in terms of dry weight than wet weight or volume, and is even more accurate if given in terms of carbon or nitrogen content, or calories.

Attempts have recently been made to compute more significant biomasses of bird populations, using physiological constants. A biomass composed of few but large individuals has a lower metabolic activity than an equal biomass composed of a large number of small individuals. In one study (Turček 1956), the importance of different species in the community was evaluated in terms of the total body surface area rather than total weight presented by each species, using the formula $N \cdot 10 \cdot W^{0.67}$, where N is the number of individuals and W the average weight of the species. In another study (Salt 1957) the number of individuals was multiplied by the mean weight of the species raised to the 0.7 power ($N \cdot W^{0.7}$). One gets the best evaluation of the importance or influence of a species in a community where metabolic activity can be measured directly and expressed in terms of calories per unit of time (Macfadyen 1957, Teal 1957).

Productivity

A characteristic of communities that has become of considerable importance in modern ecological research is productivity. The number of individuals or biomass present in a community at any one time is the *standing crop*. At the beginning of the year or reproductive season the standing crop is usually small, but as reproduction and growth take place there is an increase in the amount of organic matter making up the biomass of the community. The production of organic matter per unit of time and area is *productivity*. Productivity is commonly indicated on a yearly basis, but it is also possible to measure monthly, weekly, or daily production. Small standing crops may have a high productivity and large standing crops a low productivity, hence average biomass or standing crop differentials between different communities is not comparative of the productivity of the habitats in which these communities occur. The largest standing crop which a habitat can support without deterioration, or the maximum number of biomass of animals that can survive least favorable yet tolerable environmental conditions during a stated period of time, is the *carrying capacity*. Carrying capacity is determined not just by the amount of food available, but also by shelter, social tolerance, and other factors (Edwards and Fowle 1955). A variety of methods are being used to measure productivity of different kinds of organisms and of different habitats. It is desirable to indicate productivity as accurately as possible in descriptions or analyses of community dynamics.

SUCCESSION

Communities are in a more or less continual process of change (Clements 1916). These changes result in part from the reactions and coactions of the organisms themselves and in part from such external forces as changing physiography, changing climate, and organic evolution. The habitat is usually affected as well as the community, and as the habitat changes, new species invade it and become established, and old species disappear. These changes are especially noticeable in dominant species, since these species exert a controlling role over the composition and structure of the community as a whole. The replacement of one community by another is *succession*, and succession continues until a *climax* or final stage is reached.

Succession is a process. The series of steps or communities comprising a successional sequence leading to the climax is the *sere*. Seres are sometimes classified according to the predominant force that is bringing them about. These forces are *biotic, climatic, physiographic*, and *geologic* and their resultant seres are commonly called *bioseres, cliseres, eoseres*, and *geoseres*.

Biotic succession

Biotic succession is brought about by forces inherent within the community and in the activities of the plants and animals themselves. The most important of these activities are the organismal reactions and coactions that produce modifications in the habitat and interrelations between species. Important reactions involve filling in of ponds with plant and animal remains, the addition of organic nutrients to sterile soil, and the reduction in light intensity by increasing density of plant growth. With progressive improvement of the soil and changing light and moisture conditions, a series of new dominants come into the area. When invasion of new species occurs, intense competition develops; if the invaders are successful, the old species disappear as a new community replaces the old one.

Contributing factors that may be involved are differences in growth and dispersal rates, which are different for different species. After a forest fire or logging operation, herbaceous plant growth is immediately stimulated; since herbs grow rapidly, they become dominant within a year or two. Shrubs begin to spread, and tree suckers or seedlings also appear quickly, but because they require a longer time to reach maturity several years may elapse before they gain control of the area.

Succession is considerably influenced by the kinds of propagules available in the vicinity. Seeds, spores, and the like are dispersed more or less readily, depending on form. Some kinds of animals roam more

FIG. 3-1 **Early stages in the pond sere: open water, floating stage, emergent vegetation, swamp shrubs. Everglades National Park, Florida.**

widely or spread more readily into new areas than do other kinds. The composition of the community that develops and the rapidity with which it becomes established depends, in large part, on the rates at which different species invade.

When the volcanic island of Krakatoa in the East Indies blew up in 1883, all plant and animal life on it and on two adjacent islands was destroyed. The following year, the only living animal reported was a single small spider. In 1886, it was apparent that the pioneer plant stage consisted of a crust of blue-green algae covering the lava. A few mosses were also present, as were many ferns, and a scattering of some 15 species of flowering plants including 4 species of grass. The vegetation stage following the algae consisted predominantly of ferns, but the grasses had become dominant over most of the island. By 1906, woodland had appeared, which has since developed into an increasingly luxuriant mixed forest. Dispersal of seeds, spores, and other propagules was effected by wind, sea, animals, and man, in that descending order of importance. The order in which the propagules reached the islands greatly influenced the succession that occurred; as vegetation developed it reacted on the soil and habitat, bringing about conditions amenable to the return of the tropical rain forest (Richards 1952).

Very little study of animal life was made until 1908, and then only for three or four days. At that time, 202 species were found on Krakatoa and 29 on a nearby island. There were no earthworms, snakes, or mammals present, but there were many spiders and centipedes, a number of insects, 2 species each of land snails and lizards, and 16 species of birds. A more thorough survey in 1921 revealed 770 species of animals including rats, apparently introduced in 1918, and bats, first noticed in 1920. In 1933, 1100 species were found, including 3 species of earthworms, but true forest mammals had not yet appeared and many families of forest birds were unrepresented. As with plants, the invasion by animals depended on wind, sea, and man and other animals, in that descending order of importance. Survival and establishment of the animal species was correlated with the stage of vegetation that was reached. It is of interest, however, that scavenger species appeared first, then omnivores, herbivores, and finally predators and parasites. Succession of animals depended in large part on the speed with which they reached the island and on their finding proper food and shelter (Dammerman 1948).

Bioseres may be broadly grouped as *priseres* and *subseres,* depending on whether they develop on primary or secondary bare areas. A *primary bare area* is a sterile habitat, such as rock, sand, clay, or water. A *secondary bare area* is a denudation resulting from temporary flooding, fire, logging, cultivation, overgrazing, or other phenomenon that does not produce an extreme disturbance of the soil or substratum. Since in the latter the habitat has already supported community life, and since the soil or substratum is already in an advanced stage of development, the resulting subsere progresses rapidly and the early pioneer stages of the prisere do not usually occur. A subsere will develop following the destruction of any stage in a prisere, and the species composition of the stages in the subsere will be influenced by the particular priseral community that was destroyed.

The early stages or communities that make up the prisere depend largely on the type of bare area on which the prisere originates. As succession proceeds, however, later stages in the various seres in any area having a relatively uniform and humid climate come to be more and more alike. The successional development from widely diversified communities in initially different habitats to closely similar or identical climax communities in habitats that have also become much alike is called *convergence.*

Bioseres may occur on a small scale in microhabitats as well as in major ones. When hay infusions, prepared in the laboratory, are seeded with representative protozoans, the order of appearance of maximum or peak populations in the various species is bacteria and monads, *Colpoda*, hypotrichates, *Paramecium*, *Vorticella*, and *Amoeba*. Disappearance of species is in the same order, except that *Amoeba* precede *Paramecium* and *Vorticella*. Algae may come in at the final stage, so that a more or less balanced community is established. The succession of species appears a result of the higher reproductive rate of earlier species, and to the fact that the excreta of at least some forms, especially the hypotrichates and *Paramecium*, are toxic to them (Woodruff 1912, 1913, Eddy 1928).

Another common microsere occurs in the death and decay of trees (Graham 1925, Ingles 1931, Savely 1939). The sequence of animal species present as decay progresses depends on the species of tree, the community in which the tree occurs, the climate, and the geographic locality. The following stages have been recognized: 1) tree dying, but still with leaves and sap; 2) tree recently dead, bark beginning to loosen, termites and other insects boring into wood; 3) wood well seasoned, bark very loose or off, wood borers still predominant; 4) wood softened and permeated with fungus; fungus beetles, elaterids, and passalids common; 5) wood largely disintegrated and crumbly, snails and millipedes, occur. Wilson (1959), working in New Guinea rain forests, subdivides stages 2–5 in a different manner, each of which he names after characteristic insects found: 2) scolytid, 3) cucujid, 4) zorapteran, 5) passalid, and 6) staphylinid. Each stage also has a significantly different aggregation of resident ants. Eventually the decaying log becomes a part of the forest floor, and the animal species then present are those in general occurrence.

Climatic succession

With changes in climate, environmental conditions often surpass the limits of tolerance of established plants and animals. The result is the replacement of the existent community by another.

A most interesting clisere is the one that has occurred since the northward retreat of the continental glacier of Pleistocene time (Sears 1948, Deevey 1949, Table 21–1). Stages in this clisere may be detected

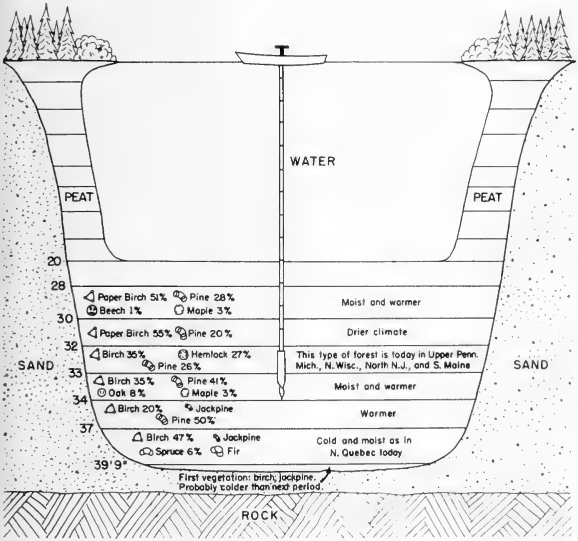


FIG. 3-2 The types of trees which have lived and died during the past few thousand years in Quebec. Instrument taking borings of lake bottom for pollen samples is operated from a boat. Symbols representing different pollen grains and the percentage which each species constitutes in the total are shown at the left. The type of climate indicated by the prevailing vegetation at the time is shown at the right (Wilson 1952).

and even the relative duration of each stage measured from an analysis of the number and persistence of different kinds of pollen grains at various depths in peat bogs. To make such studies, a core of peat is obtained from the deepest part of the bog by means of a special hand auger. The lowest portion of the core is the oldest; the most recently formed is at the top. Samples of the core at various depths are suitably prepared, examined under a microscope, and the pollen grains identified and counted. The predominant kind of pollen at any level of the core represents the probable prevailing species of plants in the vicinity at the corresponding period of time, although the proportionality between all kinds of pollen and abundance of the various species may not be exact (Davis and Goodlett 1960). Thus, during the last 20,000 years, the clisere in eastern North America is represented in simplified form by the following climaxes and climates, reading downward to present time:

spruce, fir——cold, moist
pine——cool, dry
hemlock, oak, beech——warm, moist
oak, hickory——warm, dry
beech, oak, hemlock——cool, moist

The climate is conjectured from the relation of similar flora to climate at the present time. The complete clisere occurs only in regions near the southern limit of the reach of the glacier. The later stages have not developed in more northern localities where the glacier has been gone for a shorter time and where the climate has not warmed up sufficiently. Climatic succession actually occurs at all levels in the biosere, as the seral stages leading to one climatic climax is replaced by the corresponding stages leading to another climax (Table 7–6).

Physiographic succession

Changes in the earth's surface bring a change of communities. The sea alternately inundated and retreated from the Atlantic coastal plain during the Pleistocene as ice, in which large amounts of water were tied up, alternately melted and formed. In earlier times, the sea inundated much of the continental interior, and on its recession the eosere of plant and animal communities which developed covered vast areas.

Mountain-building brings the replacement of lowland communities with new ones that invade at higher elevations. As mountains erode, the eosere progresses in the opposite direction, until base-level or peneplanation is attained. The development that the eosere will undergo with continued erosion is sometimes locally apparent in the difference between upland and floodplain forests. Stages in the erosion cycle, as it occurs in a stream, may be discerned by examination of habitat and animal life progressively from headwaters to mouth.

Geologic succession

The evolution of new forms of life and dispersal of them through the world entails replacement of pre-existing forms and gradual change in the composition and character of communities. The first organisms to appear on earth were unicellular forms confined to the sea (Table 3–1). During the Cambrian and Ordovician periods, the marine animal life differentiated rapidly into a rich variety of invertebrate types and the anlage of vertebrates. The Silurian and Devonian periods are noteworthy for the invasion of fresh water and land by both animals and plants. Fishes became predominant both in fresh water and the sea. During the remainder of the Paleozoic era, a luxuriant flora evolved, especially in swampy areas. Modern conifers, such as spruce, fir, juniper, tamarack, cypress, and yew made their appearance. Amphibians became the predominant advanced animal types, and a diversified invertebrate fauna occurred in all habitats.

In the Mesozoic era, the existing land flora of giant rushes, tree-ferns, and cycads gave way to forests of hardwoods which then spread over the world. Conifers persisted. The earliest woody angiosperms probably originated in the Jurassic and included sassafras and poplar. The forests soon contained elms, oaks, maples, and magnolias. Herbaceous angiosperms, such as grasses and sedges, appeared towards the end of the era but did not become important in North America until the drying up of the interior of the continent in the middle Cenozoic. Although the Mesozoic is predominantly the age of the giant reptiles that lived on the land and in the water and flew through the air, less conspicuous types such as the toothed birds, archaic mammals, and insects were developing rapidly.

At the beginning of the Cenozoic era, ancient types of animals, including the great reptiles and many types of invertebrates, became extinct and mammals rose to predominance. It is significant that the rich development of mammals, birds, and insects came after the worldwide establishment of the angiosperms with their rich nutrient seeds, fruits, and grasses. Pleistocene glaciation brought a major change in the habitat of these animals, and some large mammals disappeared. The last stage of the geosere, the Recent epoch, brought the dominance of man. Only future ages will determine whether this stage is climax, or whether new and different types of animal and plant life will someday evolve to replace man and

TABLE 3-1 Major steps in the geosere of the earth, especially as it applies to North America (modified from Dunbar 1949).

- Cosmic era: 3-5 billion years ago; tidal disruption of an ancestral sun and origin of earth.
- Azoic era: formation of a stable cold exterior shell to the earth; origin of oceanic depressions and continental platforms; first formation of water and a thin atmosphere.
- Archeozoic era: first plant life - bacteria, marine algae, (elevation of Laurentian Uplands and peneplation of continents).
- Proterozoic era: marine algae abundant; animal life chiefly sponges and segmented marine worms, (peneplanation of continents).
- Paleozoic era: 500 million years ago.
  - Cambrian period: marine invertebrates only.
  - Ordovician period: marine invertebrates continue predominance; rise of armored fishes.
  - Silurian period: first invasion of land by plants; rise of air-breathing scorpions and millipedes and of fresh-water fishes.
  - Devonian period: first forests and extensive land floras; diversification of fresh-water fishes, rise of labyrinthodont amphibians, and increase in land fauna, especially spiders, mites, and wingless insects.
  - Mississippian period: increase of amphibians.
  - Pennsylvanian period: luxuriant swamp floras cosmopolitan in distribution, mostly of spore-bearing types; fresh-water clams and amphibians abundant and on land, giant insects, spiders, centipedes, snails, and first reptiles.
  - Permian period: (elevation of Appalachian and Ouachita Mountains); decline of ancient flora and rise of conifers; modern insects and advanced types of amphibians and reptiles appear.
- Mesozoic era: 200 million years ago.
  - Triassic period: (desert climates); plants mostly rushes, ferns, cycads, conifers; stegocephalian amphibians and dinosaurs numerous, archaic mammals appear.
  - Jurassic period: reptiles evolve higher and more diversified forms, first toothed birds and frogs appear.
  - Lower Cretaceous period: woody Angiosperms spreading over world.
  - Upper Cretaceous period: (great inland seas, warm climate world-wide); modern genera of deciduous hardwood trees predominant, sedges and grasses appearing; clams and snails common in fresh-water, culmination of dinosaurs, toothed birds, archaic mammals (elevation of Rocky Mountains).
- Cenozoic era: 60-70 million years ago.
  - Paleocene and Eocene epochs: (inland seas recede, Appalachian region peneplained (Schooley) but later again uplifted, climate warm and humid) hardwood forests predominant, palms abundant; modern mammals and birds replace archaic forms.
- Oligocene epoch: 40 million years ago (continent peneplained); turtles, alligators, crocodile at maximum.
- Miocene epoch: 29 million years ago (western mountains becoming elevated, climate turning drier and colder); grasses disperse over open plains; insects reach full development and mammal fauna expands.
- Pliocene epoch: 12 million years ago (continued elevation of western mountains, especially Sierra Nevadas; lower Great Basin becomes arid); grasslands become extensive and desert vegetation develops in southwest; mammals at maximum and man-ape changing into man.
- Pleistocene epoch: 1 million years ago (continental glaciation); great mammals disappear.
- Psychozoic era: 25-30 thousand years ago (glaciers recede).
  - Recent epoch: man becomes predominant, rise of civilization.

Note: The epochs, Paleocene to Pliocene inclusive, are often grouped and designated the Tertiary Period, and the Pleistocene and Recent epochs the Quaternary Period.

to continue the succession into the indefinite future.

As higher types evolved in each taxonomic group, primitive forms mostly died out. The first primitive wingless insects appeared in the Devonian; in the Pennsylvanian there were giant forms of primitive dragonflies, cockroaches, and grasshoppers. One cockroach had a wingspread of nearly 12 cm. By the Permian, these giant forms disappeared and were replaced by many modern orders. During early Mesozoic, most modern families of insects were established, and by the Upper Cretaceous many modern genera are recognizable.

Of the two great groups of warm-blooded animals, the earliest mammals had originated by the Triassic. Modern orders did not become well differentiated until very late Cretaceous or early Paleocene, modern families by the Oligocene, and modern genera by the Pliocene (Simpson 1953).

Toothed birds appeared in the Jurassic and differentiation of types went on rapidly as modern orders were already represented in the Lower Cretaceous, modern families in the Eocene, modern genera in the Miocene, and modern species in the Pleistocene. The great group of songbirds evolved and dispersed through the world rather late, perhaps in the Miocene; since the Pleistocene epoch, evolution of birds has been largely limited to subspeciation.

An important aspect of the geosere is the dispersal of new types of animals and plants, for the importance of a new form depends on the extent of its distribution and the size of its population. A successful species saturates the available niches at its center of origin and thence spreads outward in all directions. Dispersal continues until an impassable barrier is reached. Tracing the origin of taxonomic groups, their phylogenetic relations with other taxonomic groups, and their dispersal is the subject matter of *zoogeography*. This knowledge is desirable for the ecological interpretation of communities, for it helps to explain their species composition and the geological history of the community itself.

The mechanics of evolution at the species level is called *speciation*, and is as much a problem of ecology as it is of zoogeography and genetics. Speciation in animals is initiated only when one population becomes isolated from another similar population so that interbreeding does not occur. This permits variation and natural selection to proceed independently in the two groups and to become fixed in the germplasm. Isolation is usually effected by geographic barriers and generally involves occupancy of new niches and development of new coactions with other members of the community. The history of the past ecological relations of species and of whole communities is the subject matter of *paleoecology*. The dynamic forces involved in these processes of speciation are among the determinants of the geosere.

The climax

We have described four types of succession as if each were entirely independent of the other three. This is not the case. All types of succession are going on simultaneously, although the relative importance of any one varies from one habitat to another. Biotic succession is most conspicuous, since it proceeds most rapidly and appears to reach a final, permanent stage in just a few decades or centuries. The climax stage of the biosere is undoubtedly more nearly stabilized, self-maintaining, and in steady state in its particular habitat than are the seral stages, yet it also is subject to gradual change over long periods of time. The climax, as well as the seral stages, changes with climate, physiographic forces, and evolutionary processes. However, the clisere usually requires a few thousands of years before changes in the community structure or composition become evident. The progress of an eosere is even slower; geosere, slowest of all. The *climax* is defined as the last stage in the biosere; no absolute stability or final permanency should be construed, since it is simultaneously a stage in the clisere, eosere, and geosere.

The climax may be recognized by the fact that in a uniform climatic area all seres tend to converge into it, and by its steady state in respect to structure, species composition, and productivity. In the climax community, all species, including the dominant species, are continually able successfully to reproduce and there is no evidence that new and different species are invading. In seral communities, on the other hand, the developing new growth, particularly evident in the dominants, contains many individuals of invading species which will eventually take over and replace species already present.

RECOGNITION OF COMMUNITIES

The community as an organic entity

Although the major community or ecosystem is the generally accepted unit of analysis in synecological studies, there is a difference of opinion as to whether the community constitutes a discrete organic entity. Two different points-of-view are incorporated in the organismic and individualistic concepts which are usually associated with the names of F. E. Clements (1916) and H. A. Gleason (1926), respectively, and more recently Phillips (1934–1935), Tischler (1951), and Emerson (1952) on one side and Bodenheimer (1938), Whittaker (1951, 1952, 1956, 1957) and Curtis (Brown and Curtis 1952) on the other. Ramensky (1926) stated the individualistic concept independently in Russia as early as 1924.

The *organismic concept* considers the community to be a supraorganism, a complex organism, or a social organism. As such, it is the highest stage in the organization of living matter; namely cell, tissue, organ, organ system, organism, species population, community. There is emergent evolution, so to speak, at each higher stage in this hierarchy; the whole is more than merely the sum of its parts. Tissues have properties, characteristics, and functions over and above those of the individual cells involved; the organ, the organ system, or whole organism functions in a way not to be predicted from a knowledge of the parts of which each consists. The species population has inherent characteristics of density, rate of natality, rate of mortality, and age distribution, while the total community has such unique functions as dominance, cooperation, trophic balance, competition, and succession which are beyond the characteristics of the individual organisms of which the community is composed. The community behaves as a unit in its competitional and successional relations with other communities, in its local and geographic distribution, in its seasonal activities and response to climate, and in its evolution. Although the community varies in its taxonomic composition and structure in different environmental situations, this variation is proportionally no greater than occurs in different cells of the same type or between individuals belonging to the same species.

The *individualistic concept* places emphasis on the species, rather than the community, as the essential unit for analysis of interrelations, activities, distribution, and evolution. Each species responds independently to the integrated influence of the various factors of the physical environment and biotic coactions. The environment may be conceived as a pattern of *gradients* with the intensity of the various factors changing gradually in space from one extreme to the other. The gradient may be a short one, as from the subterranean to the tree stratum in a forest or from the open water of a pond to a nearby swamp or climax forest, or it may be longer, as from the bottom to the top of a mountain or even from the tropical to the arctic zones of a continent. The population density of each species is distributed in a form resembling a normal curve when plotted along the gradient of a given factor, and the curves of many species in relation to various environmental gradients overlap in a heterogeneous, and apparently almost random, manner. There is seldom agreement between the limits of the distribution curves of any two species; species are not in general bound together into groups of associates which must occur together. Furthermore, the vegetation and its associated animal life very often form a *continuum* of gradually changing composition and complexity from one extreme of the environmental gradient to the other. A vegetational continuum has no sharp boundaries between individual communities of different types, and the ecologist must choose the manner in which he distinguishes these units so as best to suit his interests and objectives.

These two points-of-view are not necessarily incompatible. There is no doubt that each species is distributed according to its own physiology, its own complex interrelations with other species, and its own tolerances, and that no two species are exactly alike in their responses to the environment. On the other hand, one can be convinced that the community and its habitat, collectively the ecosystem, is a functional system and that every species of necessity occurs in and as a part of such a system so that its distribution is importantly modified by these interactions and community relations.

The community is usually recognized and identified by its most important organisms, the dominants and predominants (Shelford 1932). Subdominants and member species, however, are not usually dependent on the dominant species directly; rather, on the environmental conditions that the dominants establish. Different species of dominants in adjacent or related communities may react on the environment in a manner so nearly the same that subordinate species find suitable conditions for existence in each, although they are usually more characteristic of one than the other.

The niche that a species occupies is a finite unit of distribution that can be measured in an absolute and objective manner. The *community-stand* is an actual aggregation of organisms occurring in a particular locality. In a sense, it is a collection of niches occupied by a particular set of species, but it is something that one can see and study in the field. Because of the great variation in composition and character of community-stands in different habitats and parts of the world, they need to be evaluated and classified in some logical manner for reference purposes. *Community-types* are abstract groupings of individual community-stands which resemble one another and consequently must be defined rather arbitrarily. Different systems of community-types have been proposed, each designed to emphasize a particular point-

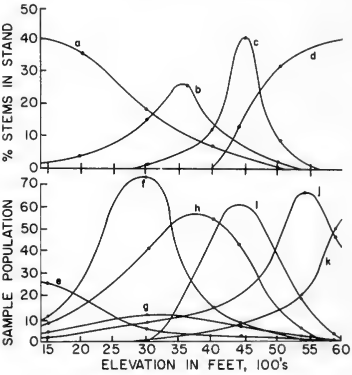


FIG. 3-3 **Continuum of tree (a,b,c,d) and foliage insect (e,f,g,h,i,j,k) species in an elevation gradient in the Smoky Mountains, Tennessee. (a) *Tsuga canadensis*; (b) *Halesia carolina*; (c) *Acer spicatum*; (d) *Fagus grandifolia*; (e) *Graphocephala coccinea*; (f) *Caecilius* sp.; (g) *Agalliopsis novella*; (h) *Polypsocus corruptus*; (i) *Anaspis rufa*; (j) *Cicadella flavoscuta*; (k) *Oncopsis* sp. (after Whittaker 1952).**

of-view. We are, in this book, using the biome system, the various parts and concepts of which will unfold as we proceed. We will consider the community as being at least analogous to an organism in being a functional unit of interacting parts and having some degree of structural uniformity. Although community-types are certainly not highly discrete and absolute units, recognition and naming of them is one way of indicating positions in the continua along environmental gradients that are occupied by particular aggregations of plant and animal species.

Physiognomy

The gross structure of a community or its physiognomy is an important basis for its recognition. In terrestrial communities, physiognomy is determined by the life forms of the dominant plant species and their spacing. The life forms that prevail in a given area depend on the climate and sometimes the substrate or other special features of the habitat and give character to the landscape. The distribution of animal communities is closely correlated with the structure of the vegetation, hence these vegetation-types need to be recognized and defined:

Desert: hot, arid habitats with scattered scrubby or thorny vegetation or, in extreme cases, none.

Steppe, plains: semi-arid grassland covered with short grasses.

Prairie: semi-humid grassland covered with mid- and tall grasses.

Chaparral: semi-arid areas covered with bushes and shrubs, usually broad-leaved evergreen.

Savanna: grassland with scattered groves of trees or shrubs.

Woodland: open stand of small deciduous or evergreen trees with undergrowth of grassland or desert vegetation.

Forest-edge: mixture of trees, shrubs, and open country, ordinarily occurring as a narrow belt on the margin of forests.

Forest: closed stand of trees forming a continuous canopy over most of the area.

Deciduous forest: broad leaves fall during cold or dry seasons.

Broad-leaved evergreen forest: no regular season of leaf fall, leaves often sclerophyllous, warm climates.

Rain forest: tall luxuriant forests, often with several strata of trees, foliage retained through-

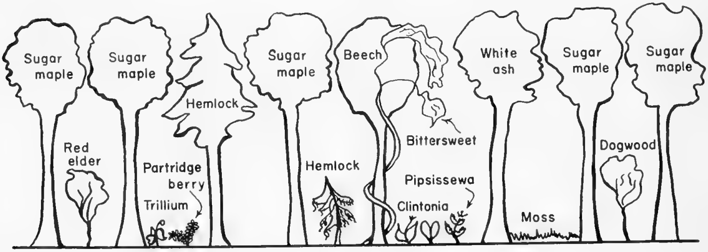
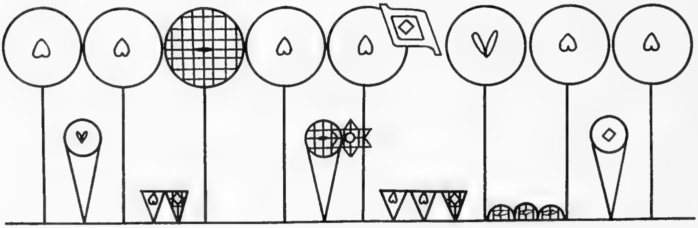


FIG. 3-4 A mixed deciduous-coniferous plant community (after Dansereau 1951). Above, a semi-realistic diagram of the community; below, symbolic structure of the community depicting life-form, size, function, leaf type, and texture.



out the year, climate continuously warm and wet.
Needle-leaved evergreen or coniferous forest: forests of pines, spruces, firs, larches, hemlocks, and the like.
Forest-tundra: stunted open growth of coniferous forests in cold climates.
Tundra: extensive flat or gently rolling treeless areas occurring in cold climates.
Alpine tundra: treeless areas at higher elevations of mountains.
Bog: wet areas in northern climates containing sphagnum, heath plants, coniferous trees.
Swamp: wet areas covered with trees or shrubs.
Marsh: wet areas containing sedges, rushes, cattails, and the like.

Inasmuch as animals choose niches in response primarily to the physical structure of the vegetation regardless of its taxonomic composition, it is helpful in describing biotic communities to show the vegetation structure in as much detail as possible. This may be done by semi-realistic diagrams or by a system of symbols (Dansereau 1951).

The 50 per cent rule

If the primary basis for community recognition is based on the life-form of the dominants, which on land is expressed in the physiognomy of the vegetation and in some aquatic habitats on the life form of the predominant animals, then the secondary breakdown of community units must be on the basis of taxonomic units. Here, the species unit is most useful, as the species is the smallest taxon having objective reality and precise interrelations with its environment.

Two aggregations of species occurring naturally in different areas or in the same area at different times are to be considered as distinct communities when at least 50 per cent of the *predominant species* of each aggregation are if not *exclusive* at least *characteristic* to the aggregation. This we may call the 50 per cent rule. The recognition of communities should not be influenced by the presence of rare species, for such are near the boundary of their habitat or geographic range. It is important to have quantitative information on the size of the populations to evaluate the importance of each species before community classification is attempted (Spärck 1935).

The distinctiveness of communities must work in both directions; that is to say, 50 per cent or more of the important species of each aggregation must be different from the other aggregation. This means that the two aggregations are more different than they are alike. If the species composition does not exhibit the 50 per cent distinction, the two aggregations are considered as belonging to the same community. If the difference approaches but does not equal 50 per cent, it is often worthwhile to designate the two aggregations as *facies* if they are seral, or *faciations* if they are climax, of the same community. It is preferable to use this criterion for differentiating communities, in the light of present ecological knowledge, rather than use more involved statistical criteria (Bray 1956). The 50 per cent rule has been earlier applied for separating zoogeographic regions (Mayr 1944).

Naming communities

Since communities are distinguished by differences in life form and taxonomic composition of the dominant or predominant organisms, these characteristics are usually used also in naming the community. Where the habitat is well defined but vegetation is largely or wholly lacking, as in many aquatic communities, habitat may be used in the terminology. Since names are largely a matter of convenience, they should be short and be derived from some easily recognized feature of the community or habitat. Very often the generic names of two, sometimes three, conspicuous dominants are used to name plant communities; two or three predominant characteristic or exclusive animal species, together with the prevailing type of vegetation or habitat, are employed to name animal communities. In case of some large communities, geographic names are more convenient.

Large geographic units, differentiated on the basis of difference in the climax type of vegetation, are called *biomes*. They are specifically named by the characteristic form of vegetation present; tundra biome, or grassland biome, for instance.

Secondary communities within the biome can be distinguished as climax or seral, respectively, by the suffixes *-iation* and *-ies*. An *association* is a climax plant community identified by the combination of dominant species present; an *associes* is an equivalent seral plant community. Thus we may speak, for instances, of the *Fagus-Acer* association, which is a climax deciduous forest community, and of the *Calamogrostis-Andropogon* associes, which is a grass stage in a sand sere (Clements and Shelford 1939).

Animal communities on land are related to different life-forms of plants or types of vegetation, but only seldom to plant communities distinguished by the taxonomic composition of the plant dominants. Thus animal communities must be analyzed and named independently of plant communities. A *biociation* is a climax animal or biotic community identified by the distinctiveness of the predominant animal species; a *biocies* is the seral equivalent. The

North American deciduous forest *biociation* is to be contrasted, for instance, with the pond-marsh *biocies*.

When two plant or animal communities merge, either by intermingling of species in the same habitat or by juxtaposition of different communities in the same region, the resultant transitional state is called an *ecotone*. Ecotones occur between consecutive communities in seral development on an area as well as between adjacent existing local or geographic communities.

SUMMARY

A community is an aggregation of organisms in a distinctive combination of species. The community and the habitat in which it occurs constitute an ecosystem. Inherent within the community are forces of dominance which control the species composition, and of influence which affects the abundance, health, and activities of organisms. Dominance is exerted primarily through reactions of organisms on the habitat, influence primarily by coactions of organisms on one another. The relative importance of each of the various species within the community is evaluated on the bases of exclusiveness, abundance, time of activity, secondary groupings, and influence. Reproduction and growth brings a production of organic matter; the rate at which formation of it takes place is called productivity.

Communities are constantly changing, the result of reactions and coactions of the organisms, and climatic, physiographic, and evolutionary processes. This change is one of succession, an orderly replacement of one community by another until a climax, especially evident in bioseres, is reached.

The community may be considered as a highly integrated self-contained organic unit or as merely an aggregation of independent species whose preferanda coincide in the same habitat. These are extreme points-of-view; an intermediate one is adopted in this book.

The gross structure of the community is the primary basis for distinguishing and recognizing it. On land, this structure is characterized by type of vegetation; in water, by the life-form of the predominant organisms, which are usually animals. Communities are then subdivided according to their taxonomic composition. An aggregation of species is given community status if at least 50 per cent of the predominant species are exclusive to or characteristic of it. Animal communities are named for the type of vegetation, life-form of predominating species, or habitat, depending on which is the most conspicuous feature; and secondarily for the predominant two or three exclusive or characteristic species that it contains or for the geographic area in which it occurs. Biomes are major geographic community units. Biociations are secondary climax communities distinguished by the distinctiveness of their predominant animal species. Biocies are the seral equivalents of biociations.

4

Background:

Measurement of Populations

The analysis of ecological communities must include a measurement of animal populations that the role played by each species may be properly evaluated. The ecologist should also be able to determine quantitatively the abundance of species at different times and different places. It is not sufficient in ecological research to indicate that a species is abundant, common, or rare; abundance must be expressed in such objective terms as lend themselves to statistical manipulations. In spite of their fundamental importance, available methods for measuring population size are only moderately satisfactory and are in need of vast improvement (Balogh 1958, Davis in Mosby 1960).

Indices of abundance are sometimes used; for instance the number of individuals or songs observed per hour, per day, or per trip; per cent (frequency) of samples in which the species was recorded; number of nests, dens, tracks, or fecal pellets per unit area; amount of food or bait consumed per unit of time, and so forth. Under certain conditions of uniform habitat and weather, random distribution of individuals, and uniform conspicuousness of the animals, indices are useful for demonstrating differences in population size within a single species as functions of time or space, but they are seldom accurate enough to allow comparisons between different species. There have been various attempts to correlate relative indices with absolute abundance (Hendrickson 1939, Bennett *et al.* 1940, Cahalane 1941, Baumgartner 1938, Emlen *et al.* 1949, Eberhardt and Van Etten 1956), but the results have been usually unsatisfactory (Clapham 1936, Dice 1952). In most types of ecological research, the aim should be to determine absolute abundance or the actual number or biomass of a species in an area of known size. The difficulty in doing so is no greater than in correcting relative indices for all the variables that are involved.

STRIP CENSUSES

This method is one of counting all individuals of birds and larger mammals seen on each side of a line of travel over a measured distance. Sometimes the count is made only of animals observed within a definite distance from the line of travel. In other cases, the effective width, and hence the area, over which the animals are being censused is computed as twice the average distance at which each species is first observed. This makes possible a quick survey of large areas in any kind of terrain, but is subject to inaccuracies of individuals omitted, especially as the distance from the trail increases (Hayne 1949a); differences in conspicuousness of different species or individuals exhibiting atypical or unusual behavior; and variations in visibility as one passes from one type of terrain or vegetation to another.

A variation of this method, often employed for counting larger animals such as deer, is to increase the width of the census strip by using a line of many observers that progresses uniformly over an area of previously fixed dimension. The animals are counted as they are driven back through the line or out between other observers stationed along the boundary (Rasmussen and Doman 1943). Helicopters may be effectively used for counting large animals in open country (Aldous 1956); faster flying aircraft are less successful (Gilbert and Grieb 1957).

SAMPLE PLOTS

Since it is seldom possible to count all the individuals present in a large area, it becomes necessary to take sample counts over small areas where accurate counting of individuals is practical. The problem then arises as to the number, size, shape, and distribution of plots required to give reliable information on species composition and the mean density for all the organisms involved. Much work on this problem has been done by plant ecologists, and their techniques should also be of use to animal ecologists.

Plot distribution and shape

Sample plots may be distributed either systematically or at random. *Systematic* arrangement of plots of uniform size spaced at equal intervals along straight lines is often preferred because of its easy application. However, if the distribution of organisms over the area shows a uniform pattern of variation, systematic sampling may indicate densities either too high or too low. Furthermore, systematic sampling does not permit the assessment of error, since statistical theory requires that the location of each sampling unit be independently determined, whereas in systematic sampling, the position of all plots is determined by the location of the first one. The completely *random* location of sample plots over an area may be somewhat more difficult to apply in the field, but the data obtained are just as precise and have the advantage that the error of sampling can be calculated (Bourdeau 1953). In order to get randomly located sample plots, a map of the entire area is subdivided into numbered plots of the proper size. The plots to be used are then selected by using tables of random numbers. If the same number comes up twice, the duplication should be discarded (Dice 1952). Other plans of sampling, such as stratified random sampling, may sometimes be preferable.

Where a habitat is perfectly uniform, the *shape* of a sample plot is not of great importance, although square plots are commonly used. Where a habitat is obviously not uniform a rectangular plot oriented with its long axis across any observed contour-, soil-, or vegetation banding will furnish less variable data than plots that are shorter and wider (Bormann 1953). Circular plots, which possess a smaller periphery than any other shape, are useful where the influx and exit of animals must be minimized.

Size

The size of plot sufficient to include an adequate sampling of the *species composition* of a particular local community varies with species involved and density of populations. Larger plots must be used for larger organisms, richer fauna, for situations in which one or a few species are so markedly predominant that minor species are scattered, and where population levels generally are low. Since the number of species included will vary with the size of the area covered in sampling, some standardization is desirable for comparing the species composition of different communities.

A standard size for sampling plots may be determined empirically (Vestal 1949). If the numbers of species found on plots of different sizes are plotted against the logarithms of the plot sizes, a sigmoid so-called species-area curve is formed. The characteristics of this curve are that an increase in the size of small sampling plots includes, at first, a considerably larger number of species, but later a size of plot is reached, varying with the kind of organisms being counted, beyond which there is little to be gained by increasing the area sampled. Two arbitrarily chosen points on the upper part of this curve, where it is concave toward the scale of plot size, have ecological significance. One of these points represents a plot fifty times the size of the other, containing twice the number of species of the other. The larger plot is close to the upper asymptote of the curve and represents a fair-sized sample plot for practically all purposes. The smaller area, located near the point of inflection and containing half the number of species, is the smallest representative area that is sufficient to identify the community, but hardly usable for any other purpose. A third point may be identified, midway between these two points on the curve, as the minimum area large enough to include all important species and about half of the minor ones. It clearly defines the community and the approximate ranking of species in points of number and biomass. The area this intermediate point represents is five times the smallest representative area and one-tenth the fair-sized area.

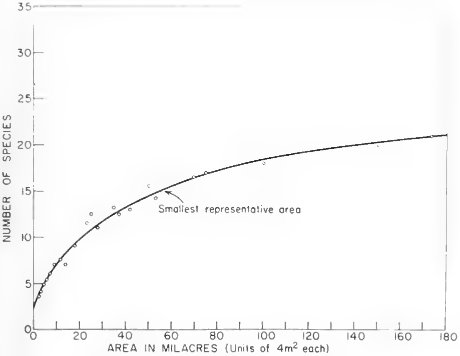
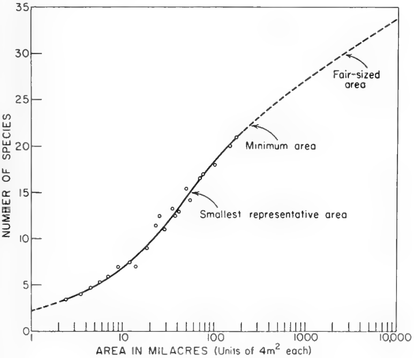


FIG. 4-1a, b **Species-area curves plotted (above) on arithmetic and (below) on logarithmic bases, to illustrate the method of determining sampling area sizes adequate for analysis of community species composition.**



The sizes of "Smallest representative," "Minimum," and "Fair-sized" areas may be determined from a sigmoid curve—of which Fig. 4-1b is an example—by the following technique.

A rectangular sheet of tracing paper is placed over the graph, the bottom edge of the paper coincident with the horizontal axis of the graph. Using the graduations on the logarithmic scale as a guide, place a mark on the bottom edge of the paper by one of the graduations. To the right of that mark, place another by that scale graduation which is 50 times the value of the first (on Fig. 4-1b, if the left mark is at 2, the right mark should be at 100). The interval between the marks represents a 50-fold increase in area. From the right mark, draw a vertical line several inches long. Now place the sheet over the graph in such a way that the bottom edge is parallel to the horizontal axis of the graph, and the left mark lies on the curve—the vertical line from the right mark should be long enough so that it will continuously intersect the curve. Keeping the bottom edge of the paper parallel to the horizontal axis of the graph, move the paper in such a way that the left mark traces along the curve. Move the sheet until the vertical line intersects the curve at a point which is twice the value of the point at which the left mark is resting on the curve, *as both values are read off the vertical scale* (on Fig. 4-1b, when the left mark rests on the curve at a point opposite 15 on the vertical scale, and the bottom edge of the tracing paper is horizontal to the horizontal axis of the graph, the vertical line intersects the curve at a point opposite 30 on the vertical scale). The point established by the left mark is the value of the "Smallest representative area," and the point established by the perpendicular line intersecting the curve is the value of the "Fair-sized area," *as both values are read in area units off the horizontal scale*. Find, by measuring, the point on the curve which lies midway between the two points just found—this is the "Minimum area," and its value is read in area units off the horizontal scale (after Vestal 1949).

In ecological sampling, fair-sized areas should be used wherever possible, but minimum-sized areas are sometimes acceptable. For evaluation of this and other procedures, see Goodall (1952). When the number of species encountered on several randomly distributed sample plots is known, it is possible to estimate statistically the actual number of species present in the whole area (Evans, Clark, and Brand 1955).

The size of the plot should also be adequate to include an accurate representation of the population densities of the various species present. Much of the difficulty of accurately determining population densities results from populations being non-randomly distributed in the space they could occupy (Cole 1946). To be *randomly distributed,* populations must have been scattered by chance rather than coercion, regardless of the proximity or distance one from another. This seldom occurs either with plants or animals. Plants reproduce by rhizomes, stolons, or suckers or by seeds concentrated near the parent plants. Animals usually lay eggs or drop young in local areas or nests, so offspring are at least temporarily concentrated. Many animals congregate socially or form colonies, concentrate on some local food supply, or are grouped closely together in certain microhabitats because of less favorable environmental conditions elsewhere. Even the attraction of male to female for reproductive purposes is a variation from random dispersal. Whenever the occurrence of one or more organisms in an area increases the likelihood that other organisms will occur nearby, this is spoken of as *contagious distribution.* Species may also exhibit *negatively contagious distributions* when they are spaced more regularly than would be expected by chance, as for instance flocking or colonial birds where each individual keeps just beyond the pecking reach of its neighbor.

When small-sized plots are used, contagious distribution shows itself in an excessive number of plots containing no individual and of plots containing a large number of individuals with a corresponding deficit of plots with intermediate numbers of individuals. This represents a deviation from the typical Poisson distribution which is expected with random distribution (Snedecor 1956). In a Poisson series, the mean number of individuals per quadrat should equal the variance according to the formula

$$\frac{\sum(x-\bar{x})^2}{\bar{x}(n-1)} = 1$$

The letter x is the number in each quadrat, $\bar{x}$ is the mean number in all quadrats, and n is the number of quadrats. If the value obtained is significantly greater than unity, then contagious distribution is indicated, if the value is less than unity, then negatively contagious distribution is indicated. For a reasonably large number of sample quadrats, say 20 or more, a deviation from unity would be considered significant if it were greater than $2\sqrt{2n/(n-1)^2}$ (Andrewartha and Birch 1954).

With contagious distribution of individuals, the aggregates themselves are often randomly distributed, in which case quadrats may be increased in size until they give a random distribution of aggregates rather than of individuals. The total population would then be computed by multiplying the number of aggregates per unit area by the average number of individuals per aggregate. When aggregation occurs but is not easily observed, then other procedures must be employed (Cole 1946a, Goodall 1952).

Number

The number of sample plots needed depends upon the precision desired for the statistical characteristics to be estimated. The degree of precision required will vary with the trustworthiness of the data and the objectives of the study. In most statistical investigations, a range of 20 to 40 replications is ample (Snedecor 1956: p. 104). Too few replications may fail to detect important differences, but too many are unrewardingly wasteful of time and energy. Any differences noted between population densities of different species on the same area, or of the same species on different areas or at different times, should be significant at least at the 5 per cent level of statistical probability. Where the number of samples is small, the differences must be relatively large to insure this level of confidence. With ecological studies in the field, there are often practical difficulties involved in obtaining a sufficient number of accurate measurements to permit reliance on minor differences in population size. It is best, therefore, to be conservative in evaluating the importance of differences in population densities. Special care must be used in evaluating the densities of rare species, as such densities are unlikely to be reliable if based on counts of less than 20 or 30 individuals (Preston 1948).

CAPTURE-RECAPTURE METHOD

Some general methods of calculating population densities need to be considered. C. G. J. Petersen, of the Danish Biological Station, working with fish in 1896; F. C. Lincoln, of the US Fish and Wildlife Service in 1930, trying to estimate the number of ducks on the North American continent; and Jackson (1933), working with insects, all independently derived a formula for determining the population size of various species of animals, much used in recent years (Ricker 1948). The method depends first on capturing a fair sample of individuals in a unit area, marking them in some distinctive manner (*Ecol.* **37**, 1956: 665–689), releasing them for rediffusion over the area, then after a short interval, retrapping the area. The ratio of marked individuals recaptured to the total number marked should theoretically be the same as the total marked and unmarked animals captured during the second trapping is to the total population or:

$$\text{Total population} = \frac{\text{total number marked}}{\text{marked individuals recaptured} \times \text{total captured}}$$

Other formulas make use of accumulating totals of marked and unmarked individuals during successive periods of trapping (DeLury 1958).

The greater the percentage of the population marked and subsequently recaptured, the greater is the accuracy of the calculations. However, there are several possible, uncontrollable sources of error: unequal mortality of marked compared with unmarked individuals; dispersal of individuals out of the area, influx of animals from outside; increase by reason of reproduction, marked animals not becoming randomly distributed among the unmarked; marked animals being recaptured with greater or less ease than unmarked ones; marks being lost or not reported, and so forth. Some of these possible errors can be corrected statistically, and a considerable body of literature has accumulated describing means of so doing (see especially *Biometrika* since 1951).

CAPTURE PER UNIT-EFFORT

In a closed or stabilized population, when the same time, traps, and effort are employed to capture or count individuals in the same area at different times and there is no loss or increment in the original population, and weather and other conditions remain the same, the number of new individuals captured or discovered with each subsequent effort becomes less and less, and should eventually reach zero. When the number of new individuals captured per unit of effort is plotted against the cumulative number of animals captured, a straight line results. A line thus derived from a few catches may be extended to zero, and the total population of animals in the area determined (DeLury 1947, Zippin 1958). A variation of this method is to use the increasing percentage of marked animals in the total number captured at successive intervals of time, as the increase in these percentages follows a definite trend that would eventually include the total population (Hayne 1949).

APPLICATION TO ANIMAL GROUPS

Mammals

The more conspicuous diurnal mammals are commonly censused by cruising or drives, but nocturnal forms, especially mice and shrews, usually have to be trapped (but see Emlen *et al.* 1957). Snap or kill traps are commonly used. When set in a variety of microhabitats they quickly gather specimens to show the species composition of the community. An early attempt at estimating abundance was expressed in terms of the number of individuals caught per trap per night. At the same site, more animals are usually caught during the first night than during later nights; 10 traps set for 10 nights will not capture as many small mammals as 100 traps set for only one night, although 100 trap-nights are involved in both instances. When the trapping procedure is standardized as to location in community, number of traps used, interval between traps, length of trap lines, number of nights trapping, and so on as has been done in the North American Census of Small Mammals (Calhoun 1956), it is possible to follow changes in relative abundance from year to year. It is not possible to relate such data to the absolute number per unit area unless the home range of each species in each locality is known (Stickel 1948).

The next advance in censusing technique was to confine the location of kill traps to a small area, usually an acre (0.4 hectare). Enough traps, a hundred or more, are included to saturate the area to the end

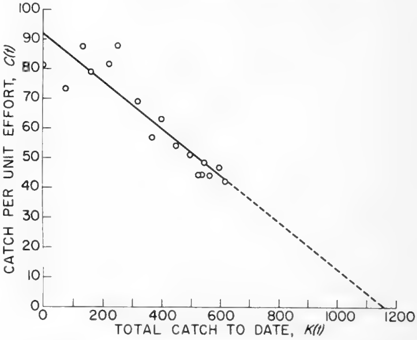


FIG. 4-2 Total population ($K = 1170$) calculated by extension of a straight line through data on successive catches per unit effort, $C(t)$, plotted against the accumulating total catch, $K(t)$ (from DeLury 1947).

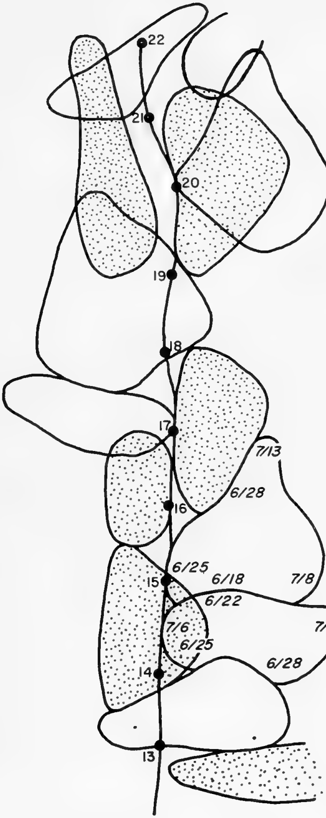


FIG. 4-3 Individual territories of birds representing two competing species, wood pewee (stippled) and least flycatcher, along a forest trail. Note that territories of individuals of the same species do not overlap, and that territories of the two species are largely but not entirely exclusive. The outline of each territory is based on observations made from the numbered points. The dates of the several data-collection trips are shown for two territories only (Kendeigh 1956).

of capturing all individuals present during a trapping period of three nights (Bole 1939). Influx and departure of animals, however, disturbs the accuracy of the measurement. Influx is usually more of a problem than escape from the area, as the trap bait and removal of captured individuals encourages invasion (Stickel 1946). Since all animals whose home ranges approach or overlap the boundary of the trapping area are likely to be caught, a correction for this error may be made by considering the census area to include a surrounding belt equal to one-half of the home range of each species concerned (Dice 1952). In order to reduce the boundary of contact with the outside area to a minimum, square or circular areas are used, rather than rectangular or irregular-shaped areas. Censuses taken in this manner and live-trap censuses sometimes give comparable results (R. M. Wetzel 1949, Buckner 1957), but in neither case can one usually be certain that he has captured all the inhabitants of the area (Fowle and Edwards 1954).

Live trapping, marking, and release of individuals is a more trustworthy means of censusing small mammals, but is more laborious and time-consuming (Blair 1941, Stickel 1946). Traps are usually distributed grid fashion at intervals of 15 to 20 meters, over several acres or hectares. Trapping is continued for a week, or until very few or no unmarked animals are captured. Marking is commonly toe clipping, ear notching, tattooing, or tags (Taber 1956). Since the animals are immediately freed, the population equilibrium is not greatly disturbed, and influx of extraneous individuals is negligible. The method has the further advantage of allowing the determination of home ranges. Individual animals differ, however, in the readiness with which they will enter traps (Geis 1955), and this will affect the accurate determination of home ranges.

The type of bait used varies with the species being trapped. Seasonal fluctuations in numbers of animals trapped may sometimes be due to variability in the acceptance of bait (Fitch 1954). For mice and shrews, a paste made of peanut butter, oatmeal flakes, and raisins is commonly used.

The most recent and promising development of technique for determining home ranges is the labeling of individuals with radioactive material, then following the movements of the freed animals by use of geiger counters (Godfrey 1954, Pendleton 1956, L. S. Miller 1957, Harrison 1958). This procedure has also been used with amphibians (Karlstrom 1957).

Birds

Airplanes have come into common use for censusing large concentrations of waterfowl. Aerial photographs are made and enlarged, and individual birds pin-pointed. Roadside counts, calling-male transects, indices derived from population structure, kill records, and a variety of other procedures are used to inventory upland game species (Hickey 1955).

For determining populations of smaller species during the nesting season, the spot-map method is commonly used and censuses thus obtained are probably reliable within plus or minus 10 per cent, if they are carefully made (Kendeigh 1944). A sample plot of uniform vegetation of at least 10 hectares (25 acres) is marked out in a grid with numbered stakes or tree tags at intervals of not over 50 meters, or the stakes may be placed along a trail. At least five, preferably more, daily counts of singing males, females, and nests are made at suitable intervals throughout the nesting season. Each time a bird is observed it is marked on a map of the plot. At the end of the season all the spots at which a species was observed are placed together on one map. Since individual birds are observed most frequently in the vicinity of their nests and within their territories, the spots fall naturally into groups so that each group indicates the presence of a breeding pair or at least a territorial male. Counting the number of groups of spots for each species gives the total population for the area. For the large predators, gallinaceous birds, or wide ranging species, census plots of much larger size are necessary than for the smaller song birds, so that procedures must be adjusted to the conditions of the habitat and the species involved. For detailed studies of small populations, the birds should be banded and color-marked for individual recognition (Hickey 1943).

Foliage arthropods

In order to determine the insect and spider composition in the herb, shrub, and tree strata of a forest, use of a variety of collecting methods is desirable; net sweepings, light traps, bait traps, adhesive snares, and the like (Hoffmann *et al.* 1949, Morris 1960). Some of these methods may be made semiquantitative to show relative abundance, but there is considerable difficulty in converting the data obtained into absolute abundance.

The use of the sweep net can be standardized to give useful and comparable estimates of population densities (Carpenter 1936). A series of 48 strokes of the net through the upper level of the herb stratum synchronized with one's pace so that successive strokes do not hit the same plants gives approximately the same number of individuals as one would find on the herbs covering one square meter if all could be captured. The net should have a diameter of 33 cm (13 in.), the strokes should be about one meter long (Shelford 1951a), and comparative samples should be taken at approximately the same time of day (Adams 1941). A similar number of strokes through the shrub foliage may be used, but the conversion to number of individuals per square meter depends on the extent and uniformity of the shrubs that cover the ground. Inaccuracies involved in sweep net sampling are the result of variations in the activity of the insects and spiders produced by changes in temperature, wind, and humidity; variations in position of the insects on the plants and hence exposure to capture; insects taking flight in advance of the collector; variations in the height of the herbs; and variations in the length and rapidity of the strokes (DeLong 1932, Hughes 1955). Differences between sexes and species in behavior and life history will also cause variations in the sampling effectiveness.

Tests on the reliability of population estimates of single species based on the sweep-net method, made by comparing the results of two different workers in the same woods at the same time, showed an agreement within 100 per cent in only 36 per cent of comparisons between single weekly collections, but in 74 per cent of comparisons between averages of weekly collections taken over the entire summer (Graves 1953). This would indicate that variations in population estimates obtained by sweep-net samples are not significant unless a good series of data is obtained, and only then when differences between averages amount to more than 100 to 200 per cent; i.e., when the larger population is at least 2 or 3 times the size of the smaller. Actually, variations in population size of the same species of insect or spider at different times or in different communities may amount to several hundred per cent, and hence the sweep net method is useful for quantitative studies.

Sampling of arthropods in the tree canopy is more difficult. In the absence of wind, small trees can be jarred or shaken so that released animals fall on a cloth spread beneath. With proper equipment, trees may be fumigated with such poisonous sprays as DDT so that the dead insects fall onto cloths spread below. To put the data on a comparative basis, the volume of the space occupied by the foliage may be measured or estimated, and the number of individuals per cubic meter calculated. In deciduous forests of eastern North America the tree canopy is commonly about 10 m thick. A useful standard for comparison with the numbers per square meter of ground, herbs, and shrubs is the number per 10 m^3.

With taller trees, samples of the foliage for visual counting of the immature stages of arthropods present may be collected with the aid of aluminum pole pruners and extension ladders, or from trestles or platforms. Foliage samples, especially of coniferous species, should consist of entire branches or longitudinal halves, since arthropods may vary in abundance from the newer apical growth to the older basal foliage. If the width of the branch at mid-length is measured, then the length of the foliated part times the width gives the foliage surface. The total foliage surface of representative trees is determined from felled individuals, and the total foliage surface per unit area may be computed from the known density of trees. If the arthropods vary in abundance at different levels in the tree, representative sampling must be taken at each level. Considerable variation in animal density also occurs from tree to tree so that sampling must be well distributed over the area under investigation (Morris 1960).

Soil animals

One must resort to a variety of methods to census the different kinds of animals in the soil because of great differences in their size, physical characteristics, and behavior (Fenton 1947, Van der Drift 1950, Kevan 1955). The *megafauna* consists of the larger millipedes, centipedes, snails, amphibians, reptiles, and small mammals. Mammals must usually be trapped. For the other forms mentioned, if there are a half-dozen workers available, a plot 10 meters on a side (100 m^2) may be marked out and the observers, forming a line at one side, may gradually work over the plot, turning over all the leaves and sticks. This gives a good count but must be repeated in various parts of the community.

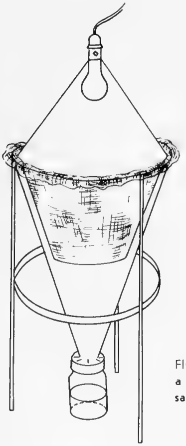


FIG. 4-4 **Tullgren modification of a Berlese funnel for quantitative sampling of soil animals.**

For quantitative sampling the fauna of fallen logs and decaying stumps, it is convenient to mark out an area 50 meters on a side (0.25 hectare) and then measure the length of all logs and the height of stumps. A medium-sized log and stump are completely torn apart and all animals counted. The total population for the whole area may then be calculated.

The *macrofauna,* consisting of the larger insects and spiders, the smaller millipedes, centipedes, and snails, and the earthworms may be censused by means of a steel ring, 7.5 cm wide, having a sharpened edge, and covering 0.1 m^2, which is pressed into the ground until it is flush with the surface. The litter and top 10–12 cm of the soil, which contain most of the ground animals, may then be sorted by hand, either in the field or in the laboratory. Samples brought in from the field should be transported in paper or plastic sacks or tight containers and sorted as soon as possible before the predatory animals in the sample have consumed prey species.

Lumbricid earthworms commonly penetrate well below the topmost few centimeters of the soil. Hand-sorting of considerable amounts of soil is both laborious and time consuming, but gives the most dependable results. In one study, small sample plots were thoroughly soaked with a potassium permanganate solution, and a later check by hand sorting indicated that 80 per cent of the adult and 100 per cent of the immature worms were forced to the surface (Evans and Guild 1947). Attempts at earthworm censusing with other chemicals have been less satisfactory (Svendson 1955). Driving worms to the surface by a discharge of alternating current from a probe thrust into the ground has also been tried (Kevan 1955).

Enchytraeid or pot-worms belong to the *mesofauna* as do the smaller arthropods, such as springtails, symphylans, pauropods, proturans, mites, and various insect larvae. Enchytraeids may be extracted quickly and efficiently by putting a layer of sand on top of a soil sample in a special container, and applying heat and water from below. This forces the animals to accumulate in the sand, from which they may be easily separated (Kevan 1955).

A common method of extracting small arthropods from litter and soil is by means of the Tullgren modification of the *Berlese funnel.* Where possible, the soil sample should be kept intact as a block and inverted into the funnel, bottom side up with an electric light bulb placed above the sample. Forced to retreat from the light and heat and the gradual drying of the soil from the top to the bottom, the animals move down the funnel and fall into the bottle of alcohol below. A week or ten days is usually required to obtain all possible animals from the sample. The procedure is subject to a number of faults, however, and must be modified for different soil types and taxonomic groups to produce the best results (Macfadyen 1953).

With the *flotation method*, the litter or soil is placed in a large pan, and warm—not hot—water is poured in to thoroughly soak and cover the soil to a depth of 1–2 cm. The warm water stimulates the animals to activity, and they come to the surface where they may be collected with forceps or suction bottle. For greater efficiency, air may be bubbled through the material to break up clumped masses; chemicals, such as magnesium sulphate, may be added to increase the specific gravity of the water (Kevan 1955).

The *microfauna* consists mostly of microscopic forms such as protozoans, rotifers, nematodes, tardigrades, and turbellarians. To quickly obtain a non-quantitative sample, a few grams of soil or litter may be placed on a screen in a glass funnel, and water, warmed to about 40°C, poured over it. The fluid collected from the funnel may then be centrifuged. A slower but more effective method for collecting nematodes is to wrap the sample in cheese-cloth or muslin and immerse it in water in a funnel that has a clamped rubber tube fastened to the stem. Let it stand for a few hours, and the nematodes will collect in the stem of this *Baerman funnel*. They may then be released into a petri dish for examination (Kevan 1955).

To obtain a good idea of the protozoans present, culturing is usually necessary. Edible bacteria are added to a non-nutrient agar or silica jelly in a petri dish, small amounts of properly prepared soil dilutions inserted at various points, and the culture incubated for two weeks. Final examination of the culture is made under the microscope, and the presence or absence of protozoans at the various points determined. Cultures may also be prepared using soil extract or hay infusion (Kevan 1955).

Fish

In small streams, a representative section of known length may be blocked off at the upper end by stretching a net from one bank to the other. Seining proceeds from the lower end up to the stretched net. There are limits, of course, to the size and depth of streams that can be examined in this manner, and unless care is taken, fish will escape around the ends or underneath the net. Seines can be used efficiently in this manner only when the bottom is free of large stones or other obstacles.

It is sometimes possible to draw long nets over measured areas of ponds and the shallow waters of lakes, but the data obtained usually give a relative abundance only. In deeper water, trammel, gill, or Fyke nets may be set, but each type of gear has limitations with reference to species, locality, and time of day. Seines, trammel and Fyke nets that catch fish alive are commonly used, however, in applying the Petersen method for obtaining absolute abundance.

When fish are removed from a body of water by gear of some sort or by sport fishing, the catch per unit-effort may be a basis for estimating total population. Creel censuses of the catch of fishermen are commonly taken to measure the yield of fish over periods of time.

In modern practice, artificial ponds are usually built in such a way that they may be drained and undesired species or surplus populations removed. Fish may be counted and measured in these operations, and only those species which are desired for replenishing the population restored to the pond.

Small bodies of water, or representative areas of larger bodies, can be blocked off with nets and censused by the use of a poison, such as rotenone (powdered derris root). Fish are killed and float to the surface of the water where they may be collected and counted. This method cannot, of course, be used where the population is to be left undisturbed. The poison also kills most zooplankton and some, but not all, other kinds of invertebrates (Brown and Ball 1942).

A less drastic method, that of shocking, is most effective in small streams. Two electrodes are inserted into the water and the electric charge temporarily stuns the fish so that they float to the surface where they can be captured. After the desired data are obtained, the fish are returned to the water and recover rapidly (Lagler 1952).

Plankton

Plankton nets are commonly made of silk bolting cloth; number 20 or 25 is ordinarily the finest mesh used. Tow nets are made with a conical bag attached to a wire frame, to which the tow string is attached by means of cords. Collections may be removed by turning the net inside out in a jar of water, or the organisms may be concentrated in a vial screwed in at the tip of the cone.

For surface plankton, it suffices to use the plankton net as a sieve and pour through it a known quantity of water. The tow net may be dragged behind a boat either at the surface or submerged to any depth by means of weights attached to the tow line.

Since the depth at which plankton occur varies with the time of day, vertical hauls sampling all depths are preferred. Comparison of plankton populations at different times or in different areas had best be made in terms of unit surface area. The Wis-

FIG. 4-5 **A Fyke fish trap (courtesy Illinois State Natural History Survey).**

consin plankton net is especially designed for this purpose. Closing nets or traps can be made so that they may be lowered to any desired depth, then closed and brought to the surface. This enables the investigator to determine at what depths the organisms occur. The Kemmerer sampler is used extensively for bringing up known volumes of water from measured depths for plankton or for chemical analyses. Nannoplankton, which passes through the finest tow net, needs to be filtered out or centrifuged out for quantitative measurement (Ballantine 1953).

Net plankton is ordinarily counted with the use of a Sedgwick-Rafter cell that holds exactly one cubic centimeter at a time, and the number present calculated per unit volume or surface area of the pond or lake. The volume of water filtered is equal to the area of the net opening, times the distance pulled, times a correction factor. No plankton net filters out all the organisms from the column of water through which it is dragged. The efficiency of such nets depends on fineness of mesh, rapidity with which it is pulled, and the abundance of organisms present. Fine-mesh nets offer resistance to water flow, which is further inhibited as the pores become clogged with organisms, so that a part of the water column is diverted around the net as it is pulled. A correction coefficient must be determined for each net and for each different rate at which it is pulled. This may be done by comparing the quantity of catch obtained in the tow net with the density obtained through use of plankton-traps or the Kemmerer sampler. Detailed instructions for constructing different kinds of nets, and statements concerning the advantages, disadvantages, and possible errors in the use of different methods are given by Sverdrup *et al.* (1942) and Welch (1948).

Bottom organisms

Dip-nets are commonly used for obtaining macroscopic bottom organisms and those attached to submerged vegetation. In shallow water, bottom organisms may be scooped out from a bottomless cylinder covering a known area. We find that four good scoops with a dip-net are necessary to get most of the organisms from a cylinder covering 0.2 m^2, so we sometimes consider two scoopsfull with a dip-net as equivalent to 0.1 m^2 when the cylinder is not used. The Surber swift-water net is standard equipment

FIG. 4-6 **A fish-shocker in use (courtesy Illinois State Natural History Survey).**

for sampling rocky stream bottoms. A frame marks out 0.1 m^2, and a net downstream catches organisms dislodged as the rocks are removed into a pail, for closer examination (Fig. 5–2a).

Dredges of various shapes and sizes may be pulled along the bottom for measured distances to get organisms in deep-water, but quantitative determinations obtained in this way give population estimates that are generally too low. The dredge commonly does not dig sufficiently deep into the bottom; often it skips and slides along the surface without picking up all the organisms that are present. Much more reliable are the Ekman bottom sampler, on soft bottoms, and the heavier Petersen sampler, used also on sand and harder bottoms (Fig. 6–9). For microscopic organisms small core samples are usually collected and brought back to the laboratory for examination.

The bottom samples obtained in various ways must ordinarily be washed through sieves to remove the debris, and the animals put into vials or jars for identification and counting. The size of mesh to be used in the sieve depends on one's objectives (Reish 1959). We find four nesting sieves efficient, with the top sieve having a coarse mesh (2 per inch) and the lower ones of increasing fineness (10, 20, 30 meshes per inch) to capture smaller organisms. Suppliers of limnological and oceanographic apparatus and supplies have been listed by Ryther *et al.* (1959). It should also be noted that for on-site studies of animals under water, increasing use is being made of photography and even television. The bottom may also be explored at first hand using diving equipment.

SUMMARY

Although determination of relative abundance is sometimes useful in projects of limited scope, the measurement of absolute abundance is generally to be preferred. Measurement of absolute abundance requires the counting of individual animals or measurement of their biomasses on strip censuses or sample plots. The size, number, shape, and distribution of sample plots and methods of measuring population densities present special problems that must be adjusted for each habitat and group of organisms concerned. The development of improved methods of population sampling is one of the major needs of ecology today.

5

Local Habitats, Communities and Succession

Streams

When rainwater falls on an uneven surface, it collects in depressions. As the water overflows them, the current erodes a narrow channel that deepens with each succeeding shower and may eventually drain the depression. There is usually also a lateral meandering of the stream, by which a valley is formed. The site of the headwaters of such streams is impermanent, and continued erosion forces the headwaters and the channel farther and farther back into the upland. The stream is at first a temporary one, dependent for its waterflow on rainfall runoff, but when its channel is cut below the level of the groundwater table the stream becomes permanent, fed by general, continuous seepage. The headwaters of such a stream are therefore its youngest portions physiographically, and the stream is progressively more aged towards its mouth.

In hilly or mountainous terrain, water may accumulate in large basins until ponds or lakes are formed. In the Great Basin of North America, such lakes have not found an outlet to the sea, and evaporation has left them with a very high salt content. Ordinarily, however, the water level in such a lake will rise until it overflows at the lowest point on the perimeter. Then the waters continue to flow downward until they eventually reach the sea. Streams springing from fixed headwaters (melting snowfields and glaciers, springs) carve valleys that are of essentially the same age throughout. Streams less than 3 m (10 ft) wide are usually called *creeks* or *brooks*; *rivers* are streams 3 m or more wide.

A river system in *youth* is characterized by valleys that are narrow and steepsided; the flow of water is usually fast, there are few tributaries, and there are many waterfalls, ponds, and lakes along its course. As the river system matures, its valleys become wider, its slopes more gentle, and its tributaries more numerous and longer. Many ponds and lakes are drained, and waterfalls are worn down to rapids or riffles. The areas of upland are well dissected, and the land is thoroughly drained. In *old age,* the river system has reached *base-level.* The upland has been worn down to low ridges between tributary river valleys, and the region as a whole is called a *peneplain.* There are no lakes, ponds, or rapids, and the flow of water is sluggish (Strahler 1951).

HABITATS

Exclusive of its lakes, the principal habitats in a stream are *falls, rapids* or *riffles, sand-bottom pools,* and *mud-bottom ponds.* The character of the bottom depends primarily on the velocity of the water current, which, along with the volume of stream flow, can be readily measured (Robins and

Crawford 1954). Water flowing at the rate of about 50 cm-sec is considered swift-flowing; velocities greater than 300 cm-sec rarely occur. Fast currents roll or slide pebbles and rocks along the bottom; move sand partly by rolling and partly by buoyant transportation; and carry fine materials, such as silt and organic matter, in suspension (Twenhofel 1939).

In places where the topographic gradient is steep, the stream bottom will be composed largely of cobble and boulders too heavy to move, and smaller pebbles which are trapped by obstructions. This habitat is called a *rapids*, if extensive and turbulent; *riffles*, if of a lesser order.

When the gradient is less steep and the water current thus slower, gravel (particle size 2–64 mm) is deposited first, then sand (0.06–2 mm), but the finer materials are carried along. Only when the current becomes negligible does the suspended material settle so that silt (0.004–0.062 mm) or mud-bottom pools or ponds are formed. Clay has a particle size even smaller (Morgans 1956). These mud-bottomed pools are the most fertile parts of the stream because of the presence of organic matter entrained in the silt. The rate at which oxygen diffuses into water from the atmosphere increases as the turbulence of the water increases; rapids therefore have, often, the highest oxygen content of a stream's waters. Ordinarily, however, oxygen is near saturation in all parts of a flowing, non-polluted stream. In a general way, riffles, sand- and mud-bottom pools represent three stages in the aging of a stream, and ecological study of them gives a good idea of what the eosere would be over a long period of time.

Trout streams do not normally exceed 24°C maximum summer temperature; streams with higher summer temperatures are more characteristically occupied by species of Centrarchidae and Esocidae (Ricker 1934). Streams have been classified into a variety of different types, using the most characteristic fish present as a basis (Van Deusen 1954). The salt content of stream waters depends both in quantity and in chemical nature on the fertility of the land drained or the rock strata which produce the springs.

STREAM BIOCIES

When quantitative sampling is made of the invertebrate populations of streams, one finds that there is a sharp distinction of species found in riffles and those found in mud-bottomed pools (Table 5–1). The sand-bottom pool habitat has few characteristic indigenous invertebrate species, but it is occupied by small numbers of individuals of species otherwise occurring abundantly in the other two habitats. The unstable bottom apparently prevents the development of a characteristic community. The unionid clams are really the only invertebrate group to become established in this habitat with any degree of success, although they are not exclusive to it. There are, however, several fish species (Table 5–2) that find sandy pools a favorite habitat, although they depend in large part upon riffle organisms for their food. Many fish overwinter in the deeper, more quiescent sand-bottom pools, especially since low water temperature makes them too sluggish to withstand rapid currents.

Mud-bottom pools form in backwaters of the main stream, behind natural or artificial dams in the main channel, or where the current is sluggish. Very often, aquatic vegetation fringes the edges of these pools. These quiet pools are essentially young stages in the development of ponds and support many animal species indigenous to ponds. Such pond animals as aquatic annelids, dragonfly and damselfly naiads, and burrowing mayfly naiads commonly occur also on the muddy margins of streams in which the main channel has a sand, gravel, or rocky bottom.

The *stream biocies* consists most typically, therefore, of the inhabitants of the riffles and sand-bottom pools found throughout the course of the river. The riffle and pool organisms make up two different *facies* in this community. Mud-bottom pools and sluggish streams are occupied by the pond-marsh biocies, to be later described.

Plants are not abundant in the stream biocies, although the upper surfaces of rocks in a riffles may be completely covered with branched filamentous algae (particularly *Cladophora*), and a few species of water mosses (Fontinalaceae) may occur. Diatoms, mostly sessile forms, may be numerous in early Spring and again in the Autumn. Dominance in the true sense, such as occurs in terrestrial communities, does not exist, although the algae and mosses passively provide food and shelter for active forms.

The most characteristic and abundant animal forms of the stream biocies are the caddisfly larvae, mayfly naiads, stonefly naiads, fly larvae, crayfish, snails and clams, sponges and bryozoans, and fish, each occupying its own particular niche (Berg 1948). Plankton is mostly absent in swift-running water (Carpenter 1928, Coker 1954), but may be abundant in sluggish, pond-like stretches of large rivers. The fishes listed in Table 5–2 are mostly warm-water fishes. In the colder waters of mountain and northern streams, the fish fauna changes. Trout, sculpins, and sticklebacks become the most conspicuous species. Streams that empty into the ocean may have a special fauna of *anadromous* ("upstream") fish, such as salmon, shad, striped bass, and some trout, that spend much of their lives in the sea but migrate into fresh-water streams to spawn, and *catadromous* fish, such as the eel, which migrate "downstream" into the sea to reproduce. There are a few vertebrates other than

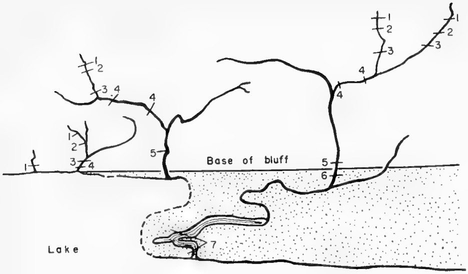


FIG. 5-1 **Diagrammatic arrangement of streams of different physiographic age on the south shore of Lake Michigan. Each number shows the location of that pool nearest a headwaters which first contains these fish: (1) creek chub; (2) redbelly dace; (3) blacknose dace; (4) suckers; minnows; (5) grass pickerel; bluntnose minnow; (6) sunfish, bass; (7) northern pike, lake chubsucker, and others (after Shelford 1913).**

fish commonly found in streams. Some salamander species occur only in fast mountain streams; other species are more typical of pond-like pools. The belted kingfisher feeds on stream fishes, and nests in adjacent clay banks. In the western mountains, the water ouzel feeds under water on the insect larvae and naiads of the riffles. Muskrats make their burrows in the stream banks and feed on vegetation and clams. Mink patrol the streams for the muskrats and fish that serve them as food. The once-abundant otter is now absent from most localities. Beaver dam streams to enlarge the pools in which they build their lodges and find shelter. Beaver feed on the bark and cambium of aspen, willow, and other trees and shrubs occurring on the shores of the stream.

ADJUSTMENTS TO CURRENT

Probably the characteristic of a stream most critical to the life therein is the current. All organisms that occur in streams must adjust to it to maintain constant position. Torrential floods scour the stream bed, move rocks and sand, cut new channels, and destroy entire populations. Recovery after such catastrophes, however, may take place within a few weeks or months, especially by those species possessing short life cycles (Moffett 1936, Surber 1936). Position is ordinarily maintained by clinging to the substratum, avoidance of the current, or vigorous swimming, and requires a good development of orientation behavior.

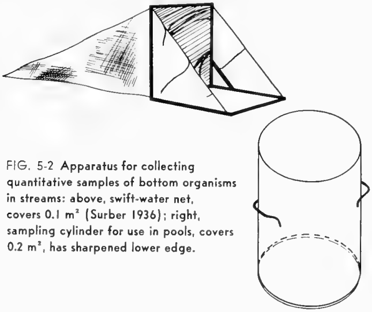


FIG. 5-2 **Apparatus for collecting quantitative samples of bottom organisms in streams: above, swift-water net, covers 0.1 m^2 (Surber 1936); right, sampling cylinder for use in pools, covers 0.2 m^2, has sharpened lower edge.**

Clinging mechanisms

The growth form of fresh-water sponges is affected by a number of factors, but in riffles sponges are usually simple encrustations. In quieter water, long, slender, finger-like processes may form. The distribution of species depends both on current and organic content of the water (Jewell 1935).

Plumatella is a common bryozoan that forms an encrusting, plant-like, branching colony on the underside of rocks or fallen trees in swift water. *Pectinatella*, on the other hand, forms a gelatinous spherical ball, and is more commonly found in ponds or slow-flowing portions of streams.

Turbellarians, such as *Planaria,* and swift-water snails, such as *Goniobasis* and *Pleurocera,* and the limpet *Ferrissia*, cling to the substratum by means of flat, slimy, adherent body or foot surfaces, and are most common on the protected lower surfaces of rocks.

Mayfly naiads have efficient adaptations which enable some of them to tolerate currents up to 300 cm-sec (Dodds and Hisaw 1924). The animals cling to the smooth undersurfaces of the rocks, keeping their heads toward the current and their bodies parallel with it as they move sideways, forward, and back. The head is flattened, and when pressed firmly against the substratum the water current exerts a downward pressure which helps to hold the animal in position. Compared with forms found in quieter

TABLE 5-1 Size and distribution of invertebrate populations in stream habitats of the Vermilion River, Illinois, as determined by class studies through eight years.

		Number per square meter		
Common name	Classification	Riffles	Sand bottom pool	Mud bottom pool
Caddisfly larva	Trichoptera	1,006		
Mayfly naiads	Heptageniidae, Baetidae	248		
Hellgrammite	*Corydalis*	46		
Riffle beetle larva	Psephenidae	19		
Riffle beetle adult	Psephenidae	4		
Limpet snail	*Ferrissia tarda*	2		
Bryozoan	*Plumatella*	+		
Fresh-water sponge	Spongillinae	+		
Flatworm	*Planaria*	+		
Broad-shouldered water strider	*Rhagovelia*	+		
Stonefly naiad	Plecoptera	61	1	
Snails	*Goniobasis livescens,* *Pleurocera acuta*	39	2	
White midge fly larva	*Tanypus*	16	0	5
Horse fly larva	Tabanidae	8	1	1
Fingernail clam	*Sphaerium*	8	+	+
Crayfish	*Orconectes propinquus*	6	1	4
Damselfly naiad	Zygoptera	4	2	7
Dragonfly naiad	Anisoptera	2	4	7
Clams (28 species)	Unionidae	++	++	+
Crayfish	*Orconectes virilis*	+	+	+
Snail	*Physa gyrina*	+	0	1
Red midge fly larva	*Tendipes*	+	1	8
Aquatic annelid	Chaetopoda	+	1	134
Burrowing mayfly naiad	*Hexagenia*	+	+	139
Water boatmen	Corixidae			6
Alderfly larva	Sialidae			4
Fishfly larva	*Chauliodes*			2
Crawling water beetle	Haliplidae			1
Amphipod	*Hyalella*			1
Predaceous diving beetle	Dytiscidae			+
Backswimmer	Notonectidae			+
Water scorpion	*Ranatra*			+
Aquatic isopod	Asellidae			+
Whirl-i-gig beetle	Gyrinidae			+
Springtail	*Podura aquatica*			+
Mayfly naiad	*Caenis*			+
Snail	*Gyraulus parvus*			+
Snail	Lymneidae			+
Total taxa		24	14	26
Total individuals		1469+	13+	320+

water, they show a larger thorax and legs, a smaller abdomen, absence of hair on the caudal cerci, shorter middle cercus, and smaller gill lamellae. These modifications enhance body streamlining and reduce the drag of the water. Furthermore, the legs are articulated in a way which allows the current to press them firmly against the substratum. The body itself swings freely in the current.

Mayfly naiads that occur in quiet waters do not have these modifications. They commonly spend most of their time in burrows, dug into the mud. They come out at night to swim around and search for food. The abdomen of the mud-inhabiting forms is thick, with little taper, sometimes bowed ventrally, and the three terminal cerci are provided with long stiff hairs that overlap and make an excellent oar for swimming.

Stonefly naiads are not limited to stony habitats. Some species occur in the masses of leaves that lodge against rocks or along the banks, in the algae grow-

TABLE 5-2 **Distribution of predominant fish species in stream habitats of central Illinois (after Thompson and Hunt 1930).**

Common Name	Riffles	Gravel and sand bottom pools	Mud bottom pools
Suckermouth minnow	+		
Banded darter	+		
Bigeye chub	+		
Log perch	+		
Green-sided darter	+		
Stonecat	+		
Hog sucker	+	+	
Fantail darter	+	+	
Steelcolor minnow	+	+	
Common shiner	+	+	+
Channel catfish	+	+	+
Hornyhead chub	+	+	+
Stoneroller minnow		+	
Silverjaw minnow		+	
River shiner		+	
Reffin shiner		+	
Rainbow darter		+	
Quillback carpsucker		+	
Smallmouth bass		+	
White crappie		+	
Orangespotted sunfish		+	
Longear sunfish		+	+
Green sunfish		+	+
Bluntnose minnow		+	+
White sucker		+	+
Northern redhorse		+	+
Shorthead redhorse		+	+
Creek chub		+	+
Johnny darter		+	+
Golden shiner			+
Creek chubsucker			+
Grass pickerel			+
Blackstripe topminnow			+
Pirateperch			+
Freshwater drum			+
Gizzard shad			+
Highfin carpsucker			+
Largemouth bass			+
Bigmouth buffalo			+
Carp			+
Black crappie			+
Black bullhead			+
Total species	12	23	24

ing on the rocks, on sand bottoms, and in small mud-bottom streams rich in organic matter. The general form of the body is similar to that of swift-water mayfly naiads, although the gills are filamentous and located at the base of the legs.

Caddisfly larvae occur most abundantly in streams with medium to swift currents, but some species occur only in sluggish rivers, in lakes, or in pond vegetation. Caddisfly larvae are of especial interest because of the cases they construct, in which the pupae also occur later. In some species these cases are portable. They are made of pieces of leaves, twigs, sand grains, or stones which are cemented or tied together with silk that the animals secrete. In standing or sluggish water, the cases are often large and made of buoyant plant material, or they may be made of sand grains, more fragile and slender. In swift water, the cases are stout, cylindrical, tapered posteriorly, and are usually smaller and more solidly constructed of sand, small pebbles, or rock fragments (Dodds and Hisaw 1925). The Hydropsychidae, Philopotamidae, and Psychomyiidae are unique in spinning fixed abodes in the form of a finger, a trumpet, or a tube. The Hydropsychidae erect a net at the front end of the tube to catch particles of food washed down with the current. Some psychomyiid larvae, particularly *Phylocentropus,* burrow into sand and cement the burrow walls into fairly rigid cases. Some larvae belonging to the Rhyacophilidae are free-living. Found in algal growth, they crawl around seeking food, and are provided with large abdominal hooks as clinging devices to supplement the legs for clinging. However, they form a stone case, or cocoon, for pupation (Ross 1944).

The black fly larvae, Simuliidae, are often very abundant in the swift waters of mountain brooks and northern streams. The larvae secrete from their salivary glands a delicate silken thread by which they attach to the rocky substratum, and by manipulation of which they can move short distances. At the posterior end of the semi-erect body is a circlet of rows of outwardly directed hooks which, when the muscles of the disk are relaxed, move outwards and catch on to a silk web placed there previously by the larva; the anterior end of the body then swings freely in the current. There is a fan-like food-gathering organ on each side of the mouth. Before pupation, the larvae spin a sedentary cocoon. The pointed end faces the current and the other end, open, faces downstream. Out of it, the peculiar gills of the pupa float in the water (Hora 1930, Nielsen 1950).

The net-veined midge larvae, Blepharoceridae, are unique in possessing six unpaired suckers on the ventral side, by means of which they fasten to the substratum. The original segmentation of the body is almost obliterated; it has been replaced by a secondary segmentation correspondent with the number of suckers.

Adult riffle beetles (Psephenidae, Dryopidae, Elmidae) are small in size and are the only coleopterans that live in or near running water. The legs are not fitted for swimming, but rather possess hooked claws for clutching the substratum. The body is covered with silken hairs that hold a thin film of air about it when the beetle is submerged. The larvae are disc-shaped and pressed close upon the substratum, to which they cling with their legs and backward-directed spines. They are sometimes called water pennies. When ready to pupate the larvae crawl out of the water.

Avoiding the current

Diminutive body and appendage sizes and assumption of a stream-line shape keep the amount of surface exposed to the full impact of the current at a minimum. The conical shape of the limpet *Ferrissia* and the flatter cone of water pennies offer little resistance to water flow. Flat bodies, such as are found in many swift-water animals, appear to be not only an adaptation lowering resistance to current but also to escape it by enabling the animals to seek shelter in crevices and underneath stones (Dodds and Hisaw 1924, Nielsen 1950). Most species, even those with specialized means of clinging to the bottom, are more abundant on the undersides of rocks in riffles than they are on the uppersides. Some species, however, such as the free-living caddisfly larvae, rotifers, tardigrades, water mites, and protozoans, find shelter within the mass of algae that may cover the top of the rocks. The hellgrammite, tabanid fly larvae, and stream crayfishes possess no special structures for withstanding currents and only occur in riffles providing protection or lodgement underneath and between rocks. Even swift-water fishes, strong swimmers, take maximum advantage of whatever protection is available.

The clams avoid the full force of stream current, and at the same time retain position, by lodging their bodies between stones. In pools, they bury themselves in an oblique position in the gravel, sand, or mud. Their posterior ends are directed upstream (according to Dr. Max Matteson), and their siphons usually maintain contact with open water so there can be circulation through the mantle cavity, for gaining food and oxygen. Clams occurring in pools one-half to one meter in depth may remain more or less sedentary, but those occurring in shallower waters move around considerably, especially in response to changes in water level and temperature.

Swimming

Locomotion of swift-water invertebrates is, in the main, restricted to short-distance crawling. Mayfly naiads that occur in riffles do not swim, although related species frequenting quiet waters do so, regularly. Only the more vigorous fishes can maintain position in swift currents by swimming, and many of them do so only when feeding. At other times they congregate in the pools that occur between riffles. Salmon and trout are well known for their ability to swim against strong currents, an accomplishment of sheer force of powerful, muscular, tails. The subfamily of darters, Etheostominae, which contains a variety of brightly-colored small fish, are especially adapted to live in the riffles. The air bladder of the darters has become very degenerate, even absent, so that the specific gravity of the body is increased.

TABLE 5-3 Rheotactic responses of invertebrates from riffles and pools (from Shelford 1914).

Velocity of current	4-6 cm/sec				10-12 cm/sec				16-20 cm/sec			
Response in percentages	Positive	Indifferent	Negative	Inactive	Positive	Indifferent	Negative	Inactive	Positive	Indifferent	Negative	Inactive
RIFFLES ANIMALS												
Crayfish, *Orconectes virilis*	30	40	28	2	54	8	16	22	78	2	6	14
Snail, *Goniobasis livescens*	45	27	28	0	65	22	0	13	76	7	0	17
Caddisfly larva, *Hydropsyche* sp.	23	26	16	35	18	9	6	67	26	2	4	68
Damselfly naiad, *Argia* sp.	79	0	17	4	63	18	4	15	63	4	0	33
Stonefly naiad, *Perla* sp.	31	24	3	42	65	6	15	14	61	3	3	33
Mayfly naiad, Heptageninae	25	12	14	49	52	3	0	45	52	3	0	45
Water penny, *Psephenus* sp.	26	32	36	6	67	26	0	7	74	15	11	0
Averages	37	23	20	20	55	13	6	26	62	5	3	30
POOL ANIMALS												
Damselfly naiad, *Calopteryx maculata*	78	0	22	0	59	8	0	33	63	0	0	37
Snail, *Campeloma subsolidum*	51	32	6	11	80	0	0	20	10	0	0	90
Burrowing dragonfly naiad, *Macromia* sp.	17	36	41	6	12	72	10	6	0	0	0	100
Clam, *Anodontoides ferussacianus*	16	66	18	0	17	67	16	0	0	0	0	100
Fingernail clam, *Sphaerium* sp.	17	66	17	0	16	67	17	0	0	0	0	100
Averages	36	40	21	3	37	43	9	12	15	0	0	85

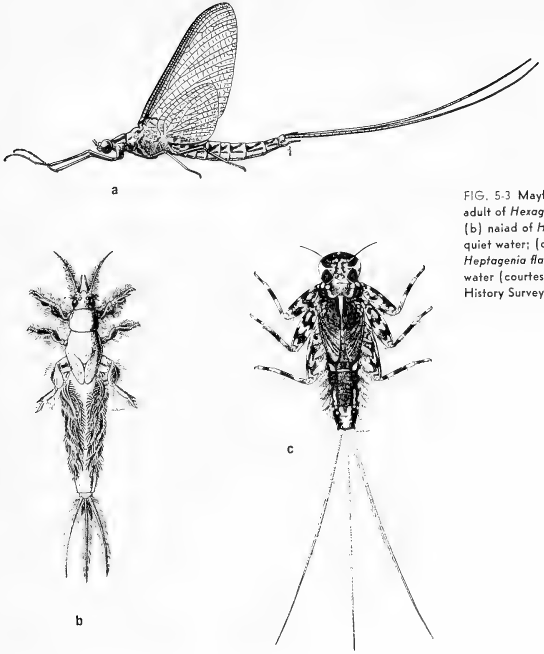


FIG. 5-3 Mayfly naiads: (a) adult of *Hexagenia limbata;* (b) naiad of *H. limbata* from quiet water; (c) naiad of *Heptagenia flavescens* from swift water (courtesy Illinois Natural History Survey).

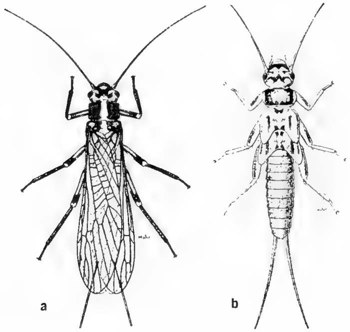


FIG. 5-4 Stonefly: (a) adult; (b) naiad, *Isoperla confusa* (courtesy Illinois Natural History Survey).

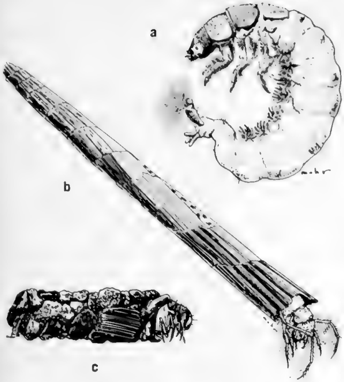
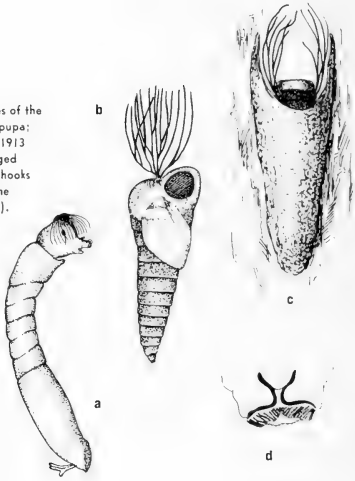


FIG. 5-5 (a) External features of a caddisfly larva; (b) larva and case from a weedy lake; (c) larva and case from a spring-fed brook (courtesy Illinois Natural History Survey).

FIG. 5-6 Immature stages of the black fly: (a) larva; (b) pupa; (c) pupa case (Shelford 1913 after Lugger); (d) enlarged detail of arrangement of hooks on the posterior end of the larva (after Nielson 1950).



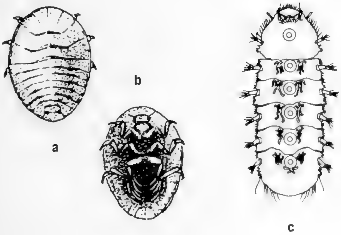


FIG. 5-7 Water pennies, larva of the psephenid beetle: (a) dorsal and (b) ventral views (Shelford 1913); and (c) larva of the net-veined midge; showing the central row of six suckers (after Hora 1930).

Their fan-shaped pectoral fins are enlarged, and project at right angles from the lower side of the body. When at rest they maintain position by contact with the bottom, fins lodged between pebbles or the body partly buried. They never float suspended in the water, as do other fish; when disturbed, they dart swiftly from one anchorage to another. The Etheostominae are confined to North America east of the Rocky Mountains.

Stream fishes are in general quite sensitive to current, and the discontinuous distribution of a species within the same stream may be closely correlated with gradient (Trautman 1942, Burton and Odum 1945). The smallmouth bass, for instance, is mostly absent in southern streams of gradient less than 40 cm/km (2 ft/mi); is of moderate abundance in gradients up to 135 cm/km (7 ft/mi); is very abundant in gradients of 135–380 cm/km (7–20 ft/mi); and becomes less common again, until it disappears altogether, in gradients above 475 cm/km (25 ft/mi). Perhaps streams with very slow current do not provide suitable gravel nest-sites for spawning, and in streams with very fast currents they are unable to maintain position.

Salamanders that live in swift mountain streams generally have short limbs and toes, reduced size of fins, smaller lungs in the adult and shorter gills in the larvae, and relatively few large eggs, which they fasten to the underside of flat rocks (Noble 1931).

Orientation behavior

Structural adaptations for withstanding or avoiding current are of no avail without appropriate behavior responses to make use of them. The rheotactic responses of animals may be tested either in the field or in the laboratory by means of special apparatus.

When animals from riffles and those from pools are compared (Table 5–3), it is apparent that, at low current velocities, responses of the two groups of animals are nearly the same. The elongate body, notably of stream animals, brings an automatic turning into the current much as wind directs a weathervane. As the velocity of current is increased, however, there is a marked increase in the percentage of riffle animals that face into or move against the current, while a very large percentage of pool animals are swept away by the current or are forced to withdraw into their shells. Caddisfly larvae, free of their cases, are not very able to withstand a strong current, although within their cases they readily maintain position.

Blackfly larvae can tolerate water currents as swift as 180 cm/sec, and studies indicate that their clinging to the substratum is a response to current rather than to any associated factor, such as food or oxygen requirement (Wu 1931).

When tested experimentally, 80 per cent of the stream crayfish *Orconectes propinquus* were able to maintain position in currents of 50 cm/sec, but only about 20 per cent of the pond crayfish *O. fodiens* were able to do so (Bovbjerg 1952).

Fishes generally respond to current by showing nearly 100 per cent positive response, regardless of whether they be taken from streams or ponds. Since the response involves a tendency to swim upstream, other factors must be involved for the fish to maintain a constant location in the stream; otherwise they would all move to its headwaters.

Some stream fishes, such as the blacknose dace and the common shiner, can be shown experimentally to respond visually to landmarks on stream bank and bottom to maintain their location. Some pool fishes, such as the sunfish and topminnow, likewise respond visually, but much more sluggishly, and irregularly. Darters are entirely unresponsive to visual stimuli, depending on the tactile stimulus of contact with the bottom for maintaining position (Lyon 1905, Clausen 1931). Smell may be important to some fish for orientation. The backswimmer *Notonecta* (Schulz 1931) and whirl-i-gig beetle *Dineutus* (Brown and Hatch 1929) have also been shown to use visual orientation in running water.

RESPONSES TO BOTTOM

The segregation of stream animals between riffles, and sand- and mud-bottom pools may be, in part, a response to type of bottom. With no current flowing, the species listed in Table 5–3 were, in another experiment, given a choice between a hard bottom and a sand bottom. Eighty-five per cent of the riffles animals selected the hard bottom, but only 10 per cent of the pool animals did so. Of the pool animals, all species made 100 per cent response to sand, except the damselfly naiad, *Calopteryx maculata,* which divided equally between the two types of bottom. When the riffles animals were given a choice between loose stones and a bare bottom, nearly all individuals selected the stones, and they distributed themselves among the stones or on top or underneath in the manner one would expect of them under natural conditions (Shelford 1914). Stream crayfish, when given a choice between mud and cinders, oriented 88 per cent to the cinders, while the pond crayfish responded 40 per cent to cinders and 60 per cent to mud (Bovbjerg 1952).

Type of bottom is important to invertebrates for support and locomotion. Sand bottoms are noteworthy as unstable and shifting. Insect larvae and naiads find footing very uncertain; planarians, sponges, and bryozoans find no stable anchorage; and rock-inhabiting snails and limpets are quickly buried. Clams, however, find a sandy bottom suitable, if it is firmly packed, as they are adapted to burrowing and plowing their way through a loose substratum. They are able also to move through a mud bottom, but where silting is heavy they close their valves to avoid an accumulation of silt within the mantle cavity and on the gills. The anodontas seem to be the most tolerant of mud bottoms.

Some of the mayfly naiads, such as *Hexagenia*, are adapted to burrowing in mud, and the surface of the bottom in shallow water is often closely dotted with the openings of their burrows (Hunt 1953). These burrows are relatively permanent in compact mud but would quickly collapse in loose sand. The genus *Caenis* is peculiar in possessing covers at the anterior end of the abdomen; they protect the gills from becoming clogged with silt. Midge fly larvae and aquatic annelids exist in mud bottoms; they would be ground to bits among moving sand particles. The pond crayfish will burrow into mud down to water level as a pond dries up, but stream crayfish will not do so and consequently suffer high mortality (Bovbjerg 1952).

The bottom is important to invertebrates and vertebrates alike for placement of eggs. Some caddisfly eggs are fastened to smooth rock surfaces in long strings by a cement-like substance. The eggs of other species occur in jelly-like masses and may be secured to plant stems or other submerged objects. Jelly-like masses of snail eggs are often quite common on the undersides of rocks in riffles. Some fish, such as the fantail darter (Lake 1936), make nests in small cavities under stones, but other species, for instance the rainbow darter (Reeves 1907), creek chub (Reighard 1908), and river chub (Reighard 1943), build nests in gravel bottoms in the upper parts of riffles. Some of the suckers (Reighard 1920) spawn in shallow water; their eggs scatter downstream, finding lodgment in various riffles.

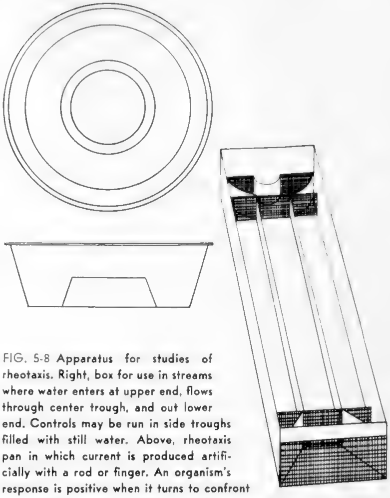


FIG. 5-8 **Apparatus for studies of rheotaxis. Right, box for use in streams where water enters at upper end, flows through center trough, and out lower end. Controls may be run in side troughs filled with still water. Above, rheotaxis pan in which current is produced artificially with a rod or finger. An organism's response is positive when it turns to confront the current; negative, when it faces downstream; indifferent, when it orients crossways.**

RESPIRATION AND OXYGEN REQUIREMENTS

Oxygen is usually ample in streams, often saturating the water in turbulent riffles. The oxygen concentration is sometimes low, however, in sluggish streams and standing pools. The difference in oxygen tension of the two habitats is reflected in the respiratory adaptations of the organisms that inhabit them.

The lamelliform gills of the mayfly naiads inhabiting mud-bottom pools are larger in size than those of species inhabiting streams, are doubled in number on the anterior abdominal segments of some species, and are almost continuously flicked back and forth for better aeration. The gills of naiads living in riffles, or in waters in which the oxygen content is high, may have the surface area of the gills reduced by two-thirds in proportion to body weight, compared with mud-dwelling forms. They are never flicked, since the water movement continually brings oxygen to them (Dodds and Hisaw 1924). Other species do not flick their gills at high oxygen tensions, but will do so when tension is reduced. In some swift water species, there appears to be sufficient oxygen diffusion through the general body surface to make gills inessential equipment (Wingfield 1939).

Caddisfly larvae have filamentous gills, and there is some evidence that they increase in number as body size increases and oxygen content of the water decreases. It is probable that oxygen also diffuses readily through the thin skin. A constant current of water is maintained through their cases by undulations of the abdomen. Stonefly naiads have poorly developed filamentous gills, located on the thorax, or have none at all. As a result, they are more sensitive to variation in oxygen supply than are the other forms mentioned.

The respiratory equipment of pond-inhabiting animals permits them not only to live in habitats with lower oxygen tensions but also to survive longer at high water temperatures. Often, these animals display relatively low rates of general body metabolism and oxygen requirement. Such relations between riffle and pond animals have been observed for mayfly naiads, caddisfly larvae, isopods, crayfish, and fishes (Allee 1912–13, Wells, 1918, Fox *et al.* 1935, Clausen 1936, Whitney 1939, Bovbjerg 1952), and to some extent for limpet snails (Berg 1951).

RESPONSES TO STREAM SIZE

Of the species of clams indigenous to Michigan, the 3 commonest are largely limited to creeks, 14 others to medium-sized rivers, and 5 to large rivers (Van der Schalie 1941). In central Illinois, the number of species of fish per collection increased from about 4.5 in streams draining 4 sq km to 15.5 in streams draining 500 sq km of upland. At the same time the number of fish decreased from 9 to 2.5 per sq m of water surface (Thompson and Hunt 1930). Large species of fish can occur only in stream with sufficient volume of water to permit freedom of movement; small fish may find orientation difficult in large rivers. The preference of fish for streams of specific size is evident in the tendency for some species to travel upstream in times of flood and downstream in times of drought.

An increased number of species downstream correlates with greater variety of available niches and moderate environmental conditions. In many instances the correlation between distribution of species and stream size, or volume, is not direct but dependent on associated changes in temperature, type of bottom, fertility, silting, pollution, and other factors.

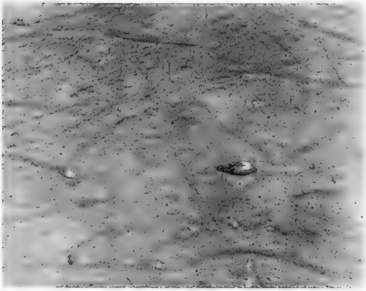


FIG. 5-9 **Clam tracks in a sandy pool (courtesy R.E. Rundus, 1956).**

Headwaters

The headwaters of drainage streams present a highly variable habitat. During dry periods, pools shrink and may disappear; temperature may be very high in summer and the water largely converted to ice in winter; there may be a lack of oxygen, an excess of carbon dioxide, and a high acidity; fishes and other organisms may become greatly overcrowded. In times of heavy rain, on the other hand, the stream is swollen, there is considerable erosion of materials into the stream, and animals are washed downstream. At all times food is likely to be scarce.

Only the hardiest species can exist under these conditions. The creek chub is a remarkably hardy fish; it may be found in large numbers in shrunken pools, stirring up the water with tail action and gaping for air at the water surface. Crayfish burrow into the bottom when the pool dries up. Small snails may survive desiccation of habitat by crawling under rocks or into crevices, secreting a mucous membrane across the aperture of their shells, and remaining dormant until water returns. The occurrence of insect larvae and naiads is hazardous, for if the aquatic stages of their life cycles are characteristically prolonged, they perish at times of low water or drought.

Temperature and altitude

In drainage streams the temperature of the headwaters is variable, but as the water volume increases downstream and becomes more constant, the range of temperature variation decreases. The headwaters of spring-fed streams, or of streams arising at high elevations, usually have a progressive increase in temperature downstream.

Some species of stonefly and mayfly naiads and caddisfly larvae are absent from the headwaters of Ontario streams because the temperature never gets high enough to permit them to complete their life cycle. More species are present downstream, and the headwaters species tend to emerge earlier and earlier in the summer while the waters are still cold. Still further downstream, the headwaters species disappear altogether. Species that are limited to the lower portions of the stream emerge late in the season, when the waters are the warmest. Closely related species are thus segregated to different positions in the stream by temperature tolerances. Headwaters species have generally a northerly distribution over the continent and the downstream species a southerly distribution (Ide 1935, Sprules 1947). Linear distribution of fish in streams may be, in part, a result of differences in temperature tolerance. Brook trout, for instance, do best in waters cooler than 19°C in Virginia, while some varieties of introduced rainbow trout prefer waters above 19°C (Burton and Odum 1945). The altitudinal zonation of various species of invertebrates and fish in mountain streams is well defined, and is in large part contingent on differences in temperature (Dodds and Hisaw 1925).

Shape and size of individuals

In the Tennessee River, riffles snails of the genus *Io* show a progressive change in shape from the headwaters on downstream. There is a decrease in shell diameter, a decrease in globosity, and an increase in number and length of spines (Adams 1915). However, the riffles snail *Pleurocera* was found to increase in globosity downstream in Michigan (Goodrich 1937). Some pond snails, such as *Lymnaea stagnailis* and *Galba palustris,* develop a larger foot and shell aperture when exposed to wave action (Baker 1919). Primitive types of clams, on the other hand, such as *Fusconaia, Amblema, Quadrula, Pleurobema,* and others, change progressively downstream from a large, compressed, smooth shell to one that is shorter, more obese, and sculptured with tubercles (Ortman 1920). Some species of clams show no such changes in shape. In some fish of central Asia (Nikolski 1933), the body changes downstream from a torpedo-shape to a flatter, longer form. These changes are probably a result of downstream reduction of water current, increase in amount of calcium in the water, and higher temperatures. The formation of spines and tubercles, for instance, would require an abundance of calcium and quiet water.

EVOLUTION

In all probability species inhabiting quiet waters are ancestral to those occurring in running waters (Dodds and Hisaw 1925, Hora 1930). Invasion of stream habitats requires mechanisms for contending with the force of current, and orientation behavior for maintaining position. Convergent evolution has occurred in many kinds of animals under the influence of current, as shown by similarities in structure and habits (Shelford 1914a). Inducements to the invasion of swift waters have doubtless been new sources of food, escape from enemies, and avoidance of competition with the abundant life of lakes and ponds. As adaptations to stream habitats evolved, animals have largely lost their ability to occupy quiet waters. They no longer can tolerate the lower oxygen tension, silt bottoms, and the absence of current which brings them food and oxygen, and, in some forms, such as the Hydropsychidae, helps build their shelters and nests.

LIFE HISTORIES

The life-cycle of stream insects is remarkable for the long duration of the immature stage in many species and the brief life of the adult. The naiads of mayflies pass through a number of molts (20–40), and this immature stage may last from six weeks to two years. When ready to emerge, the naiad comes to the water surface or crawls out onto a stone, molts into a subimago, and flies away. Within a few minutes, or a period of one to two days at the longest, the subimago undergoes another molt, unique in insects, into the fully mature adult. The adult insect does not eat and lives only a few hours or days; during this time reproduction takes place. Mating occurs in flight, hundreds or thousands of individuals swarming in flight together. The females lay their eggs almost immediately after mating. In some species, deposition is made upon the water surface, the eggs sinking to the bottom; in other species the female crawls down into the water and attaches the eggs, as they are laid, to a rock surface. The eggs have a viscid surface or filaments and quickly become attached to submerged objects. Embryonic life may last 11 to 23 days, at the end of which time the naiad is fully formed (Needham *et al.* 1935, Burks 1953, Hunt 1953).

The life-cycle of stoneflies is also 1, 2, or possibly 3 years long in different species, of which time all but a brief interval is spent in the water (Frison 1935). Molting into the adult occurs after the naiad crawls out of the water onto a rock or other projecting object, and there is no subsequent molt in the adult stage. Adult diurnal stoneflies may feed, although the adults of nocturnal species apparently do not. It is of great interest that many species emerge, mate, feed, and carry on all essential activities during the coldest months of the year (Frison 1935). At all seasons, the eggs may be dropped into the water while the female is in flight over the water, or as she alights on its surface. The eggs are mucilaginous and may contain surface filaments or hooks.

Caddisfly larvae pupate submerged in cases. As the pupa approaches the adult form, it leaves the case; and, after crawling and swimming, emerges either upon the water surface or on some protruding object. Larval life in different species may be as short as 25 to 80 days, but since overwintering occurs in this stage it may be greatly prolonged. The pupation period is ordinarily shorter than the larval period, and the adults, which probably feed, may live from several days to a few weeks. Species living in temperate climates have either one or two generations per year. Some females drop their eggs while in flight but others crawl under the water to deposit them. The eggs are laid in masses in either a single-layered, cement-like encrusting form or in a jelly or gelatinous matrix that swells in water. Eggs are sometimes deposited on objects above water. Usually, 10 to 24 days are required for their hatching (Balduf 1939).

The common hellgrammite of North America appears to require three years to complete its life-cycle, of which it spends two years and eleven months as an aquatic larva. When ready to pupate, the larva crawls out of the water and underneath some loose stone or piece of wood. The adults do not eat and live only a few days. The female lays her eggs in masses attached to supports situated near water or to the upper surface of leaves. Upon hatching, the larvae make their way back into the water (Balduf 1939).

In the crayfish *Orconectes propinquus* copulation occurs in cool climates from July to November. Further southward, copulation is delayed until September, continues until cold winter weather, and is renewed again during March and April. Eggs are laid beginning in late March or early April and are carried around by the female, attached to her pleopods, or swimmerets. The eggs hatch in 4 to 6 weeks, and the young are carried for another week or two before they become free-swimming. The majority of the young become sexually mature at the end of the first growing season in early October (Van Deventer 1937).

The female adult black fly deposits her eggs in a mass or string on a stone or other object at water level during late afternoon, usually with only the tip of the abdomen submerged. If the eggs become exposed to the air they do not hatch; normally, the larvae appear in four or five days at medium water temperature of 20°–22°C. The larval stage persists 13 to 17 days, the pupal period a little more than 4 days, and the adult stage a little over a week when the adults feed, or only 5 or 6 days when they do not (Wu 1931).

Stream snails attach their eggs in a jelly mass to the sides of stones during late spring and summer, and development leads directly to the adult. Clams of the family Unionidae, however, have a peculiar mode of reproduction. The sexes are separate, and fertilization of the eggs takes place in the suprabranchial chambers of the female. Development takes place through several weeks in these marsupial gills, and each egg grows into a minute glochidium. These larvae are later shed into the water, where further development requires that the glochidia become attached to the gills, skin, or fins of fish. The larvae may be parasitic, feeding on nutrients absorbed from the fish; this stage may last from 9 to 24 days. Later, the cyst formed by the fish around the glochidium weakens, and the young animal escapes to take up a free-living existence. Breeding occurs from May to August in *Quadrula* and *Unio,* while in some species (*Anodonta, Lampsilis*) breeding does not occur until late in the summer and the glochidia are retained in the female over winter.

The life history of clams is of special significance in showing that dispersal depends, to a large extent, on the movements of the fish to which the clams are attached. There is evidence that some species of clams cling to particular species of fish only, so that distribution of the two forms in the stream is closely correlated. The fingernail clams Sphaeriidae, on the other hand, are hermaphroditic and lack the glochidial stage. The fingernail clams are annuals; the larger unionid clams may live 10 to 15 years (Coker *et al.* 1922, Boycott 1936, Matteson 1948).

Some sponges, and perhaps also bryozoans, are perennial, although they may become fragmented as a result of floods or freezing during the winter; they may die during times of low water. Both kinds of animals have vegetative buds, gemmules in sponges and statoblasts in bryozoans, that become free of the parent body. The buds are adapted to withstand unfavorable drought or winter periods, and to germinate and form new colonies when favorable conditions return.

The nesting habits of some stream fishes have already been mentioned. Some of the darters and dace defend their nests, or small territories around their nests, against intruders; other species appear to not do so. Individuals of territorial species do little wandering, and it is possible that a darter may persist through several generations in the same riffles. There is increasing evidence that some larger species of stream and pond fishes have definite home areas, and that the fish population of a small stream with riffle-pool development may be considered as a series of discrete, natural units. This has been demonstrated with tagged individuals for species of bass, sunfish, suckers, and bullheads (Gerking 1953). Homing tendencies, however, are developed to varying degrees, and some species appear to move around in a quite random manner (Thompson 1933).

FOOD COACTIONS

The basic food substances for stream animals are detritus, diatoms, and filamentous algae. Detritus consists of dead fragments of plants; partially decomposed, finely divided, plant material; and a certain amount of dead animal matter. Plankton, either plant or animal, is not normally a common source of food, except in outlets from the lakes and ponds from which they derive and in the sluggish waters near the mouth of the stream. Larger aquatic plants are not characteristic of swift flowing streams; they occur in sluggish pools. Filamentous algae, however, may be abundant in riffles, and a rich microflora of diatoms, with scattered protozoans, may furnish a thin slimy film over the surface of rocks. Animals are adapted to these food resources as filter feeders, microflora eaters, or carnivores (Nielsen 1950).

The caddisfly larva *Hydropsyche* is a fine example of a filter feeder. This species and related forms construct silken nets at the entrances of their shelters and strain out food particles brought down by the current. The anterior legs of some caddisfly larvae and mayfly naiads are furnished with brushes of hairlike setae which catch and transfer the detritus to the mouth as the animal faces the current. Black fly larvae have a pair of fans at the anterior end of the body. These fans are of long, curved setae. The larva folds them periodically, and the mandibles comb or brush off the detritus that collects. Clams siphon water through the mantle cavity, and detritus material and plankton are carried to the mouth through the activity of the cilia of the mantle, gills, and labial palps. Sponges and bryozoans also take detritus into body cavities for feeding purposes.

Feeding on the microflora and filamentous algae are planaria, snails, and various insects. Some caddisfly larvae have mouthparts specially adapted to scrape the thin film of microflora from the surface of rocks. The maxillae of mayfly naiads serve as a comb or brush with which diatoms are swept up into the mouth.

Carnivorous species may also be partly herbivorous (Table 5–4). Too, there is apt to be seasonal variation in food habits and there are differences of habit between closely related species. Fall and winter stonefly naiads are largely herbivorous, but spring and summer forms comprise genera that are either carnivorous, herbivorous, or omnivorous. Hellgrammites are largely carnivorous, feeding on immature insects. Crayfish are omnivorous; they appear to prefer dead and decaying material. The smaller fish, including the darters, are largely insectivorous, but also consume some plant material. Suckers, carp, and catfish feed on bottom debris as well as small living animals and plants. Young bass and trout are largely dependent on insects for food, but as they grow larger they turn also to young crayfish and small fish. The population density of fishes is ultimately determined, therefore, by the abundance of invertebrates and, when fishes rely on vision for finding their food, also on the turbidity of the water.

The average weight of food in the stomach of fantail darters of all sizes, sampled from October to May in New York State, was found to be 0.01354 g (Daiber 1956). If the average biomass of the living food averages 2.83 g/m² of bottom, then one individual of this species could get 209 full meals from one square meter if it captured everything that was there. Similarly, mottled sculpins could obtain 130 meals from a square meter. It would be interesting to know what actual percentage of the invertebrate population can be readily captured by fish and how frequently the fish feed, for correlation with the density of the fish population. Fish, however, also depend to a considerable extent, especially in summer, on small terrestrial organisms that fall, or are washed, into the stream.

BIOMASS AND PRODUCTIVITY

Of the kinds of animals present in one short coastal stream in California, the caddisfly larvae were found to be not the most populous. But when size was considered, they constituted more bulk than any other invertebrate group (Table 5–5). The invertebrate biomass per unit area of riffles is invariably much greater than in sand-bottom pools, whether biomass be computed in terms of wet weight, dry weight, or volume. However, the abundance of species within the riffles depends on whether the stones are loose or are fastened to the bottom, and on whether or not they are covered with algae, moss, or other vegetation (Percival and Whitehead 1929). The biomass of mud-bottom pools may sometimes exceed that of the riffles, especially if it contains the burrowing mayfly naiad *Hexagenia* (Behney 1937, Forbes 1928, Lyman 1943, Needham 1932, O'Connell and Campbell 1953, Pennak and Van Gerpen 1947, Smith and Moyle 1944). In the mud-bottom Silver Springs stream in Florida, the dry weight biomass of plants averaged 809 g/m², herbivores 37 g/m², small carnivores 11 g/m², and large carnivores 1.5 g/m² (Odum 1957a).

Insect populations in streams vary with the season (Table 5-6). Peak populations commonly occur during late spring and again in autumn (Daiber 1956, Lyman 1943, Needham 1934, 1938, Stehr and Branson 1938). Populations become reduced in summer because of low water; in winter, because of low temperature and ice.

Small streams tend to have greater densities of insect populations per unit area than do large streams. In New York State, streams up to width 2 m have biomasses that average 22.2 g/m² wet weight; from 2 to 4 m, 18.0 g/m²; from 4 to 6 m, 10.1 g/m²; and over 6 m, 7.7 g/m² (Needham 1934). In small streams, the distribution of organisms is nearly uniform from one side to the other, but in large streams there is a decrease in density from the sides toward midstream (Behney 1937). Larger streams actually

TABLE 5-4 Food habits of immature stream insects in Yellowstone National Park, Wyoming (Muttkowski and Smith 1929).

Insect	Number of specimens examined	Per cent food types consumed		
		Animal	Plant	Detritus
Stonefly naiads	80	54	22	24
Mayfly naiads	109	4	30	66
Caddisfly larvae	115	28	54	18
Diptera larvae	20	0	77	23

contain more organisms, however, in spite of lower densities per unit area, because they have a much larger total bottom surface. The reason for this variation in density per unit area is not clear, but it may be that per given population of sexually mature adult insects in the surrounding region, small streams offer less area than large streams, over which the females can spread their egg-laying.

The standing crop of fish in Indiana streams varies from 5.2 to 106 g/m^2 (46–939 lbs/acre) wet weight for minnows, suckers, centrarchids, darters, and bullheads (Gerking 1949) to 2.7–4.2 g/m^2 (24–37 lbs/acre) for rock bass (Scott 1949). The fish crop in warm water streams is generally higher than in cool trout streams, a relation that also holds for the biomass of invertebrates (Pennak and Van Gerpen 1947). Fish are usually more abundant in relatively deep streams than in shallower ones. Brook trout and three other species in one stream in New York State averaged 10.9 g/m^2 (97.5 lbs/acre), a ratio of 1:2.1 to the invertebrate food supply (Moore *et al.* 1934).

Of a stream, the richness of a fauna and the size of the biomass that develops depend largely on the fertility and chemical composition of the water. Hardwater streams, with an abundance of salts in solution, tend to have a large and more varied fauna than do softwater streams. Calcium salts, in particular, are required by mollusks for building their shells, and by crayfish for the exoskeleton. The salts and organic matter which are basic substances in all aquatic food chains depend directly on the fertility of the soil over which the water drains. Streams draining areas of fertile soil usually have an abundance of stream organisms; biomasses of both invertebrate organisms and fish in streams occurring in areas of poor soil are low.

The productivity of insects in Algonquin Provincial Park, Ontario, was periodically measured during one summer by collecting, in cages a yard square, all insects as they emerged from the water and transformed into adults. The count varied over different kinds of bottom between June 1 and August 31, 1940, as follows: rubble 6603, gravel 1636, sand 1079, mud 2618 individuals per sq m. Various mountain streams in different parts of the country have shown an annual productivity of trout taken by fishermen of 2.2 to 3.9 g/m^2 (20 to 35 lbs/acre) wet weight (Surber 1937).

TABLE 5-5 Relation between numbers per m^2 and biomass of insect groups in a riffles of a California coastal stream during February and March (after Needham 1934).

Insect	Total number of individuals	Per cent	Wet weight	
			Grams	Per cent
Caddisfly larvae and pupae	742	22.2	5.66	43.9
Mayfly naiads	1,853	55.5	3.61	28.0
Fly larvae and pupae	343	10.3	1.02	7.9
Stonefly naiads	260	7.8	1.58	12.2
Miscellaneous	137	4.1	1.02	7.9
Totals	3,335		12.89	

APPLIED ECOLOGY

The chief problems in applied ecology of streams are those of erosion and silting, pollution, and maintenance of biotic productivity at the highest possible level.

Erosion and silting

Stream erosion becomes considerable when upland vegetation is so reduced that there is little or no retardation of runoff from heavy rains. Dredging and stream straightening for drainage purposes usually eliminates the riffles habitat. The bare, hard clay that often emerges as the new stream bottom supports very little animal life.

Continuous erosion throws a heavy load of fine silt into the stream. This is detrimental. It makes the water opaque; reduces or prevents photosynthesis in algae, water moss, and other plant life; handicaps those fish and other animals that depend on sight for finding and capturing food; and clogs the filtering mechanism of various invertebrates. Clams are ordinarily closed less than 50 per cent of the time, but in silted waters they may stay closed up to 95 per cent of the time. Clams secrete mucous to keep the mantle cavity cleansed, but when silting is heavy this may not be sufficient and mortality will result (Ellis 1936). Deposition of silt on rock or sand bottom may bring a considerable change in species composition of animals present. During the last several decades, greatly increased soil erosion in agricultural areas has reduced pan and game fishes in our streams, and rough fish, such as carp, have taken their place.

Chronically muddy streams may often be cleared by reforesting the watershed, and by practicing mod-

TABLE 5-6 Seasonal variation in invertebrate populations per m² in a California coastal stream (Needham 1934).

Month	Number of individuals	Wet weight in grams	Predominant species
February	2,862	7.89	Mayfly naiads
March–April	2,324	9.76	Mayfly naiads
May	18,254	52.94	Blackfly larvae and pupae
August	4,524	19.37	Caddisfly larvae and pupae
November	6,531	23.03	Mayfly naiads

ern erosion control in cultivated areas. With slower runoff, more rainwater soaks into the ground, and the water table is raised. It is also desirable to maintain vegetation on the immediate stream banks to slow up undercutting. Streambank vegetation is also beneficial for shading the water and keeping it cool enough for such fish as trout. If artificial dams are necessary, they should be small, and located where the drainage begins in the numerous headwaters of the streams. Contour plowing, strip planting, and sod ditches also slow up water movement in hilly areas and should be practiced.

Pollution

Pollution occurs when foreign substances are introduced into a body of water in amounts sufficient to change its character and chemical composition. This type of pollution is of two forms: industrial wastes, such as those from lead and zinc works, tanneries, breweries, paper mills, gas plants, mines, atomic energy plants, etc.; and organic sewage. Industrial and mine wastes are often acid, and extreme acidity will kill fish and other organisms. Clams are greatly reduced or disappear altogether in acid waters. Industrial wastes contain a great variety of chemical compounds, including salts of the heavy metals, and many of them are very toxic to fish. Young fish and species of small fish appear especially sensitive, and the polluting materials may cause physical or chemical injury to the gills without actually being absorbed into the body (Doudoroff and Katz 1953).

The control of radioactive wastes from uranium mills and other atomic energy plants has become an especially serious problem in modern times. No stream can purify itself of these wastes. However, they become diluted downstream, undergo natural decay, settle out in the mud bottom, and are taken up by organisms. Organisms take up elements at equal rates whether they are radioactive or not. Radioactive elements may thus accumulate and become concentrated in organisms to an extent many thousands of times greater than their concentration in water. This is of potential harm to man (Tsivoglou *et al.* 1957). Fortunately, streams are but little used at the present time for the disposal of radioactive wastes. The ecological significance of radioactive wastes and fallout from atomic explosions has been summarized by Odum (1959).

The introduction of small quantities of organic wastes may increase the size and productivity of animal populations by adding to the basic nitrogen supply. The limit of the sewage load that a stream can carry without harm is, however, low and soon reached. As fresh organic material oxidizes, carbon dioxide and toxic gases are released into the stream, and there is a drastic reduction in the oxygen content. Fermentation is more rapid in summer than in winter, and may begin in wastes before they are discharged into the stream. The decomposing organic material continues to be oxidized as it is carried downstream, and when this action is completed the stream is again pure (Coker 1954).

There have been many attempts to determine the degree to which a stream is polluted, by means of chemical analyses of the water. There is difficulty, however, in evaluating the extent to which each of the many chemical compounds to be found is harmful to the various kinds of organisms. There is considerable variation in this respect, even between different stages in the life-cycle of the same species. Furthermore, the sewage load may vary from time to time, and infrequent heavy loads may wipe out the animal life in localities where chemical measurements made at other times do not indicate harmful pollution.

Various investigators (Richardson 1928, Ellis 1937, Paine and Gaufin 1956, Gaufin and Tarzwell 1956) have attempted to use invertebrate animals as indicators of pollution. The presence of midge fly larvae *Tendipes riparius, Glyptotendipes,* mosquito larva *Culex pipiens,* rattail maggot, and sludge fly delimit zones of septic pollution. There are relatively few species that can tolerate septic conditions, but those that do may become very abundant. The oligochaete worms *Tubifex* and *Limnodrilus,* and certain midge fly larvae, such as *Tendipes plumosus,* indicate low oxygen. In general, pond invertebrates are much more tolerant of low oxygen concentration than are those belonging to stream habitats. Species especially tolerant of pollution are those that have adaptations for obtaining oxygen at the water surface, such as the dipteran larvae of Culicidae, Syrphidae, and Stratiomyidae, aquatic Coleoptera and Hemiptera, and pulmonate snails. Gill-bearing species generally require clean water of high oxygen content. Among fish, pond species such as carp, bullhead, perch, and crappie are relatively more tolerant than stream species.

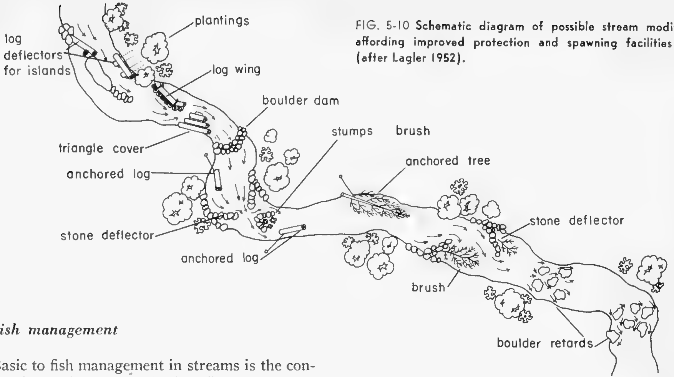


FIG. 5-10 **Schematic diagram of possible stream modifications affording improved protection and spawning facilities to fish (after Lagler 1952).**

Fish management

Basic to fish management in streams is the control of soil erosion and pollution. In clean, clear streams, both invertebrates and fish can attain high populations through normal reproduction. Artificial propagation and release of reared fish into streams to improve fishing is not necessary except where habitats have been depleted of breeding stock or where the fishing pressure is excessive. The artificial raising and releasing of fish of suitable size for quick recapture in sport fishing is expensive but sometimes justified in highly populated areas. In most regions the fish manager is better concerned with improving habitats and letting the fish repopulate them to full carrying capacity on their own accord.

Stream fishes suitable for sport and food are primarily those inhabiting the pools rather than the riffles. The carrying capacity of streams can sometimes be raised by artificially increasing the number of pools without destroying too many of the riffles, the main source of fish food. The interspersion of ponds along the stream also increases its fertility, since they are the sources of plankton, detritus, and dislodged or escaping organisms. The formation of pools may often be done inexpensively by making simple log dams or deflectors. Occasionally, it may be desirable to haul in gravel from elsewhere to make spawning beds and to provide artificial log or brush shelters (Needham 1938, Lagler 1952).

There has been a country-wide practice of introducing species of fish into streams where they did not originally occur. The result has been to greatly mix up and modify the fish fauna; original primitive communities no longer prevail. This is unfortunate for ecological research. The U.S. National Park Service is, however, attempting to preserve a certain number of natural stream areas in their original condition, prohibitng fishing therein (Kendeigh 1942a).

SUMMARY

Streams contain riffles, sand-, and mud-bottom pools. Inhabitants of the riffles and sand-bottom pools constitute a distinct stream biocies. Mud-bottom pools are inhabited by species from the pond-marsh biocies. Animals adjust to the action of water current by clinging mechanisms, avoidance, or vigorous swimming. They are generally positively rheotactic, and several forms maintain orientation to a particular position in the stream by means of visual landmarks. Segregation to different habitats depends largely on differential response to the substratum; that is, preference respectively for rock, sand, or mud. Animals occurring in mud-bottom pools are usually negatively rheotactic, or become helpless in strong current. They also have adaptations tolerant of lower oxygen concentrations in the water. Changes in the size of the stream, occasioned by various physical factors, also affect the responses of animals. Stream animals have apparently evolved from ancestral types that occupied the quiet waters of lakes and ponds. The life cycles of many stream insects are remarkable for the long duration of immature stages and the brief life of adults. Animals have various adaptations to feed on detritus in the water, on diatoms, on filamentous algae, or for being carnivorous. Density of individuals, biomass, and productivity of invertebrates are ordinarily less in sand-bottom pools than in either riffles or mud-bottom pools. Clams and game fish, however, inhabit sand-bottom pools. Fish management requires the proper interdigitation of pools and riffles, as well as control of erosion, silting, and pollution.

6

Local Habitats, Communities, and Succession:

Lakes

Lakes are large bodies of fresh water, often deep enough to have a pronounced thermal stratification for part of the year. Typically, shores are barren and wave-swept (Muttkowski 1918).

Lakes are formed in youthful stages of river system development. Water from upland runoff, groundwater seepage, springs, and melting snowfields and glaciers collects in basins. As the basins fill to overflowing, erosion of outlets starts; as it goes on, outlets are deepened and water level of the lake drops. Products of erosion, carried into the basin by wind and water, and the products of animal and plant decay accumulate, making the water shallow.

Morphometry aside, the essential distinction between lake and stream habitats is the characteristic of water movement; continuous, rapid flow is the characteristic of the stream, the *lotic* habitat. The lake is a *lentic* habitat; the water is essentially a standing, quiescent body, although at times wind action stirs surface layer and margins into great turbulence. Habitat factors associated with the lentic environment are uniquely modified to it (Welch 1948, Hutchinson 1957).

HABITAT

Pressure, density, and buoyancy

The pressure imposed on a lake-dwelling organism is the weight of the column of water above it plus the weight of the atmosphere. Most lakes have a maximum depth of less than 30 meters; the Great Lakes of North America vary from 64 to 393 meters in depth, Crater Lake in Oregon is the deepest on the continent, 608 meters (Welch 1952). Maximum pressures are much less than in the ocean, and organisms appear to adjust to them readily. The absence of animal life from deep water is ordinarily a consequence of low oxygen supply, or low temperature, rather than pressure.

The density of water varies inversely with temperature and directly with the concentration of dissolved substances. Water is most dense at approximately 4°C. Water becomes progressively less dense as it is cooled below +4°C; ice expands markedly (i.e., becomes less dense) the colder it gets. It is because the coldest water is at the surface in winter that ice forms there, rather than at the bottom. In summer, the coldest waters of deep lakes are at the bottom. Dissolved salts increase the density of water; the density of most inland waterbodies is much less than that of the ocean. When great evaporation occurs in a lake having no outlet, as in the Great Basin, the lake may come to contain a higher percentage of salts than the ocean. The few species capable of living in these very salty lakes include some algae and Protozoa, the brine shrimp *Artemia gracilis,* and the immature stages of two brine flies, *Ephydra gracilis* and *E. hians.* There are no fish in the Great Salt Lake of Utah (Woodbury 1936).

By the law of Archimedes, the buoyancy of an object is equal to the weight of the water it displaces. Buoyancy varies with the density of water, and is influenced by the factors that affect density. Viscosity, the measure of the internal friction of water, varies inversely with temperature and also influences buoyancy.

An organism will sink unless it keeps station by swimming movements, or unless it has special adaptations to decrease the specific gravity of the body and take advantage of any turbulence in the water. Such adaptations take several forms: absorption of large amounts of water to form jelly-like tissues; storage of gas or air bubbles within the body; formation of lightweight fat deposits within the body, or oil droplets within the cell; increase of surface area in proportion to body mass, which increases frictional resistance (Davis 1955). When an organism so equipped dies, the special mechanisms quickly cease to function, and it sinks to the bottom. If dead organisms did not sink to the bottom, living organisms, with the exception of some bacteria, could not exist in an aquatic habitat.

An interesting phenomenon is *cyclomorphosis,* a seasonal change in body form that develops in many plankton organisms, both plant and animal, including protozoans, cladocerans, and rotifers. In general, the summer generations have higher crests, longer spines, longer beaks, or longer stalks, than do the winter generations. It is believed that the increased surface area provided in the summer forms is induced by the higher water temperatures obtaining then, and may be an adaptation to the decreased buoyancy of the water at this season, but factors other than temperature also appear to be involved (Brooks 1946).

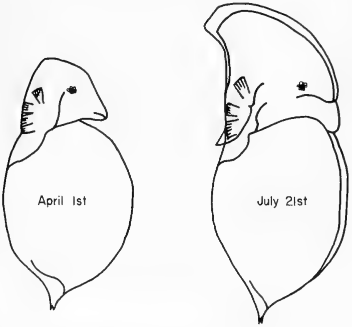


FIG. 6-1 **Cyclomorphosis of *Daphnia retrocurva* in a Connecticut lake (from Brooks 1946).**

Light

The daily alternation of light and darkness establishes a rhythm in the activities of many aquatic organisms. Light is essential to plant photosynthesis; some fish require light by which to feed. Many organisms orient to light, and some are sensitive to light of particular wavelengths, notably ultraviolet. Small, soft-bodied, bottom-dwelling organisms are particularly sensitive to light, and it is thought that the evolution of pigmentation, chitinous exoskeletons, shells, cases, and similar structures may have helped certain otherwise photosensitive species to survive in shallow, well-lighted areas (Welch 1952).

A common way to measure the relative transparency of water is to lower a *Secchi disk,* a white plate 20 cm in diameter attached to a cord marked off in linear units, marking the depth at which the disk disappears from sight. The disk is lowered a bit farther, then raised until it reappears, and that depth marked. The two depths are averaged. The light intensity at the depth of disappearance of the disk is usually about 5 per cent of that at the surface (Hutchinson 1957). Other more exact procedures employ photographic methods, pyrlimnometers, or photoelectric cells (Shelford 1929).

The depth to which light penetrates into water is affected by intensity of the light, angle of ray incidence, reflection at the surface, scattering within the water, and absorption. Penetration anywhere is reduced when the sun is away from the zenith; is less in waters at high latitudes; and is much less in winter compared with summer. About 10 per cent of the light falling on Lake Mendota, Wisconsin, during the spring and summer is reflected; about 15 per cent during the autumn (Juday 1940). In the unusually clear waters of Crystal Lake, Wisconsin, measurements with a pyrlimnometer indicated only a small surface reflection light loss, a penetration of 67 per cent of full intensity to a depth of one meter, and 10.5 per cent of full intensity at 10 meters (Birge and Juday 1929). In pure water, red light is absorbed most rapidly, at a rate of 64.5 per cent per meter; orange, at 23.5 per cent per meter; yellow, at 3.9 per cent; green, at 1.1 per cent; blue at only 0.52 per cent. Blue penetrates the farthest. Violet is absorbed at 1.63 per cent per meter. Very little ultraviolet penetrates the water, and nearly all the infrared is absorbed in the first meter (Clarke 1939, Ruttner 1953).

Suspended material in water produces *turbidity,* and reduces light penetration. In western Lake Erie, the depth to which 1.0 per cent of surface light penetrates varies from 9.7 m when turbidity is 5 ppm, to 0.8 m when turbidity is 115 ppm (Chandler 1942). Since phytoplankton require light for photosynthesis, abundance varies inversely with turbidity. Light penetration is also affected by the abundance of organisms themselves, both phyto- and zooplankton.

An appreciable amount of light passes through ice in the winter. This enables phytoplankton photosynthesis to continue. In eutrophic lakes many fish may suffocate when snow overlies surface ice, preventing photosynthesis and, thus, the generation of oxygen (Greenbank 1945).

The *apparent color* of water bodies may be the result variously of sky reflections, the color of the bottom, suspended materials, or of plants and animals. But apart from these extraneous factors, water often has an intrinsic color deriving from its chemical contents. The blue color of pure water is a result of blue-light scattering by water molecules. Iron gives water a yellow hue. A green color is usually associated with high concentrations of calcium carbonate. Water from bogs or swamps contains humic materials and is often dark brown. Many waters are essentially colorless. In a Wisconsin lake showing practically no color, maximum photosynthesis of algae occurred at one meter depth on bright days; some photosynthesis occurred down as far as 15 meters. In a highly colored lake, maximum photosynthesis occurred at 0.25 meter, none at 2 meters (Schomer 1934).

Photosynthesis releases oxygen into the water; respiration and decomposition absorb it. The upper layer of a lake, where photosynthesis predominates, is called the *trophogenic zone.* Below this zone there may still be considerable photosynthesis, but oxygen absorption is greater than oxygen release. The deeper portion of a lake is called the *tropholytic zone.* The two zones are separated by a thin layer where the oxygen gains from photosynthesis during the daylight hours are balanced by the respiratory and decomposition losses during the day and night. This is the *compensation depth,* to which generally about one per cent of the full sunlight at the water's surface penetrates. The compensation level in a dark-colored bog may lie less than a meter below the surface; in a deep, clear lake it may be 100 m down.

Wind and currents

Wind is an important environmental factor of lakes because of water currents it generates. The effect of wind action depends largely on the extent of the exposed water surface, the presence or absence of protecting upland, and the configuration of the lake relative to the prevailing wind direction.

Waves may become sizable in large lakes, but the forward motion of a wave does not involve any great mass of water. The rate of movement of surface water is usually less than 5 per cent of the velocity of the wind. The wave form moves on while the water beneath undergoes a more nearly cycloidal motion, except along the shore, where the wave mass progresses forward and breaks as surf. The water washes back off the beach as an undertow, only to be carried forward again by the incoming waves. The problem of maintaining position here is similar to the problem of maintaining position in streams. The depth of wave action in the open lake and along the shore depends largely on the strength of the wind (Ruttner 1953).

In summer, surface water is warmed by solar radiation and its density, weight, and viscosity decrease. In deep lakes the warm water piles up on the exposed shore until, moving down along the bottom, it encounters colder and denser waters, which resist mixing. The warm water is then diverted horizontally to the opposite shore. Thus the lake beomes stratified horizontally into an upper *epilimnion,* where the water circulates and is fairly turbulent, and a lower *hypolimnion,* which is relatively undisturbed. This difference in circulation in deep lakes is closely correlated with differences in temperature and oxygen characteristics; it is of considerable importance in the distribution of the biota.

Temperature

The thermal conductivity of water is very low; but because of the thorough mixing of the waters in the epilimnion during the summer by wind action, the temperature is nearly uniform down to the thermocline. The *thermocline* is the zone of most rapid temperature decrease, generally involving a drop of

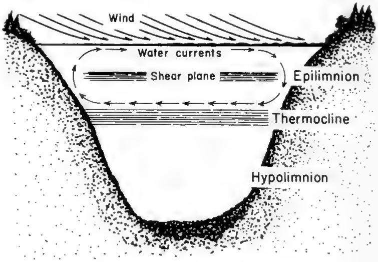


FIG. 6-2 Water currents and thermal stratification in a deep lake.

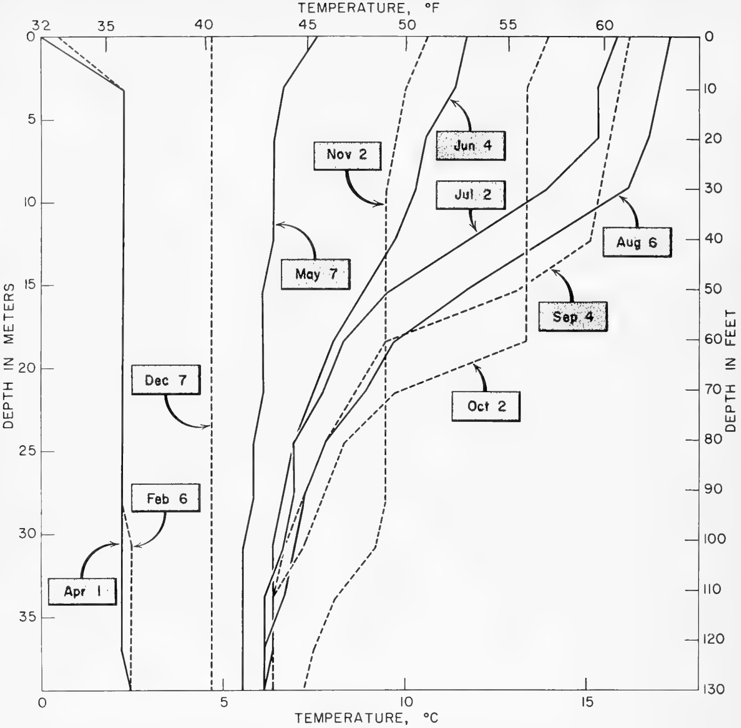


FIG. 6-3 **Vertical temperature distribution throughout a year in a dimictic lake of the second order—Convict Lake, California; elevation 2308 m (from Reimers and Combs 1956).**

at least 1°C per meter of depth (Birge 1904) and occasionally as much as 7°C per meter. The thermocline, as here defined, equals the *metalimnion* of some authorities who have a different conception of the thermocline (Hutchinson 1957). When the thermocline forms, early in the season, it is close to the surface. As the season progresses, it sinks lower, increasing the volume of the epilimnion and decreasing the volume of the hypolimnion. The temperature of the hypolimnion is fairly uniform, although it declines gradually from the lower edge of the thermocline to the bottom, where it is seldom below 4°C.

During the autumn, the surface water cools and the thermocline sinks. The epilimnion increases in thickness until it includes the entire lake. The waters are then uniform in temperature and density, at all depths. Even slight winds produce complete circulation. This is the *autumn overturn,* which may last for the several weeks, until ice forms.

As surface waters cool below 4°C they no longer sink, and ice may form. Less dense than the underlying water, it floats. Immediately below the ice, the temperature of the water is very close to 0°C, but in one or two meters of additional depth it usually rises rapidly to 4°C, although in some lakes temperatures below 4°C occur even at considerable depths.

As the ice melts during the spring and the surface waters warm up, a *spring overturn* occurs when the water at all depths is at the same temperature. The time and duration of the spring overturn depends on weather conditions; it may last several weeks. It often occurs intermittently, however, corresponding with changes in weather and water temperatures.

When a lake has two overturns during the year, it is called a *dimictic lake.* Such lakes are characteristic of, but not limited to, temperate climates. In warm, oceanic climates and in the tropics, the surface waters may not cool sufficiently to permit complete circulation, except during the coldest period of winter. Lakes undergoing a single overturn are called *warm monomictic.* The temperature of the water in the hypolimnion of such a lake is never lower, of course, than the mean air temperature during the period of the last complete circulation; in warm climates this may be several degrees above 4°C. On the other hand, lakes in polar or alpine regions may never warm above 4°C, and complete circulation occurs only in the middle of the summer. These are *cold monomictic* lakes (Hutchinson 1957). The three types of lakes were formerly called temperate, tropical, and polar, but this terminology is undesirable since their geographical segregation is not precise.

Lakes of the first order are those in which the bottom water remains at or near 4°C throughout the year, and while one or two circulation periods are possible, there is often none. In *lakes of the second order,* the temperature of the bottom water rises above 4°C during the summer, and there are one or two regular circulation periods during the year. *Lakes of the third order* do not develop thermal stratification, and circulation of water is more or less continuous (Whipple 1927). In general, lakes over 90 meters in depth belong to the first order; those between about 8 and 90 meters belong to the second order; and those less than 8 meters to the third order.

The specific heat of water is greater than most other substances; accordingly, a vast amount of heat must be absorbed to cause a temperature change. Temperature change is, in any event, slow. Much of the energy of solar radiation is lost by reflection from the water surface. The rest of the radiation is absorbed by the water, the solutes, and the suspended material. But much of the diurnal energy increment may be dissipated by re-radiation at night or in cloudy weather, by evaporation, and by convectional cooling. The amount of heat actually retained by a lake to melt its winter ice and warm it from the winter minimum up to the summer maximum is its *annual heat budget* (Table 6-1). For many dimictic lakes this is between 20,000 and 40,000 g-cal/m² of surface; there is wide variation in different kinds of lakes. The annual heat budget is important in determining a lake's productivity.

TABLE 6-1 **Monthly change in cumulative heat budget and solar radiation in the Bass Islands region (depth 7.5 m) of western Lake Erie, in 1941. A 20.3 cm ice covering formed in mid-January, melted in late March. The maximum heat budget, reached on July 30, was 19,575 g-cal/cm². The heat budget was about 15 per cent of the total solar radiation received during the year (after Chandler 1944).**

	g-cal/cm²			g-cal/cm²	
Month	Heat budget	Solar radiation	Month	Heat budget	Solar radiation
January	105	3,364	July	18,765	17,291
February	206	5,849	August	18,112	16,375
March	581	10,201	September	16,331	12,737
April	6,405	13,952	October	11,115	6,829
May	12,581	17,156	November	4,350	4,147
June	16,369	15,960	December	1,369	2,599

Oxygen

The distribution of oxygen at various depths depends upon the presence or absence of a thermocline, the amount of vegetation, and the organic nature of the bottom. The amount of oxygen in water is only one-fortieth to one-twentieth of that present in an equal volume of air when the two are at equilibrium, although their partial pressures are the same. Diffusion of oxygen from the air into comparatively sedentary water occurs very slowly; agitation of the water increases the surface area and promotes a faster rate of equilibration.

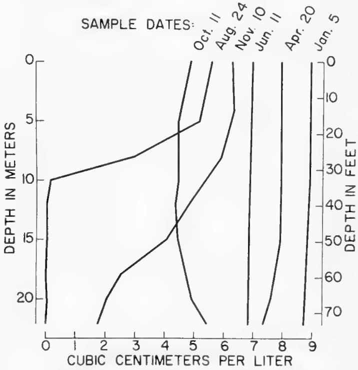


FIG. 6-4 **Changes in the vertical distribution of oxygen throughout a year in a dimictic eutrophic lake—Lake Mendota, Wisconsin (after Birge and Juday 1911).**

The amount of oxygen released by plants varies with their abundance and time of day; photosynthesis can take place in light. Phytoplankton and the rooted vegetation restricted to the shore line are important sources of oxygen to the water. With rapid photosynthesis in relatively small volumes of water, the water may be supersaturated with oxygen for short periods of time.

The oxygen supply of lakes is reduced in various ways; most notably through the respiration of animals and plants and the decomposition of organic matter. As lake waters warm up during the summer, their capacity to hold oxygen is reduced and oxygen may be released into the atmosphere. The saturation capacity of water at 0°C is 10.2 cc per liter, but at 25°C it is only 5.8 cc per liter. In some lakes, decomposition of organic material at the bottom may deplete the hypolimnion of its oxygen content for several weeks during the summer; perhaps lower than the level minimal to the support of life. This is called the *summer stagnation period.* During the winter, if the lake is covered with ice and snow, there may be a *winter stagnation period.* The oxygen supply of the deep waters is renewed with the autumn and spring overturns. Before decomposition can proceed very far there must be calcium in the water. Hence, decomposition is slow in soft or acid waters.

At temperatures of 15°–26°C oxygen concentrations of less than 2.4 cc/l (3.5 ppm) are fatal within 24 hours to several species of fish. From 0°–4°C, oxygen concentrations can decline through 48 hours to 1.4 cc/l (2.0 ppm), or even to 0.7 cc/l liter (1.0 ppm), before the same mortality results (Moore 1942). Some planktonic invertebrates can tolerate oxygen concentrations as low as 0.2 cc/l (0.3 ppm) and, for short periods, even 0.1 cc/l (0.1 ppm). Some bottom-dwelling protozoans, annelids, mollusks, and insect larvae may survive actual anaerobic conditions for periods of days, even weeks. Organisms that tolerate a lack of oxygen do so by creating an oxygen debt; that is, the lactic acid and other breakdown products produced in consequence of muscular activity simply accumulate until conditions permit oxidation of them. In true anaerobes these acid waste products are eliminated from the body; no oxidation debt is established.

European workers, principally Thienemann and Naumann, have devised a classification of lake habitats into three main categories on the basis of fertility and the amount of oxygen in the hypolimnion during the summer concentration. The oxygen concentration in the hypolimnion is, of course, a reflection of the fertility of the lake, since it is inversely proportional to the amount of decaying organic matter. Dystrophic lakes contain considerable organic matter but are infertile because the organic matter does not completely decompose and there is release of organic acids.

Oligotrophic lakes are usually deep (over 18 meters) with very little shallow water, and little vegetation around margins. Bottom contours are V-shaped; they are low in fertility, rich in oxygen in the hypolimnion (*orthograde* distribution), low in CO_2, and the color of the water varies from blue to green. The volume of the epilimnion is usually less than the volume of the hypolimnion. The fish population is not large. Characteristic species are lake trout, whitefish, and cisco. The midge fly larva, *Tanytarsus,* predominates. Plankton is not abundant. The Finger Lakes of New York are of this type.

Eutrophic lakes are usually less than 18 meters deep, the bottom contour is U-shaped, water color varies from green to yellow or brownish green, and there are larger areas of shallow waters and more marsh vegetation. Fertility is high, and because of rich bottom humus the oxygen content of the hypolimnion is greatly reduced during the summer (*clinograde* distribution). The CO_2 content is accordingly high. The volume of the epilimnion is usually greater than that of the hypolimnion. Plankton is abundant. The midge fly larva *Tendipes* is very numerous and the culicid larvae *Chaoborus* is usually present. The bottom fauna is rich, and there is a large fish population in the epilimnion. Characteristic fish species are the largemouth bass, perch, sunfish, and pike. These lakes occur in relatively mature river systems; many lakes in Minnesota and Wisconsin are of this type.

Dystrophic lakes are bog-like, very rich in marginal vegetation and organic content. Oxygen is likely to be scarce at all depths. The water is usually conspicuously colored, yellow to brown, and may be acidic because of organic acids and incompletely oxidized decomposition products. Plankton, bottom organisms, and fish are usually scarce, but blue-green algae are sometimes abundant. *Tendipes* may predominate among the bottom forms, but at times only *Chaoborus* is present. Characteristic fish are sticklebacks and mud minnows. Many lakes of northern latitudes are dystrophic in type.

All gradations exist between these three types of lakes, and individual lakes are often difficult to classify. *Oligotrophy* is indicated if the loss of oxygen in the hypolimnion during the summer is not over 0.025 $mg/cm^2/day$; *eutrophy,* if it is over 0.055; *mesotrophy,* if it is between the two (Hutchinson 1957). A lake may change from one type to another as succession proceeds (Lindeman 1942). Probably all lakes start as oligotrophic, but as they accumulate vegetation and decaying organic matter, they change into eutrophic lakes; or, if the organic matter does not completely decompose, into dystrophic lakes.

Eutrophic lakes may later develop into ponds and marshes; dystrophic lakes, into bogs. Biotic succession is scarcely discernible, however, in very large or very deep lakes. The Great Lakes, for instance, will endure until erosion lowers their outlets.

Carbon dioxide and other gases

Carbon dioxide is required by plants for photosynthesis. Its presence in lake waters tends to vary inversely with oxygen. Carbon dioxide is derived from the atmosphere, the respiration of both animals and plants, decaying organic matter, ground water, and bicarbonate salts. It may occur in either the *free* state (dissolved CO_2), *half-bound* state (HCO_3), or *fixed* state (CO_3). These three states are associated respectively with pH values 7, 7 to 10, and above 10. Algae and some rooted aquatic vegetation are able to obtain the half-bound CO_2 from the soluble bicarbonate salts, thereby converting them into the less soluble carbonates:

$$Ca(HCO_3)_2 \rightleftharpoons CaCO_3 + CO_2 + H_2O$$

Mollusks, a few insects, and some bacteria are also able to precipitate carbonates. Carbonates precipitate as to make conspicuous marl deposits on the bottom of some lakes. When marl formation becomes considerable, there is a decrease in lake fertility and a consequent decrease in animal life present, including bottom-inhabiting organisms.

When there is sufficient free carbon dioxide in the water derived from sources other than carbonates, they are converted back into bicarbonates and marl does not form. The degree of *alkalinity* of a lake is measured by the amount of carbon dioxide or acid required to convert the excess carbonates into bicarbonates, yielding neutral water. *Soft-water lakes* contain not over 5 cc/l fixed carbon dioxide; *medium-class lakes* contain 5 to 22 cc/l; *hard-water lakes* may have from 22 to as high as 50 cc/l (Birge and Juday 1911).

Marsh gas (methane) evolves from organic matter decomposing at the bottom. It rises in bubbles to the surface of the water. Methane formation may be extensive during the summer stagnation period. Methane does not appear to be particularly toxic to organisms until it is generated in very large amounts.

Hydrogen sulphide results from anaerobic decomposition of sulphurous organic matter. It may be conspicuous in sewage-polluted waters. It is inherently very poisonous.

Nitrogen occurs in water by reason of diffusion from the atmosphere. When present in excessive amount it has been known to form bubbles in the circulatory systems of fish causing death, but this does not commonly occur in natural waters.

Ammonia may occur naturally in water, a result of decomposition of organic matter. Ammonia may also be dumped into streams and lakes from industrial plants, often in concentrations toxic to fish. Fish are apparently unable to detect the presence of ammonia in water.

Dissolved solids

Falling rain may contain as much as 30 to 40 ppm of solids, and the runoff dissolves more as it drains over the upland into streams and lakes. Water draining off siliceous or sandy soils may contain 50 to 80 ppm of dissolved minerals; off more fertile calcareous soils, 300 to 660 ppm. Lake waters commonly vary from about 15 to 350 ppm of dissolved minerals, although in some lakes of the Great Basin, the total dissolved salts exceed 100,000 ppm. The ocean contains only 33,000 to 37,370 ppm.

Inorganic salts especially important for plants include ammonium salts, nitrites, and nitrates as sources of nitrogen; phosphates to supply phosphorus which, with nitrogen and sulphur, are raw materials for protein synthesis; silicates, which furnish silicon to diatoms and sponges; and salts of calcium, magnesium, manganese, iron, copper, sodium, and potassium for proper development of chlorophyll and growth of plants and, indirectly, of animals. Mollusks require calcium salts for shells. Crayfish and other arthropods require calcium for the carapace; vertebrates, for their skeleton. Absence of these necessary salts in lake waters limits the kinds and abundance of animals that can live there. Phosphorus and nitrogen are the most likely to be deficient. Nutrient salts tend to accumulate in the deeper waters and at the lake bottom, but they are brought to the surface at the autumn and spring overturns. Lakes in prairie regions tend to have more salts than those in deciduous or hardwood forests, which, in turn, have more salts than lakes in coniferous forest areas (Moyle 1956). The total dissolved content of a lake is important in determining its general level of productivity (Northcote and Larkin 1956).

Little is known about the amount of amino acids, fats, and carbohydrates occurring in natural bodies of water and how much of this nutrient material may be directly absorbed by organisms. Dissolved organic matter is derived chiefly from plankton remains, and other dead plants and animals as well as from bottom mud and external sources. In Wisconsin lakes, there is about 15 mg/l, of which crude protein constitutes 15 per cent, fats or ether extract 1 per cent, and carbohydrates about 83 per cent. Dissolved organic material becomes higher, of course, in dystrophic lakes and peat bogs (Birge and Juday 1934).

Hydrogen-ion concentration

The acidity or alkalinity of water depends on the ratio between the H^+ (or hydronium, H_3O^+) and OH^- ions. The amount of acidity or alkalinity is commonly expressed in terms of potential hydrogen ions in a pH scale. The values on this scale represent the logarithm of the reciprocal of the normality of free hydrogn ions. When the number of H^+ ions is equal to the number of OH^- ions, the pH value is 7, the value which represents absolute neutrality. All pH values less than 7 indicate a greater number of H^+ ions than OH^- ions, which is to say the closer the pH value approaches 0, the more acid the water. Above pH 7, there is a preponderance of OH^- ions; the higher the pH value, up to 14, the more alkaline is the water.

The hydrogen-ion concentration of most unpolluted lakes and streams is normally between pH 6.0 and 9.0, but extreme values of pH 1.7 and pH 12.0 occasionally occur (Hutchinson 1957). In some bodies of water, the pH value fluctuates considerably. Hydrogen-ion concentration increases (low pH values) with active decomposition of organic matter.

In general, aquatic animals can tolerate great changes in pH, although the range of toleration varies between species. Mollusks are not ordinarily found in acid lakes, but some snails can survive pH as low as 6, and the fingernail clam *Pisidium* down to pH 5.7. At the lower pH values, the shells of mollusks become thin, fragile, and transparent, but it is believed that the cuticular covering is partially protective and prevents complete dissolution of the calcium carbonate by the acid (Jewell and Brown 1929). In *Campeloma* snails, the apex of the shell may completely dissolve, exposing the apex of the visceral mass. Most fish can tolerate pH 4.5 to 9.5 provided there is plenty of oxygen (Brown and Jewell 1926, Wiebe 1931), and many invertebrates will tolerate even greater extremes. Fish as individuals become acclimated to certain pH values, and will select those values when given choice in a gradient. Such acclimation of individuals may have an effect on their choice of natural habitats, although when forced into a habitat with a different hydrogen-ion concentration, they change their acclimation. Although the direct ecological importance of differences in hydrogen-ion concentrations is doubtful, the measurement of pH may serve as an index of other environmental conditions, such as the amount of available carbon dioxide (with which it varies inversely), dissolved oxygen (with which it varies directly), dissolved salts, etc. Sometimes the difference in species of plankton found in bodies of water with permanently different pH values, for example in granite and limestone, is very striking (Reed and Klugh 1924).

LAKE BIOCIES

If we reserve ponds and peat bogs to separate consideration, there remain two major lake communities. They differ in species composition, abundance of organisms, distribution of niches, productivity, and physical characteristics. Inasmuch as these two communities correspond fairly well to the oligotrophic and eutrophic types of lakes, we may name them simply the *oligotrophic* and *eutrophic* lake biocies. Various facies of each community, or intermediate types (Deevey 1941) are affected by variations in the abundance of component species and correspond to differences in temperature, depth, fertility, and other features of the habitat. The communities that occur in dystrophic lakes; for instance, are an impoverished facies of the eutrophic lake biocies. In spite of taxonomic differences in constituent species, each lake biocies contains organisms belonging to the same life-forms and with similar mores so they may be discussed together.

Depending largely on their morphological adaptations and behavior, aquatic organisms are, for convenience, divided into plankton, neuston, nekton, and benthos, although the differences between the groups are not precise. *Seston* is a collective term that includes all small particulate matter, both living and non-living, that floats or swims in the water. *Plankton* are free-floating or barely motile organisms, either plant (*phytoplankton*) or animal (*zooplankton*), that are readily transported by water currents. Most plankton are microscopically small, although some forms are visible to the unaided eye. Species that can be caught with a net are called *net plankton* to distinguish them from the minute varieties that pass through No. 20 silk bolting cloth meshes. The latter include most protozoan, bacterial, and fungal forms, collectively called *nannoplankton*. Organisms that depend on the surface film for a substratum are called *neuston* and are more important in the quiet waters of ponds than in lakes. *Nekton* are larger animals that are capable of locomotion independent of water currents. Aquatic birds that swim and dive are included in this group. *Benthos* organisms are attached to or dependent on the bottom for support; there are sessile, creeping, and burrowing forms.

PLANKTON

Fresh-water plankton (Welch 1952, Pennak 1946, Davis 1955) includes representatives from the photosynthetic algae, Bacillariaceae (diatoms), Myxophyceae (blue-green), and Chlorophyceae (green), and occasional other form such as *Wolffia* among the higher plants; the non-photosynthetic bacteria and other fungi; and among the zooplankton, all classes of Protozoa except Sporozoa, Rotatoria, Entomostraca (especially Cladocera, Copepoda, and Ostracoda), some immature Diptera, the statoblasts and gemmules of bryozoans and sponges, the rare fresh-water jellyfish, *Craspedacusta,* and occasional aquatic mites, gastrotrichs, and others. Fresh-water plankton lack many forms common in the plankton of the ocean. On the other hand, the rotifers, aquatic insects, and water-mites are mostly absent from the sea, and the Cladocera are only poorly represented. It is probable that plankton evolved from benthonic forms occurring near the shore (Ruttner 1953), and many species of groups listed above, notably Ostracoda and Rotatoria, are still largely benthonic in behavior.

The algae in fresh water may vary in numbers from hundreds of thousands to tens of millions of cells per liter; Protozoa, from thousands to hundreds of thousands of individuals per liter; and the rotifers and entomostracans, from less than ten to hundreds per liter.

Distribution

Many species of plankton are nearly worldwide in distribution, particularly those that occur in the larger lakes. Cosmopolitan distribution and the many primitive types of the plankton community indicate that its origin is ancient. Some plankton, however, such as species of the genus *Pseudodiaptomus,* have a very limited distribution.

The plankton found in the open water of small to medium-sized lakes is seldom more than one to three species of copepods, two to four species of cladocerans, and three to seven species of rotifers, although the species change from one time of the year to another. It is also unusual to find more than one species of the same genus at the same time. When two do occur, one of them is usually much more abundant than the other. It is commonplace to find that 80 per cent or more of all limnetic copepods present belong to a single species; 78 per cent of all cladocerans to a single species, and 64 per cent of all rotifers to a single species (Pennak 1957).

In any one lake the horizontal distribution of the plankton may be irregular because of water currents, inflowing streams, irregularity of shore line, or swarming of a particular species in local areas. The vertical variations in the composition and abundance of species is even more striking. The chlorophyll-bearing algae require light and are most numerous in the upper stratum, although diatoms commonly occur at greater depths (Fritsch 1931). The vertical distribution of zooplankton varies widely with the species, but it is strikingly affected by light, food, gravity, dissolved gases, particularly oxygen, and thermal stratification. Few zooplankton occur in the hypolimnion of eutrophic lakes during the summer stagnation period, but occur at all depths during the spring and autumn overturns.

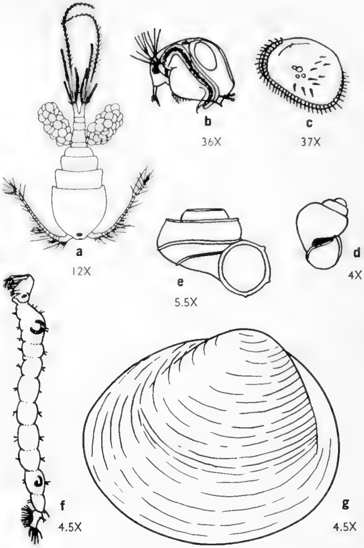


FIG. 6-5 **Common invertebrates found in lakes. (a) Copepod, (b) cladoceran, (c) ostracod, (d) the snail *Amnicola limosa,* (e) the snail *Valvata tricarinata,* (f) the ghost larva *Chaoborus albipes,* (g) the fingernail clam *Pisidium.* (Modified from various sources, Pennak 1953.)**

Diel movements

Several species of net zooplankton exhibit pronounced vertical migrations, moving upward into surface strata during the night and returning to greater depths during the day. In some instances this daily shifting of position may extend to 60 or more meters, in other instances it may be only a fraction of a meter, and some species do not exhibit the phenomenon at all (Langford 1938). A common explanation of these movements is that the animals are negatively geotatic by nature, but that during the day this drive is suppressed by a negative phototaxism and can be expressed only at night (Parker 1902). An alternative explanation is that zooplankton actively orient to a band of optimum light intensity and move up and down at different times to avoid light of too great or too little intensity (Cushing 1951, Hardy and Bainbridge 1954).

These diel movements are most widespread among Cladocera and Copepoda, but other species are also involved. One of the most interesting cases is the dipteran larva *Chaoborus punctipennis* that rests on the lake bottom during the daylight hours but is often teeming in the surface waters at night. It appears that the buoyancy of this larva varies with the size of its two pairs of air-sacs (Damant 1924). There are a few rotifers, *Mysis* among the Malacostraca, and *Ceratium* among the Mastigophora, in which vertical day and night movements have been demonstrated (Pennak 1944).

Seasonal distribution

The different species of plankton vary in their response to seasonal changes in the physical and chemical nature of the water, in number of generations per year, and in time of occurrence. Accordingly there is a marked seasonal variation in total numbers dur-

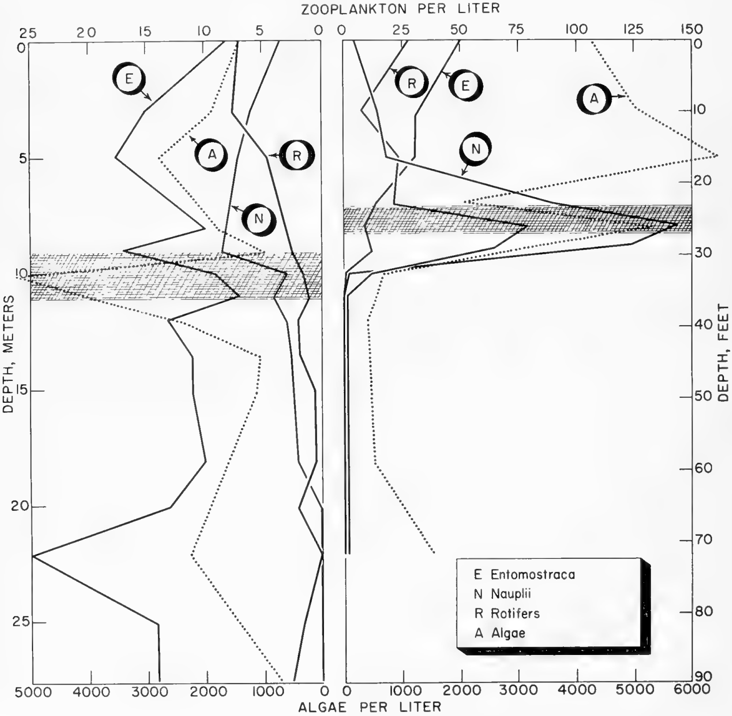


FIG. 6-6 Vertical distribution of net plankton (left) in an oligotrophic lake and (right) in a eutrophic lake, Wisconsin. Note that the horizontal scale is different for the two lakes, and for the algae as compared with the zooplankton. The cross-hatched horizontal belts show the region of the thermocline (from Birge and Juday 1911).

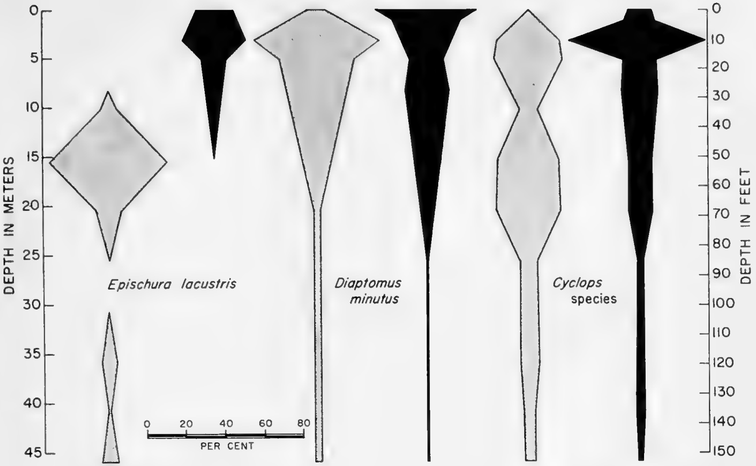


FIG. 6-7 **Vertical distribution of three species of copepods in the daytime (stippled) and at night (black) in the oligotrophic Lake Nipissing, Ontario, on a July day, when the thermocline occurred between 12 and 15 m (from Langford 1938).**

ing the year. In larger and deeper lakes, a maximum population usually occurs between April and early June, a minimum in August, a second maximum in late September or October, and the yearly minimum in late winter, February or March. However, not all species follow this schedule; some species have a maximum in the spring and not in the autumn, or vice versa; and some species reach greatest abundance during the general summer or winter minimum.

A species can also exhibit alternate increases and decreases in population at other times; these, as well as fluctuations in total plankton, are called *pulses*. At times, especially during the summer when the water is warm, an algal form, most commonly a blue-green species, may become so abundant that it discolors the water; these irruptions are known as *blooms*. The death and decay of such masses of vegetation may so deplete the oxygen supply that great mortality of fish and other animals results. In some cases the algae produce chemicals toxic to animals.

The ways in which environmental factors control seasonal and other changes in population are not all clearly understood, but it is significant that the maxima in total plankton of deep lakes often come at the times of the two annual overturns, times when food and oxygen are abundantly distributed at all depths. But the bimodal curve may also be found in shallow lakes and ponds that do not possess thermoclines. In small lakes, however, there is greater irregularity, and one, two, three, or no maxima may occur at various times of the year (Pennak 1946). Periods of high rainfall, which means increased drainage of nutrients into a lake, may be a factor of importance in producing maxima; seasonal changes in water temperature and oxygen tension certainly are important. There appears to be no relation between the pulses of net phytoplankton and zooplankton suggesting exclusive dependency of the latter on the former.

BENTHOS

Divisions

The lake bottom can be divided into a littoral zone and a profundal zone.

The *littoral zone* extends from the water's edge to the limit of rooted aquatic vegetation. It may be subdivided into the *eulittoral zone*, between high and low water marks at the water's edge where the beat-

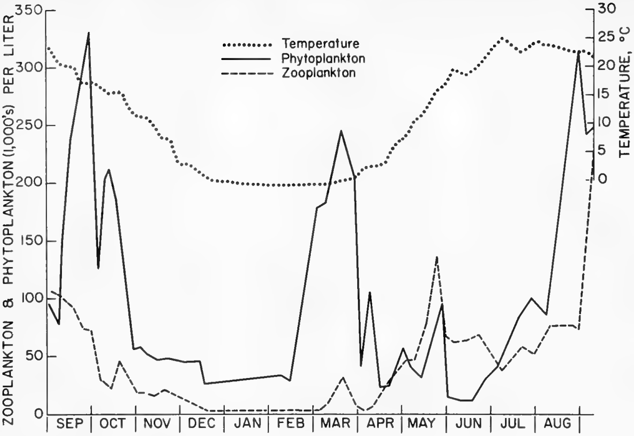


FIG. 6-8 **Seasonal plankton populations in western Lake Erie through a year (after Chandler 1940).**

ing of waves is most effective, and the *sublittoral zone*, which extends from the lower limit of wave action to the lower limit of rooted vegetation. Where such vegetation is absent, the sublittoral zone may be considered the bottom of the epilimnion down to the thermocline.

The *profundal zone* is the entire bottom below the rooted vegetation, or commonly the bottom of the hypolimnion. The boundary lines between the zones are variable and change with the depth of the thermocline. The open water of the lake above the bottom is known as the *limnetic zone*.

Littoral zone

The bottom of the littoral zone may be rock, cobble, gravel, sand, or mud. The muddy shallows of protected bays may have considerable rooted vegetation; they are essentially pond habitats. Differentiation of species distribution is primarily between the hard bottom and mud bottom habitats; sand bottom habitats are transitional (Table 6–2). Sand bottoms ordinarily have the lowest population of most species except clams because they are unstable habitats at best; indeed, they are often destructive by reason of the action of sand grains grinding on each other (Rawson 1930, Krecker and Lancaster 1933, Lyman 1956). A lake-bottom and a streambed of similar composition will contain many of the same kinds of organisms because of the similarity in the physical conditions of existence. The respective species compositions, however, are often different.

Oneida Lake in New York has an unusually high mollusk population. Baker (1918) recorded 59 species and varieties. It is interesting that most of them occurred on mud and sand bottoms. The highest populations were 1890 individuals per m^2 on mud at depths less than two meters, and 1573 individuals per m^2 on sand. On rocks and gravels there were only 656 individuals per m^2.

In eutrophic Douglas Lake, Michigan, bottom deposits in the littoral areas show zonation down to a depth of about 18 m. Beginning at the shoreline, there are belts of barren, wave-washed sand, muddy sand, sandy mud, and deep-water soft black ooze, in that order. The average number of macroscopic benthic animals is large, varying in the different types of bottom from 369 to 1178 to 3822 to 1713 per m^2, respectively. The abundance of animals is related not only to the nature of the bottom but also to depth and vegetation present. Where vegetation was scarce there were only 162 animals per m^2, but with increasing density of plants from sparse to common to abundant the population of animals rose to 1531, 2525, and 4407 per m^2, respectively. Vegetation was most dense at depths of 7 to 14 m in mixtures of sand and mud. Most abundant animal species in decreasing

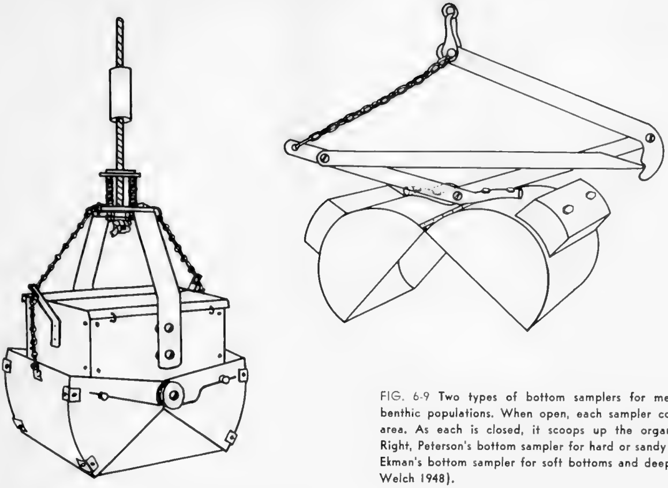


FIG. 6-9 **Two types of bottom samplers for measurement of benthic populations. When open, each sampler covers a known area. As each is closed, it scoops up the organisms present. Right, Peterson's bottom sampler for hard or sandy bottoms; left, Ekman's bottom sampler for soft bottoms and deep water (from Welch 1948).**

order were the amphipod *Hyalella azteca,* the dipteran larvae *Tendipes* and *Protenthes,* the snail *Amnicola,* tubificid worms, and the sphaerid *Pisidium* (Eggleton 1952). For comparison, the depth distribution of animals in an oligotrophic lake is shown in Fig. 6–10.

There is also a fauna of microscopic animals inhabiting the bottom. This consists of Protozoa, *Hydra,* Rhabdocoela (flatworm), Nematoda, Rotatoria, Gastrotricha, Oligochaeta, Cladocera, Copepoda, Ostracoda, Acarina (mites), and Tardigrada. These organisms are often very numerous in the thin organic ooze-film that covers mud bottoms (Bigelow 1928), but may penetrate underlying deposits to depths of 20 cm. Sand bottoms also support a varied and abundant microfauna (Pennak 1940, Cole 1955). In general, number of microfauna species and individuals varies inversely as the depth of water; only a few species remain active in the profundal zone during the summer stagnation period (Moore 1939). Bacteria, a source of food, are abundant in the bottom at all depths.

Much of the bottom fauna of the littoral zone consists of immature stages of otherwise terrestrial insects. The pulmonate snails and water mites have evolved from terrestrial species. Other aquatic species, however, have related forms in the sea and this may indicate their evolutionary origin. The fundamental problem involved in dispersal from the sea into fresh water would be that of osmoregulation, and the ability to live in fresh water has doubtless constituted a selection factor in the origin of this community.

Profundal zone

In oligotrophic lakes, species characteristic of the littoral zone are found at much greater depths than they are in eutrophic lakes, in which the oxygen supply during the summer stagnation period is reduced. The amphipod *Pontoporeia* occurs only in the deeper oxygenated cold waters of some northern lakes (Adamstone 1924). It is a relic from the glacial period, when it was probably more widely distributed. The profundal benthos of one oligotrophic lake in British Columbia increased from 470 individuals per m^2 in January to 1270 in August (Ricker 1952).

The most common bottom organisms are the annelids *Tubifex* and *Limnodrilus,* and the insect larvae *Tendipes, Chaoborus, Protenthes.* There may be a few mollusks, *Pisidium,* and *Musculium* for instance, nematodes, and other forms, including a microscopic fauna (Eggleton 1931).

The midge larvae represent a variety of species. Fifty species occur in one small lake in Algonquin Park, Ontario, that has a pH range of 4.6 to 6.6 and thermal stratification in summer with ample oxy-

TABLE 6-2 **Size and distribution of invertebrate populations on different types of bottom in the littoral zone of western Lake Erie (after Shelford and Boesel 1942).**

Common name	Classification	Number per m^2 cobble and gravel	sand	mud
Midge fly larva	*Cricotopus exilis* & others	1,000		
Caddisfly larva	*Hydropsyche*	70		
Mayfly naiads	*Stenonema tripunctatum, S. pulchellum, S. interpunctatum*	15		
Snail	*Physa* sp.	13		
Water penny	*Psephenus contei*	7		
Sponge colonies	Spongillinae	3		
Snail	*Planorbula crissilabris*	2		
Leech	*Glossiphonia*	2		
Snail	*Amnicola limosa porata*	1		
Mayfly naiads	*Baetis, Centroptilum*	+		
Clam	*Elliptio dilatatus sterkii*	+		
Damselfly naiad	*Argia moesta*	+		
Midge fly larva	*Tendipes pallidus*	+		
Bryozoan colonies	*Plumatella*	32	+	
Parnid beetle & larva	*Stenelmis crenata*	17	+	
Caddisfly larva	Trichoptera	2	1	
Clam	*Leptodea fragilis*	+	1	
Flatworm	*Planaria*	+	+	
Snail	*Goniobasis livescens*	12	1	2
Midge fly larva	Chironomidae	1	2	1
Clam	*Amblema costata*	+	0	+
Clam	*Lampsilis siliuoidea rosacea*	+	2	1
Clam	*Obovaria subrotunda*		1	
Clam	*Lampsilis ventricosa*		+	
Mayfly naiad	*Ephemera*		+	
Alderfly larva	Sialidae		+	
Midge fly larva	*Tendipes flavus*		+	
Parnid beetle larva	*Stenelmis bicarinatus*		+	
Clam	*Anodonta subglobosa*		+	
Clam	*Micromya fabilis*		+	
Snail	*Pleurocera acuta*		7	+
Clam	*Fusconaia flava parvula*		1	+
Mayfly naiads	*Hexagenia occulata, H. rigida*		+	33
Midge fly larva	*Tendipes digitatus*		1	6
Midge fly larva	*Procladius culiciformis*		+	3
Amphipod	*Gammarus limnaeus*		+	+
Water boatman	*Arctocorixa lineata*		+	+
Midge fly larva	*Tendipes decorus*			1
Snail	*Valvata tricarinata*			1
Leech	*Herpobdella punctata*			1
Amphipod	*Gammarus fasciatus*			+
Leech	*Glossiphonia stagnalis*			+
Crayfish	*Cambarus argillicola*			+
Mite	*Limnesia undulata*			+
Midge fly larva	*Cricotopus trifasciatus*			+
Clam	*Protera alata*			+
Clam	*Ligumia nasuta*			+
Clam	*Truncilia donaciformis*			+
Total taxa		22	23	22
Total individuals		1,177	17	49

gen in the hypolimnion. Of this number, 33 species are confined to the littoral and sublittoral zones, 7 to the profundal zone, and 10 occur throughout (Miller 1941).

The bottom mud of eutrophic lakes commonly consists of a thin, upper, brown, detritus layer of newly deposited organic matter that has drifted down from above; a relatively thick gray layer containing many fecal pellets and much organic matter, as well as diatoms; and a relatively barren bottom layer. In England's Lake Windemere, 85 per cent of all bottom organisms occur 6 meters below the surface, and 100 per cent 12 meters below the surface in the upper layers (Humphries 1936).

Maximum populations of insect larvae in eutrophic lakes are ordinarily reached during the winter. Minimum populations occur during late spring and summer, both in the littoral and profundal zones, because many immature insects have completed their development and emerged, as adults (Eggleton 1931, Ball and Hayne 1952). Although relatively few genera make up the bottom fauna, populations may at times be enormous. *Chaoborus* larvae alone have been recorded in populations of 97,000 individuals per square meter, and *Tendipes* larvae at 26,000 individuals per square meter (Deevey 1941).

Summer stagnation period

The low concentrations or complete disappearance of oxygen in the hypolimnion of eutrophic lakes for periods of several days or weeks in the summer requires special adjustments by organisms. Some bacteria are truly anaerobic, and perhaps some animals are, too, but most forms simply accumulate an oxygen debt that is repaid when the autumnal overturn takes place. It is of interest that the annelid worms and those midge fly larvae that tolerate the lowest oxygen concentrations possess hemoglobin in the blood, the pigment which has the greatest capacity and efficiency in transporting oxygen at low tensions. Tubificid worms extrude farther from their tubes and wave their tails more vigorously for a time as the oxygen content becomes reduced. The nightly excursions of *Chaoborus* larvae into the oxygenated epilimnion is certainly an opportunity for replenishment of their oxygen needs. A considerable proportion of the larvae migrate out of the profundal zone during the spring, and do not return until autumn or early winter (Wood 1956). The copepods *Cyclops bicuspidata, Canthocamptus staphylinoides,* and perhaps others, encyst and lie on the bottom during the summer period (Moore 1939), although this action has not definitely been related to any particular environmental factors (Cole 1953). Some midge fly larvae also form cocoons inactive.

NEKTON

The nekton of lakes consists principally of fish. There is an interesting small shrimp, *Mysis relicta,* found in the deeper waters of many northern lakes of North America that is often included with the nekton. This species is believed to be a relic of

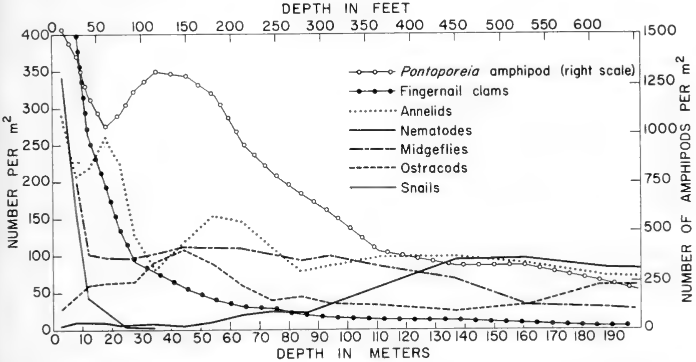


FIG. 6-10 Variation with depth in abundances of various organisms in oligotrophic Great Slave Lake (Rawson 1953).

a marine fauna that happened to get cut off from the sea in some past geological period, yet was able to survive as the water became fresh.

Numbers and species of fish are more concentrated in the littoral zone of lakes than in the open, deeper waters of the *limnetic* zone. Limnetic species, however, invade shallow waters for spawning. In deep waters, fish tend to remain close to the bottom, where their food supply is located, unless there is a deficiency in oxygen there. Caged fish, lowered to various depths in a eutrophic lake, did not survive long below the thermocline (Smith 1925). Fish may, however, make short excursions into the hypolimnion.

In a study of fishes in six Wisconsin lakes, Pearse (1934) found that *Usually most fishes per unit area occur in muddy, vegetation-filled, shallow ponds, but the characteristic fishes (carp, crappie, sunfish, dogfish) are not the most desirable for food. Rich eutrophic lakes produce considerable quantities of desirable fishes (perch, largemouth bass, white bass, rock bass). Oligotrophic lakes produce littoral game fish of good quality and size (smallmouth bass, wall-eyed pike, pickerel) and ciscoes in deep water.* The average catch with gill nets in two oligotrophic lakes was 3.5 per hour; in two eutrophic lakes, 4.2 per hour; and in two shallow lakes or ponds, 5.1 per hour.

In the littoral zone, fish species are segregated according to the composition of the bottom, as are the invertebrates. The species living over rock and gravel bottoms in lakes are mostly different from those inhabiting similar bottoms in streams, but the mud bottom forms are nearly the same as in ponds (Shelford and Boesel 1942, Nash 1950).

Amphibians and reptiles do not commonly occur in lakes except around margins supporting attached aquatic vegetation, and here pond species occur. Such pond mammals as the muskrat, mink, and otter are not typical of lakes as such, although they are frequently found in shallow littoral waters. There are a number of bird species, however, that occur most commonly in lakes: American and red-breasted mergansers, loons, pelicans, cormorants, terns, gulls, ospreys, bald eagles, and swallows. These species get their living from the lake, but nest on neighboring shores or islands. In addition, there are many pond and marsh birds that occur along vegetated lake margins.

FOOD CYCLE

The lake is a closely knit ecosystem whose inhabitants are largely independent of the rest of the world but very much dependent on each other for existence. It is almost a microcosm in itself (Forbes 1887), but it depends on the insolation of the sun for energy, rain and snow for water supply, and on minerals dissolved out of the surrounding uplands for the basic nutrient salts essential to the formation and functioning of protoplasm.

Basic to this food cycle are the bacteria. A few bacteria occur free-floating in the water. For the most part, however, they are either attached to algae, to other plankton organisms, to submerged objects, or occur on the bottom as part of the benthos (Henrici 1939). Their number varies from one place and time to another, as do the numbers of other organisms; they are more abundant in eutrophic than oligotrophic lakes. Their action is to transform the dead organic matter into nutrients, especially nitrates, that the green plants then absorb.

The phytoplankton are the next link in the food cycle because of their ability to manufacture carbohydrates with the aid of sunlight and to anabolize proteins after absorbing nitrogen and other compounds dissolved in the water. Rooted vegetation around the lake margin is important in this respect, although in large lakes the proportion of food substances formed by marginal vegetation is small as compared to the amount manufactured by phytoplankton. In Wisconsin lakes, the daily production of glucose during clear days in August varies from 14 to 44 kg per hectare (12 to 39 lb/acre) (Manning and Juday 1941).

Zooplankton feed upon phytoplankton, Protozoa, bacteria, detritus, and each other. Some species appear to discriminate in their choice of food, but most species filter out and ingest all particulate matter, within size limits, non-living as well as living, with which they come in contact. The ratio of number of entomostraca to number of phytoplankton cells has been found to vary from 1:1,800 to 1:63,000. Ratios of rotifers to phytoplankton vary from 1:50 to 1:37,500 (Pennak 1946). The plant cells, however, are much smaller than individual animals. The mean ratio of zooplankton to phytoplankton by volume is commonly about 1:4 (Davis 1958), but in alpine and northern oligotrophic lakes, the ratio may be reversed (Pennak 1955, Rawson 1956). In the nannoplankton, Protozoa depend largely upon bacteria, although some forms feed also on algae and detritus; a few species prey chiefly upon other protozoans (Picken 1937).

When the plankton dies, it settles to the bottom and furnishes food for the benthos. The accumulation of dead plankton and other aquatic organisms on the bottom may be extensive enough to form a distinctive brownish layer. The benthic midge fly and other insect larvae, annelids, clams including the sphaeriids, snails, and bottom-dwelling entomostraca feed on this detritus layer, on organic matter held in suspension, and on algal plankton and attached forms.

The variety of their food habits is reflected in certain anatomical adaptations of fish. Fish feeding on bottom matter have soft-lipped sucking mouths; fish feeding on plankton have numerous slender gill-rakers; fish feeding on other fish have large mouths and sharp teeth. The adults of some fish, such as the cisco, gizzard shad, paddlefish, and sunfish, consume large quantities of plankton. The gizzard shad also feeds on bottom mud, straining organic particles out of it and grinding them up in a stomach that resembles the gizzard of a chicken. Sturgeon, whitefish, buffalo fish, carp, catfish, bullheads, suckers, sunfish, and many others feed largely on bottom annelids, insect larvae, mollusks, and vegetation in shallow waters. As many as 354 midge fly larvae have been found in a single whitefish stomach; 331 were found in a sturgeon stomach (Adamstone and Harkness 1923). Bass, crappies, perch, pike, gar, and lake trout feed principally on other fish. The bottom feeders scoop up the bottom ooze indiscriminately; several forms maintain contact with the bottom by means of sensitive barbels hanging from the chin, but plankton-feeders and carnivorous species depend largely on sight for seizing individual prey.

Young fish of many species live largely on plankton, even though as adults they feed on something quite different. A 10-centimeter perch requires 150 mg dry weight of food per day during the summer, the equivalent of about 37,500 *Cyclops*. The perch would have to consume *Cyclops* at a rate of 26 per minute throughout the day in order to ingest such a total. A 20-centimeter perch would require 600,000 *Cyclops* per day, ingested at a rate of 417 per minute, which is doubtless beyond its efficiency of intake. By consuming only four small fish 0.3 g dry weight each, the perch could obtain the same energy intake (Allen 1935).

Most lake-inhabiting birds subsist mainly on fish, diving for their food. Gulls take only dead fish, which they find floating on the surface or washed up on the shore. Swallows skimming over the water surface consume enoromus numbers of emerging adult midge flies and other insects.

BIOMASS AND PRODUCTIVITY

The dry weight of total organic matter of seston in 529 fresh-water lakes was found to range from 0.23 to 12.0 mg/l with an average of about 1.36 mg/l (Birge and Juday 1934). Of this, living plankton organisms constituted an amount ranging from 20 to 80 per cent. The biomass of green phytoplankton is usually, but not always, greater than the zooplankton. The biomass of net plankton may be only one-third to one-tenth of the total net and nannoplankton. Net plankton is generally more abundant in hard water than in soft water, more abundant in eutrophic lakes than oligotrophic lakes (Rawson 1953). The dry weight of net plankton during the summer in 18 lakes of western Canada and in 2 lakes of Wisconsin varied from 0.9 to 17.7 mg/l, and averaged 5.0 mg/m^2 of water surface area (Rawson 1955).

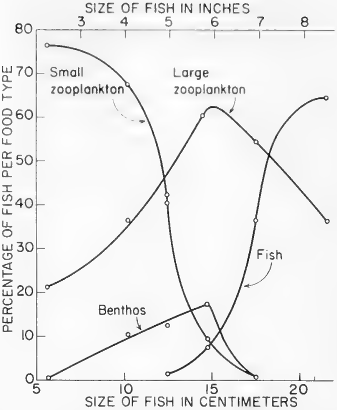


FIG. 6-11 **Change in food habits of perch as they age and increase in size (after Allen 1935).**

The biomass of benthos varies with the nature of the bottom, amount of vegetation, and depth. When computed for the total bottom of 10 Canadian lakes exceeding 11 m in depth, it was found to vary from 0.07 to 2.47 g/m^2, and average 0.63 g/m^2 dry weight, not counting the shells of mollusks (Rawson 1955). The mean of 36 lakes in Connecticut ranging in depth from 1.1 to 11.1 m varied from 1.09 to 34.8 g/m^2, and averaged 7.5 g/m^2 (Deevey 1941). The bottom fauna of various European lakes has been found to range from 0.69 to 5.65 g/m^2.

When lakes of different depths are analyzed, it is found that the mean biomass of both net plankton and benthos exist in inverse relation with mean lake depth (Table 6–3). This may indicate that the morphometric characteristics of a lake affect its carrying capacity, a factor additional to those of dissolved salt content, oxygen content, and temperature.

The biomass of plankton is generally greater than the biomass of benthos. In addition to the five Canadian lakes listed in Table 6–3, Deevey (1940) found the ratio between plankton and benthos in five other lakes likewise to vary from 3.8:1 to 10.0:1. In one eutrophic lake in Michigan, the standing biomass of

TABLE 6-3 **Interrelations between depth, biomass of plankton, and biomass of benthos in five Canadian lakes (from Rawson 1955).**

Average depth, meters	Average dry weight of net plankton, g/m^2	Average dry weight of benthos,[1] g/m^2	Ratio total biomass, plankton/benthos
11	9.05	2.47	2.3
26	3.65	0.41	4.5
38	3.2	0.45	5.7
69.5	2.6	0.20	7.2
120	0.9	0.07	9.6

[1] Minus weight of shells in mollusks

fish to benthos was in the ratio of 2.7:1 (Ball 1948).

The measurement of productivity is difficult, and methods presently in use require several assumptions. If, throughout the year, the plankton population of Lake Mendota, Wisconsin, should replace itself every two weeks, then the annual productivity is 624 grams ash-free, dry, organic matter per square meter of water surface. Of this amount, 585 g would come from phytoplankton and 39 g from zooplankton. The benthos reproduces less rapidly, nekton, still less so. The annual productions of bottom fauna and fish in Lake Mendota is estimated at 4.5 and 0.5 g/m^2 respectively, and the large aquatic vegetation at 51.2 g/m^2 (Juday 1940). Disregarding the large aquatic plants, the ratio of productivity between plankton and benthos is approximately 139:1; between benthos and nekton, 9:1; and between plankton, benthos, and nekton taken together, 1248:9:1. The ratio of annual productivity between plankton and benthos is much higher, therefore, than is the ratio of their biomasses or standing crops. No attempt was made in this study to determine the standing crop of fish.

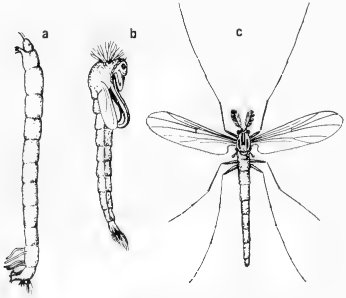


FIG. 6-12 **(a) Larva, (b) pupa, and (c) adult of a midge fly (from Shelford 1913 after Johannsen).**

In a detailed study of the net productivity of the benthos in the Russian Lake Beloie (Borutsky 1939), it was found that the standing crop increased during the year by 125 per cent. Of this total biomass, 55 per cent died without being eaten by other organisms or was replaced by the small biomass of new eggs being laid; 14 per cent was consumed by other organisms, chiefly fish; and 6 per cent emerged as adults that subsequently left the lake ecosystem. The remaining 25 per cent constituted the standing crop of the following year. However, this standing crop was only 56 per cent of what it was the year before, so these percentages are not representative of stabilized populations.

It was estimated that in Costello Lake, Ontario, the standing population of midge fly larvae was replaced during the 135 days of summer eight or nine times in the epilimnion, and two or three times in the hypolimnion. Consumption of larvae by fish was small in shallow waters but amounted to 50 per cent of the standing crop in deep water (Miller 1941).

LIFE HISTORIES

Although most *midge fly larvae,* Chironomidae, are aquatic, some forms live in decaying organic matter, under bark, or in the ground. The earliest larval stage is a wiggler, which may be carried by the current or may squirm about from place to place. Later, this wiggler larva becomes sluggish and builds a case or tube, open at both ends, by cementing particles of sand, debris, or silt about itself with mucous from its salivary glands. Construction is accomplished in about three hours. The larvae extend themselves from these cases for feeding, and in some species may even move the cases to better feeding areas. The larval period is the longest part of the life cycle; it lasts at least two months (Macdonald 1956). Most of the pupation period, which is probably less than a week, is spent in the larval case, but towards the end the pupa swims to the surface of the water. At this time it is preyed upon extensively by fish. The adult imago struggles out of the case and flies off. The adult lifespan is probably short, as there is no evidence that they feed. They may occur in immense swarms in the evening. Eggs are laid in masses of several hundred or in sticky gelatinous strings that float at the surface attached to some object or sink to the bottom. The eggs hatch in a few days, and the cycle is repeated (Cavanaugh and Tilden 1930, Johnson and Munger 1930). Some larvae (e.g. *Procladius, Tanypus*) are carnivorous rather than herbivorous or saprophagous. They do not build cases, but roam over the bottom. The number of generations varies in different species from two per year, to one per year, or one in two years, and depends in part on the depth and temperature of their habitats (Miller 1941).

The *tubificid worms* do not leave the lake bottom. Many of them occur in tubes or cases, similar to the habit of midge fly larvae. It is evident by the presence of sexually mature adults and the reproductive cocoons that reproduction occurs principally during the periods of autumn and, especially, spring overturns. There follows a large increase in numbers of small immature worms (Eggleton 1931).

It is obviously impossible to include a description of the life history of all species. The cisco or lake herring has been selected to illustrate the life-history of a lake fish (Cahn 1927, Fry 1937).

The *cisco* spends much of the year in deep water, feeding very largely on plankton, strained out by specialized gill rakers. Because its food habits require a large volume of water to be passed through its gill-rakers, the fish swim almost constantly, usually in a constant and definite direction, in schools of from twenty to several hundred individuals. During hot summers the cisco may leave the cool, deep, but oxygen-poor carbon dioxide-rich waters and ascend into the epilimnion. There they are sometimes killed in large numbers by temperatures higher than they are able to tolerate. The fish spawn in November or December, when the water temperature drops to 4°C. For this purpose the fish move into water only one to three meters deep, or even up into rivers. The males precede the females by two to five days. When the females arrive, several males consort with each. When she is ready to spawn, the female descends to within 20 cm of the bottom and sheds about 15,000 eggs. At the same time, the accompanying males discharge sperm, and fertilization is completed. The eggs are viscous and become attached to rocks or bottom debris. No nest is made and no further attention is paid to the eggs. Incubation may last 10 to 12 weeks; hatching normally occurs in late March. The young fish later return to deep water and reach breeding condition in three years. Doubtless the slow rate of development in this species is related to the low temperature of the habitat. After spawning is completed, the adults may remain in shallow water until water temperatures reach 20°C. This temperature is above their preferendum, although they can tolerate temperatures up to at least 25°C.

APPLIED ECOLOGY

Applied ecology involves the management of lakes and the control of their resources for man's benefit. Aside from their use in transportation, in industry, and as sources of drinking water, lakes are of importance to man for fishing, swimming, sightseeing, and boating. For swimming, clean, clear water with a sand bottom is desirable. Sewage and industrial wastes must be diverted or eliminated for reasons of health and the appearance of the water. Algal growth, when excessive, can be controlled with copper sulphate; and rooted vegetation can be reduced by sodium arsenite treatment. When chemical treatment of water is limited to low concentrations administered with discretion, there is generally no great harm to fish; some invertebrates, such as midge fly larvae, mayfly naiads, and fresh-water shrimp, are adversely affected (Machenthun 1958).

Where there is excessive erosion of the surrounding upland, silting may render the waters of small lakes turbid, decreasing the growth of algae, a basic food substance for lake organisms. The rapid accumulation of silt on lake bottoms covers up bottom organisms, clogs the gills of mollusks, and generally reduces the lake's productivity. The obvious remedy is the control of erosion at the source.

The management of large lakes to the end of increasing fish productivity is difficult because of the area and depth of water involved. Where commercial fishing is commonly practiced in large lakes, a careful yearly catch record for each species should be maintained. This will suggest regulations such that annual cropping will not exceed annual production. To improve fishing and increase productivity there must be an increase in a lake's carrying capacity. Carrying capacity depends on maintenance of good chemical and physical characteristics of the water, an abundance of food, plenty of breeding areas, and exclusion of exotic predators. The drastic decline in the annual yield of lake trout in the Great Lakes is attributed to invasion by the predaceous sea lamprey. Artificial fertilization of lakes presents greater problems than it does for ponds, but may eventually prove practicable (Hasler and Einsele 1948).

Pollution is usually a local problem in large lakes. A moderate pollution of organic wastes may in fact fertilize a lake and produce an increase in the plankton and bottom organisms which serve as fish food. Excessive pollution, however, must be controlled, as it interferes with the use of the lake for recreation and as a water supply.

The smaller the lake the more practicable becomes management of the habitat. The water level may be manipulated, by damming, to increase the area of shallow water available for spawning at certain seasons, or lowered at other times to permit growth of marginal vegetation or prevent spawning of undesirable species. Artificial shelters or spawning areas may sometimes be created, yielding a significant improvement (Hubbs and Eschmeyer 1938). In general, rearing small fish in hatcheries for later release has not proven economically practicable. Any proposed introduction of exotic species should be investigated with considerable skepticism.

SUMMARY

Important factors in aquatic habitats are pressure, density, light, current, temperature, oxygen, carbon-dioxide and other gases, dissolved solids, and hydrogen-ion concentration. Of special importance in many lakes is the occurrence of a thermocline that divides the water into an epilimnion and a hypolimnion. The hypolimnion retains a low temperature throughout the year, and in some lakes becomes deficient in oxygen in late summer. These differences in temperature and oxygen greatly affect local and seasonal occurrence of organisms. Lakes are classified several ways on the basis of physical characteristics; biologically, only two distinct communities, the oligotrophic and eutrophic lake biocies, are distinguishable.

The life-forms of lake organisms are chiefly plankton, benthos, and nekton. Zooplankton exhibits diel movements to greater depths in the daytime and general dispersal, including movements toward the surface, at night. Peak populations are commonly reached in late spring, and again in autumn; low points occur in summer and winter. Benthos decreases in abundance from the littoral to the profundal zone. Profundal animals in eutrophic lakes are adjusted in various ways to survive the low oxygen late summer stagnation period. Nekton includes aquatic birds as well as fish.

The lake is a closely knit ecosystem, largely independent of the rest of the world except for its solar energy, inflowing water, and mineral salts. The base of food-chains is composed of detritus, bacteria, and phytoplankton, then zooplankton and small benthic organisms, and finally fish and birds. All dead organisms, as well as their excreta during life, decompose so that their nutrient substances start the food-cycle over again. The biomass and productivity of the three life-forms usually rank, from high to low: plankton, benthos, and nekton.

The life-cycle and behavior of lake organisms are closely adjusted to the various environmental situations available. Control or management of fish production by man is difficult, except in lakes of small size.

7

Local Habitats. Communities, and Succession:

Ponds, Marshes, Swamps, and Bogs

Pond is a popular term for lakes of the third order that are small, shallow, and, when mature, have rooted vegetation over most of the bottom. There is no clear distinction between ponds and lakes of the first and second orders. The littoral zone of eutrophic lakes, for instance, is pond-like in habitat and organisms. Floating and emergent vegetation commonly occurs around the margin of ponds to form extensive tracts of marsh. The pond habitat may originate as a shallow basin, as a large pool in a stream, as the result of the filling in of a lake, or from a stream dammed by beavers, man, or landslide. Slow-flowing rivers are essentially elongated ponds, and have a similar fauna (Kofoid 1908, Richardson 1928). Because of the slight water movement in ponds, the surface film becomes an important microhabitat for some species. Pondwater temperature is often uniform at all depths, but during warm sunny weather, ponds well protected from the wind may show considerable stratification, not only in temperature, but also in oxygen content and other characteristics (Wallen 1955). Daily and seasonal variations in temperature may be great because of the small volume of water. Ice forms earlier and lasts longer in ponds than in lakes, freezing shallow ponds to the bottom in severe winters. Light penetrates to all depths, encouraging growth of vegetation except in high turbidity. Young ponds may have rocky, sandy, clay, or mud bottoms; in mature ponds, there is ordinarily an accumulation of organic matter and silt.

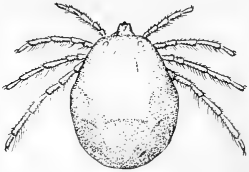
The dissolved oxygen content of ponds varies widely from temporary supersaturation when there is excessive photosynthesis of plants to near depletion when decomposition predominates. Oxygen content is often highest in the spring; very low in late summer; and sometimes low again under the winter ice cover. Oxygen content is usually higher during daylight hours than during the night because of the daytime photosynthetic cycle of plants. Oxygen may become so low at night as to become critical, especially for fish. Decomposition of organic matter evolves carbon dioxide and, at times, considerable methane, hydrogen sulphide, and other gases. In ponds, as in lakes, there is as wide variation in hydrogen-ion concentration. As ponds mature and accumulate humus, pH value decreases.

PLANT SERE

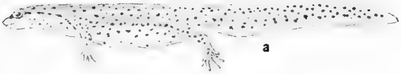
The plant hydrosere, or pond sere, typically contains the following stages and characteristic species:

Submerged vegetation: water weed, pondweed, milfoil, hornwort, naiads, buttercup, bladderwort, eelgrass, and the herb-like alga *Chara.*

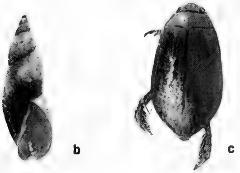
FIG. 7-1 **Pond animals (from Shelford 1913).**

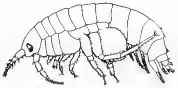


Red mite



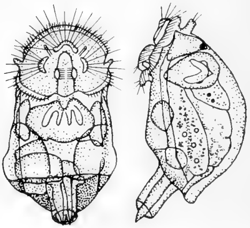
Representative animals of the emerging association. a, the common newt; b, the common pond snail; c, a predaceous diving beetle.



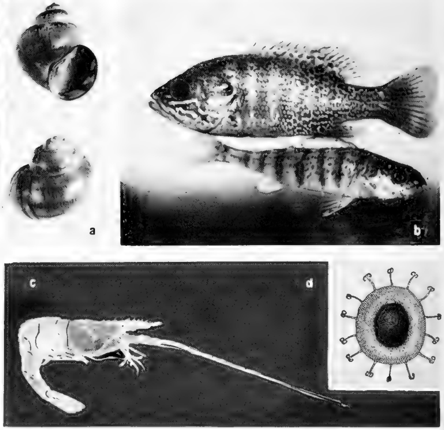


An Amphipod

A pelagic rotifer
ventral (left) and side (right) views



(Above) A garter snake feeding on the dead fish left in a dry-season pond.



(Right) Representative animals of the submerged vegetation. a, a viviparous snail; b, a green sunfish above a yellow perch, both juvenile; c, a shrimp; d, a winter body, or statoblast, of the gelatin-secreting polyzoan.

Floating vegetation (Fig. 2.8): water lily, pond lily, pondweed, smartweed, duckweed, and water hyacinth. All except the last two are rooted in the mud, often at depths of two to three meters, and may have rhizomes from which long petioles extend to the leaves floating on the surface. Duckweeds and water hyacinths are unattached floaters, and cover the surface extensively in some localities.

Emergent vegetation (marsh) The dominant species are: cattail, reed, bulrush, bur-reed, swamp loosestrife, wild rice, and sawgrass. They invade waters of over a meter depth, but in shallower waters or in secondary succession they are replaced by a sedge meadow composed of sedge, rush, and spike rush.

Swamp shrubs: buttonbush, alder, dogwood, swamp rose, and sometimes shrubby willow and cottonwood.

Swamp forest: red and silver maples, elm, ash, swamp white oak, and pin oak.

Succeeding stages depend on the climate of the region. In arid regions the swamp forest may be poorly developed, and grassland or desert vegetation may come in quickly. In the mesic climate of the Eastern states, an oak-hickory associes follows the swamp forest, replaced in turn by a climax of sugar maple-beech or mixed mesophytic forest. The hydrosere in the broad-leaved evergreen climax area of southeastern North America brings in cypress and a number of other unique species.

Vegetative debris and animal remains, together with inwashed silt, fill the basin gradually, reducing the depth of water and allowing vegetation to encroach on the periphery. As this process continues, the succession is effected. Ultimately, open water entirely disappears as the ground stratum is built up above the water table, and climax vegetation replaces all other types.

ANIMAL SERE

Animals characteristic of marshes and ponds constitute a distinct *pond-marsh biocies* which extends into sluggish or base-leveled streams and the littoral zone of eutrophic lakes. Most animal species are not restricted to a single stage or community of the plant sere, but commonly occur in several stages in varying abundance and for various activities. Fish, for instance, feed in open water but spawn in shallow water among the emergent vegetation. Submerged, floating, and emergent vegetation represent different levels or strata in a single biotic community, and each stratum has about the same degree of distinctiveness as forest community strata.

With the invasion of swamp shrubs and with the ground level well above the water table most of the year, pond and marsh species largely disappear, replaced by many characteristic new species. This animal community represents the swamp facies of the *deciduous forest-edge biocies,* which will be discussed later. The swamp forest is often quite open at its outer margin, and forest-edge species remain common. But as this forest develops a closed canopy and drier ground stratum, it is invaded by the swamp facies of the *deciduous forest biociation.* In the pond sere there is a succession of animal adaptations from aquatic to amphibious to terrestrial.

POND-MARSH BIOCIES

Neuston

The *supraneuston,* organisms which move on top of the surface film in pursuit of most of their life activities, consists of the water striders Gerridae, Veliidae, Mesoveliidae; the water measurers Hydrometridae; the whirligig beetles Gyrinidae; the springtails Collembola; some spiders; and occasional other forms. The gyrinids of several species commonly occur in social groups (Robert 1955). They are remarkable for having each eye divided by the margin of the head so that the upper portion looks into the air and the lower portion into the water. Several of the forms listed have long legs that distribute the weight of the body over a large area of surface film. The portions of the legs or body that contact the surface film are water repellant.

The undersurface of the water film supports an *infraneuston* of *Hydra,* planarians, ostracods, cladocerans, snails, and insect eggs, larvae, and pupae (mosquitoes, certain kinds of midge flies, and so forth). For all except the insects, however, the use of the surface film in this manner is usually transitory. Some cladocerans, such as *Bosmina* and *Daphnia,* occasionally break through the surface film from below, fall over onto their sides, and cannot return.

Plankton

The species of plankton found in ponds differ somewhat from those in lakes (Klugh 1927), but the transition from lake species to pond species is a gradual and progressive one. Protozoa and Rotatoria are usually more abundant in ponds than in lakes.

TABLE 7-1 **Development (ecesis) of invertebrate bottom populations (calculated in** number per m²) in strip-mine ponds of different ages, as determined by studies conducted in October, through three years. The ponds 1 and 8 years old had no rooted vegetation; the ponds 21 and 30 years old had a little vegetation in protected coves; the pond 80 years old had submerged, floating, and emergent vegetation. Range of pH: 7.1 to 8.5; locality, near Danville, Illinois.

Common name	Classification	Age of pond				
		1 yr	8 yr	21 yr	30 yr	80 yr
Red midge fly larva	*Tendipes*	16	7	6	27	25
Damselfly naiad	Zygoptera	2	23	4	22	51
Caddisfly larva	Trichoptera	1	-	-	2	3
Backswimmer	Notonectidae	+	-	-	+	3
Whirl-i-gig beetle	Gyrinidae	+	+	-	+	
Alderfly	*Sialis*		23	3	2	
Water boatman	Corixidae		13	+	1	
Burrowing mayfly naiad	*Hexagenia*		21	262	5	1
Dragonfly naiad	Anisoptera		9	4	11	27
Crawling water beetle	Haliplidae		5	+	+	+
Clam	Unionidae		5	+	-	+
White midge fly larva	*Tanypus*		3	1	35	10
Aquatic annelids	Tubificidae, Lumbriculidae		4	+	3	2
Ghost larva	*Chaoborus*		+	+	+	17
Springtails	*Podura aquatica*		+	+	+	+
Crayfish	*Orconectes propinquus*			1	1	
Fly larva	Diptera			3	+	
Water spider	Arachnida			+	+	3
Fingernail clam	*Sphaerium*			+	-	2
Mayfly naiad	*Caenis*				+	
Snail	*Physa gyrina*				14	58
Amphipod	*Hyallela*				5	105
Other mayfly naiads	Ephemerida				1	21
Aquatic isopod	*Asellus communis*				1	5
Flatworm	*Planaria*				1	1
Limpet snail	*Laevapex*				1	1
Snail	*Gyraulus parvus*				+	17
Snail	*Helisoma trivolvis*				+	9
Water scorpion	*Ranatra*				+	1
Leeches	Hirudinea					5
Snail	Lymnaeidae					2
Fingernail clam	*Pisidium*					1
Shrimp	*Palaemonetes*					1
Water strider	*Gerris*					+
Total taxa		5	3	16	27	28
Total individuals		19+	113+	284+	132+	371+

Although plankton distribution does not vary with depth as much in ponds as in lakes, seasonal fluctuations are as extensive and similar in nature. Eddy (1934) lists 15 perennial species of zoo- and phytoplankton that may be found in ponds throughout the year, 2 seasonal species which reach their peak of abundance between December and April, 4 between February and June, 12 between March and December, and 5 between July and September.

Benthos

Subaquatic animals dwell not only on the bottom but also on the stems and leaves of submerged plants. Aquatic plant species have many kinds of insects, amphipods, mites, and snails using them for the food, shelter, or reproductive sites denied them in the mud bottom below. Other kinds of insect larvae and oligochaetes are more abundant in the mud than on the plants. The undersurface of lily pads often contains many small organisms, including Protozoa, *Hydra,* flatworms, rotifers, and snails. The biomass of animals varies directly with the biomass of vegetation, and the quantity of invertebrates is especially great on those plants possessing finely dissected leaves (Gerking 1957). Very few species found in lake bottoms are not found in ponds, but the pond-marsh biocies contains many species not found in lakes.

The variety of species and number of individuals found in the bottom fauna increase with the age of the pond from the time the pond is formed until attached vegetation becomes excessive (Tables 7–1, 7–2). Coincident with the development of the bottom fauna is an increase in variety and abundance of plankton (Eddy 1934) and fish. The construction of a beaver dam in a small Ontario river changed the riffle habitat into that of a pond and brought a reduction in mayfly naiads, stonefly naiads, and caddisfly larvae within two years. Other stream animals fell from 68.7 to 15.6 per cent of the total population while midge fly larvae increased from 31.3 to 84.4 per cent (Sprules 1940). Shallow ponds develop more rapidly than deep ones, and mud bottom ponds develop more rapidly than sand- (Shelford 1911) or rock bottom ponds (Krecker 1919). The increase in number of species and individuals in ponds depends on an increase in the variety of microhabitats, types and amount of food, and vegetation. With the development of the pond into a marsh there is generally an increase in humus and an increase in bacteria effecting its decomposition, carbon dioxide, and marsh gases. Oxygen and pH decrease.

Two predominantly terrestrial orders of insects, Coleoptera and Hemiptera, have invaded the pond community but are not found in lakes except those which have pond-like margins. The Coleoptera are represented by three families of diving beetles, Haliplidae, Dytiscidae, and Hydrophilidae, and by the whirligig beetles, Gyrinidae. The haliplids are herbivorous; the dytiscids are predacious; some hydrophilids and gyrinids are predators, others are scavengers. The aquatic bugs or Hemiptera are the Corixidae, which feed on the bottom ooze, the Notonectidae, which prey upon small Entomostraca, the Nepidae, the Belostomatidae, and the Naucoridae, which are all carnivorous; and the Veliidae, Mesoveliidae, Gerridae, and Hydrometridae, which are probably both carnivores and scavengers. Some of these species, as already noted, are usually found on the surface film, but they may occasionally dive and cling to submerged vegetation. The true diving

TABLE 7-2 **Succession of dragonfly and damselfly naiads in western Lake Erie (after Kennedy 1922).**

	Lake biocies		Pond-marsh biocies			Forest-edge biocies
Dragonfly and damselfly naiads	Open lake	Lake margin with submerged vegetation	Lake margin with floating and emergent vegetation	Young pond	Mature pond	Old marsh with invading shrubs and trees
Gomphus plagiatus	++	++				
Gomphus vastus	++	++	+			
Neurocordulia yamaskinensis	++	++	+			
Macromia illinoiensis	++	++	+			
Argia moesta	++	++	++	+		
Enallagma carunculatum		++	++	++	++	
Enallagma exsulans		+	+	++	++	
Enallagma ebrium		+	+	++	++	
Ischnura verticalis		+	++	++	++	++
Tramea lacerata			+	++	++	
Anax junius			+	++	++	+
Enallagma signatum				++	++	
Libellula luctuosa				++	++	
Libellula pulchella				++	++	+
Lestes rectangularis				+	++	+
Leucorrhinia intacta					++	
Erythemis simplicicollis					++	
Plathemis lydia					++	
Nehalennia irene					+	
Pachydiplax longipennis					++	+
Lestes forcipatus					++	++
Sympetrum obtrusum					++	++
Sympetrum vicinum					++	++
Sympetrum rubicundulum					+	+
Enallagma hageni						+
Lestes uncatus						+
Lestes unguiculatus						+

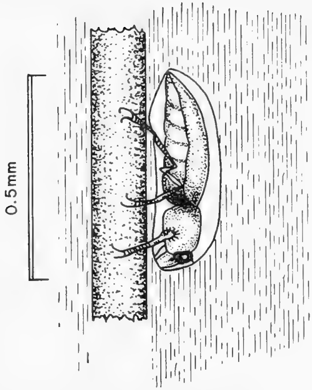


FIG. 7-2 **The beetle *Dryops* freshly submerged, crawling along a stem, encased by a bubble of air (after Thorpe 1950).**

forms, especially the beetles and some of the hemipterans, have evolved oar-like legs for rapid propulsion.

Respiratory adaptations

Air-breathing aquatic insects, as well as the pulmonate aquatic snails *Lymnea, Helisoma, Gyraulus, Physa, Laevapex,* have evolved special mechanisms and behavior for respiration. Most species rise to the surface of the water at intervals to replenish their supply of air. Insects are so buoyant that they must cling to the vegetation or some other object to maintain a submerged position. As soon as they let go of the substratum, they float to the surface and must return by swimming. Snails commonly creep to the surface along plant stems or other submerged objects, or suddenly emit mucous threads that float them to the surface (Dr. Max Matteson, personal communication). They find their way to the surface, at times of oxygen need, by negatively geotactic behavior. After they have obtained a fresh supply of oxygen, they become positively geotactic (Walter 1906). Pulmonate snails probably also absorb some oxygen from the water; indeed, some species appear never to come to the surface. The gill-bearing or branchiferous species of snails are seen to be segregated into rather distinct niches when their habitat relations are analyzed in detail (Baker 1919).

Diving beetles carry a bubble of air beneath the elytra, and the entire body of *Dryopa* is enclosed in air. The hemipteran notonectids and corixids carry a bubble over the ventral surface of the body, trapped there by hair-like setae. The spiracles of the tracheal system open into these bubbles. The body surface encompassed by and setae holding the bubble are water-repellant, or *hydrofugous.* The fresh air-bubble contains 21 per cent oxygen and 78 per cent nitrogen, the same proportion as the atmosphere. The nitrogen dissolves into the water very slowly. The carbon dioxide given off by the insect passes quickly into the water. As the insect uses up the oxygen in the bubble, it shrinks. The oxygen content of the bubble may be reduced to one per cent, or less, before the insect rises to the surface for a fresh supply; in water containing little or no oxygen, rising may occur every three or four minutes. If the water contains ample, however, oxygen will diffuse into the bubble as rapidly as it is used, and perhaps three times as fast as the nitrogen diffuses out. Under these conditions backswimmers, *Notonecta,* have survived for nearly 7 hours without coming to the

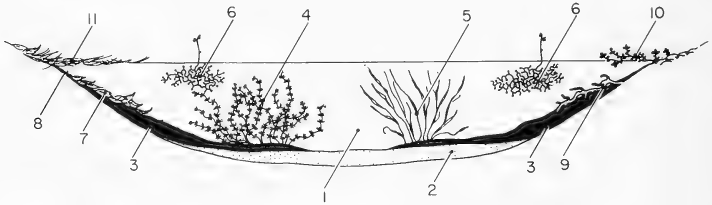


FIG. 7-3 **Dragonfly niches (after Needham 1949): (1) on sand, *Macromia;* (2) in sand, *Gomphus;* (3) in muck, *Libellula, Neurocordulia;* (4) on massed *Nitella,* damselflies; (5) on tips of *Websteria, Enallagma laurenti;* (6) in open tangles of bladderwort, *Erythemis* and damselflies; (7) in fallen brown leafage, *Pachydiplax longipennis;* (8) at sides of ditch, *Tetragoneuria, Celithemis, Erythrodiplax;* (9) on invading roots of woody plants, *Argia fumipennis;* (10) at water-line rooted green plants, damselflies; (11) in rafts of fallen pine needles, aquatic Hemiptera that are enemies of dragonfly naiads.**

surface. The bubble is really a physical gill mechanism, but functions only as long as the nitrogen present provides an adequate surface for oxygen diffusion. The insect's trip to the surface is as much to get a fresh supply of nitrogen as it is to get a fresh supply of oxygen (Wolvekamp 1955).

The air-breathing respiratory mechanisms of other aquatic insects are equally remarkable. In many larvae, *Dytiscus*, Culicidae, and other Diptera, and in the aquatic Hemiptera, only the terminal abdominal spiracles are functional. The tracheal trunks of mosquito larvae and *Dytiscus* larvae among others, store considerable air so that the animal may remain submerged for long periods. *Ranatra* and other Nepidae have long respiratory tubes extending from the tip of the abdomen so that they can cling to vegetation well below the water surface yet respire directly into the air.

Dragonfly naiads pump water through the anus, in and out of an enlarged rectum. The walls of the rectum are abundantly supplied with a network of tracheae for interchange of gases directly with the water. In the larvae of midge flies, black flies, and corixid beetles, the general body surface is richly supplied with fine tracheae for exchange of gases directly with the water. The anal papillae of midge flies and mosquito larvae are not respiratory in function, as formerly supposed, rather they serve for osmoregulation. Tracheal gills, plates, or filaments are found on many immature insects, Ephemeridae, Plecoptera, Zygoptera, Trichoptera, Neuroptera, and some Diptera, and effectively increase the area of surface available for oxygen absorption. The larvae of the beetle *Donacia* and certain Diptera including mosquitoes have a unique ability to puncture the walls of submerged plants and collect air from the intercellular spaces (Miall 1934).

Terrestrial invertebrates

The terrestrial insects found in marsh vegetation are in the main adult mosquitoes, midges, dragonflies, damselflies, mayflies, and alderflies, whose immature stages live submerged. On bare ground around ponds may be found toad bugs, shore bugs, springtails, tiger beetles, and sometimes ground beetles and pigmy locusts. Spiders become numerous throughout the vegetation, and the snail *Succinea* appears. In addition to these true marsh and pond species, invertebrates belonging to the forest-edge biocies may occasionally be found.

Fish

Fish are often very abundant (Table 7–3). Included among the species that occur are several bottom-feeders—suckers, bullheads, buffalo, and carp; the last, a species introduced from Europe. By feeding on the submerged vegetation and stirring up the bottom they may control the habitat and the composition of species present in the community. This condition, however, does not last indefinitely. Vegetation encroaches on the margins of ponds, and the fish are gradually eliminated because of the disappearance of suitable breeding sites. The mudminnow, bowfin, and bullhead are usually the last to disappear before the pond becomes a dry marsh (Shelford 1911).

TABLE 7-3 **Differences in species composition and number of individuals of fish present in two similar-sized Wisconsin ponds (Cahn 1929).**

Species	Pond with carp	Pond without carp
Carp	5,891	0
Shorthead redhorse	66	0
White crappie	17	0
Bigmouth buffalo	1	0
Northern redhorse	14	10
Walleye pike	4	20
Bowfin	7	340
Northern pike	3	380
Rock bass	1	940
Bluegill	2	1,220
Longnose gar	0	30
Pumpkinseed	0	610
Yellow perch	0	680
Black crappie	0	730
Largemouth bass	0	1,120
Total species	10	11
Total individuals	6,006	6,080

Amphibians and reptiles

Salamanders and frogs are basically aquatic animals, although they show varying degrees of adaptation to terrestrial life. *Siren* and *Necturus* have permanent external gills and spend all their lives in the water. Most other forms lay their eggs and pass through their earlier development in water, but the adults are air-breathing and wander over the land. Since their skins must be kept moist, they are confined to the vicinity of water, to humid climates, or to damp humus. A few species, such as *Plethodon cinereus* and *P. glutinosus,* lay their eggs in the cavities of well-rotted logs and seem largely non-dependent on standing water. The ability of salamanders and frogs to live temporarily away from water appears positively correlated with thickness, cornification, and relative impermeability of the skin. The aquatic tadpoles and larvae are scavengers or herbivorous in their food habits, the adults feed on in-

TABLE 7-4 **Populations of breeding birds in units of pairs per 40 hectares (100 acres) in marshes of northern Ohio (after Aldrich 1943).**

Bird species	Marsh	Swamp shrubs	Swamp forest
Virginia rail	22		
Least bittern	12		
Short-billed marsh wren	10		
Florida gallinule	5		
Sora	3		
Mallard	3		
Killdeer	1		
Long-billed marsh wren	78	3	
Red-winged blackbird	113	144	
Swamp sparrow	68	49	4
Song sparrow	8	49	12
Yellow warbler		80	
Traill's flycatcher		80	
Eastern kingbird		24	
American goldfinch		21	
Tree swallow		7	
Catbird		31	4
Green heron		7	1
Yellowthroat		28	13
Robin		3	4
Red-eyed vireo			9
Black-capped chickadee			9
Northern waterthrush			9
House wren			7
Ovenbird			7
Downy woodpecker			7
Eastern wood pewee			5
Tufted titmouse			4
White-breasted nuthatch			4
Blue jay			3
Rose-breasted grosbeak			2
Crow			2
Scarlet tanager			2
Yellow-shafted flicker			2
Crested flycatcher			2
Cardinal			1
Wood thrush			1
Veery			1
Hairy woodpecker			1
Black billed cuckoo			1
Red-shouldered hawk			1
Eastern bluebird			1
Brown-headed cowbird			1
Prothonotary warbler			1
Total species	11	13	30
Total individuals	323	526	121

sects, earthworms, or other animal matter that they catch on land (Noble 1931).

Reptiles are terrestrial. Desert reptiles never go to water. Painted, geographic, and snapping turtles bask in the sun on the shore or on protruding logs, but quickly plunge into the water to escape danger, to cool off, or to feed. The alligator and musk and soft-shelled turtles spend nearly all their time in water. The soft-shelled turtle is able to utilize dissolved oxygen in the water and hence has evolved special readaptation to water. Like other turtles, however, they lay their eggs on land, placing them in holes excavated in sand, loose soil, muck, or decaying stumps or logs. Water snakes give birth to living young that enter the water immediately. Water snakes feed on insects, small fish and amphibians, crayfish, or whatever other animal food they can find. The food of turtles is similar to that of snakes; some species are also scavengers. The cottonmouth moccasin is a prominent poisonous snake in southern marshes and swamps. The massasauga rattlesnake occurs in wet areas to the north.

Birds

Bird populations are high, and the pond-marsh, swamp shrub or forest-edge, and forest communities are especially clearly defined (Table 7–4). There is an abundance of nest-sites and food, but the aquatic and terrestrial species exploit different niches to avoid competition as much as possible. The aquatic species feed in all stages of the plant sere, beginning with the open water, but nest for the most part in the emergent vegetation (Beecher 1942). Herons commonly feed in shallow water but nest in tree-top colonies. Grebes, cormorants, and terns feed on fish in the open water; the herons, egrets, and bitterns get fish in water shallow enough for them to wade in; cranes and coots are omnivorous; ibis, stilts, snipe, and rails probe around in the mud for invertebrates; avocets sweep their curved bills back and forth through the water, catching aquatic insects; gallinules eat seeds, roots, and soft parts of succulent plants as well as some invertebrates; most ducks feed on submerged and floating vegetation and attached animal organisms; song birds inhabiting the marsh feed chiefly on insects captured outside the water.

Mammals

One of the most characteristic mammals of the marsh is the muskrat. A well-developed marsh may contain one of their haycock-shaped lodges on each acre (2.5 per hectare), with perhaps five animals per lodge during the autumn. The diet of the muskrat is largely the leaves and roots of marsh vegetation, although they also feed to some extent on crayfish, clams, snails, and sluggish fish. Overpopulations of two or three lodges per acre (5.0 to 7.5 per hectare) may lead to "eat-outs" or local destruction of the marsh vegetation (Dozier 1953).

The mink is probably the most common mammalian predator of the marsh; it is an enemy of the muskrat. Foxes, raccoons, and coyotes may invade the marsh when the water level is low. The otter preys on fish and crayfish of the marsh; it has now been exterminated from most of its former range.

The beaver makes its own marsh habitat by damming small streams, flooding the surrounding lowland. Here it builds its large lodge and feeds on the bark and twigs of adjacent aspen, willow, and cottonwood, and on the roots of aquatic plants. When the supply of aspen and other food is exhausted, the colony disappears, the dam decays, the water level subsides, and marsh vegetation invades. After some years the pond is converted into a beaver meadow.

In the southern Atlantic seaboard and Gulf states, the herbivorous rice rat is common to marsh vegetation. In northeastern Ohio, the meadow mouse attains populations averaging 58 per hectare (23/acre) in the marsh and persists in smaller numbers in the swamp shrub and swamp forest (Aldrich 1943). The smoky shrew averages 8 per hectare (3/acre) in the marsh. The cinereous shrew and short-tailed shrew are found in marsh vegetation and are common in the swamp-shrub stage (30 and 52 per hectare, 12 per acre and 21 per acre, respectively). All three of the insectivorous shrews are also found in the swamp forest. The white-footed mouse increases in numbers from the marsh through the swamp-shrub into the forest stages (2.5-22-32 per hectare, 1-9-13/acre). Moles, chipmunks, and squirrels also occur in small numbers where the ground is drier.

FOOD CHAINS IN PONDS

Many animals in ponds depend for food on floating phytoplankton, bacteria, and bottom detritus. Ponds, however, unlike lakes have additional producers of organic matter in the rooted pondweeds. Attached to the submerged pondweeds is a periphyton composed of bacteria, diatoms, and green and blue-green algae. This periphyton is important as food to many small crustaceans, immature insects, oligochaete worms, and snails (Frohne 1956). Pondweeds are consumed by insects, ducks, and herbivorous mammals. Filamentous algae are also more abundant in ponds than in lakes, and is a source of food to various immature insects and frog tadpoles. Creeping predators among the pondweeds and algae are leeches, dragonfly and damselfly naiads, and water mites. Small swimming predators are the dytiscid beetles, most of the hemipterans, and the swimming leeches *Erpobdella* and *Macrobdella*. At the top of the food chains, feeding on all these small animals, and often on plants as well, are the fish and other vertebrate groups (Lindeman 1941).

SEASONAL CHANGES AND TEMPORARY PONDS

Seasonal changes are greater in a pond than in a lake, a consequence of the smaller volume of water. Because of decreased rainfall, increased evaporation, and continuous seepage or drainage, ponds often become greatly diminished during the summer, or the open water may entirely disappear. As the volume of water shrinks, water temperature rises, and the oxygen content and pH decline. Animals must either adjust to these conditions of the pond or disappear altogether.

Under the winter ice, active pond life is slight because of the low oxygen and pH, but all groups increase in numbers as the temperature rises during the spring. In one small *Chara-cattail* pond near the south end of Lake Michigan, the snails *Amnicola* and *Helisoma deflectus,* the amphipod *Hyalella azteca,* the isopod *Lirceus danielsi,* the back swimmer *Plea striola,* and diving beetles Haliplidae attained maximum populations during April and May, but then declined in numbers through August, increasing again in the autumn. On the other hand, the water strider *Gerris,* mayfly naiads Ephemeridae, damselfly naiads Agrionidae, dragonfly naiads Libellulidae, and the snails *Physa* and *Helisoma parvus* had highest populations during June, July, and August (Petersen 1926). Maximum populations of Protozoa are also attained during the warm period of the year (Wang 1928).

Fish sometimes suffer from lack of oxygen in the winter when the ice cover lasts a long time. During the summer thermal stratification often forces them out of the deeper stagnant water. When photosynthesis is curtailed at night or in cloudy weather mortality may become high.

Bird nesting is ordinarily completed by the time marshes dry up in late summer. At this time ducks concentrate in the remaining deeper bodies of water, and other marsh species start their southward migration.

Periods of drought are times of stress and increased mortality for muskrats, since the lack of water interferes with their normal locomotion and predation upon them by invading terrestrial species increases. Intraspecific competition becomes intensified as animals become crowded together in the shrinking habitat. Many individuals undertake overland journeys to new areas (Errington 1939).

Many invertebrates have spores or eggs resistant to the effects of desiccation, enabled thus to pass over the period during which the pond is dried up. These include representatives of the protozoans, sponges, hydras, turbellarians, nematodes, annelids, bryozoans, rotifers, mollusks, crustaceans, and insects (Mozley

1932, Kenk 1949). It is an interesting experiment to collect top soil from a dried-out pool, place it in an aquarium with fresh water, and see what comes out of it (Dexter 1946). When water returns to the pond the hatching of plankton organisms and their growth to reproductive maturity is very rapid. The life cycle of some species appears shorter than could be readily sustained in a normal year; perhaps this is an adaptation to survive extreme years (Table 7–5). During years when the pond does not fill with water at all, eggs and cysts remain in a dormant condition; some have hatched in a year of good conditions after they had continued dormant for several poor years. Some, but not all, species of crayfish survive dry periods by burrowing down to the water table.

Among the more interesting inhabitants of temporary ponds are the phyllopods. The fairy shrimp is not found in permanent ponds, except those with a wide, shallow shore that dries out during the summer. Shrimp nauplii develop quickly from the egg, usually in January or February after the ice melts, but sometimes as early as November if the pond becomes filled with water after an autumn dry period. In the spring, adults mature in three or four weeks, egg-laying takes place forthwith, and the species may be gone by late May. The period when the pond is dry is passed through in the egg stage, and either the drying or freezing of the eggs facilitates their hatching (Weaver 1943).

Some toads, *Bufo* spp., *Microhyla olivacea,* and spadefoot frogs lay their eggs, after a warm spring rain, in temporary pools rather than permanent ponds. Development is rapid, and metamorphosis of the tadpoles may be completed in a month's time, before the pool evaporates (Bragg *et al.* 1950).

LIFE HISTORIES

On hatching from the egg, *copepods* first pass through six free-swimming *nauplius* stages by a series of molts, during which the small compact animal possesses only three pairs of appendages; then through five *copepodid* stages, when additional appendages are added; and, finally, into the adult form. Both sexes occur regularly.

Ostracod eggs also hatch into nauplii, but these already possess a shell like that of the adult. Several molts are required, however, before maturity. Some species always reproduce sexually; others are partially or always parthenogenetic.

The reproduction of the *cladocerans* is of special interest. Most of the time only females are present, and eggs develop parthenogenetically during the summer into more females. The thin-shelled eggs are held in a brood pouch on the dorsal side of the body, and the young are well grown before they are set free. There are no free-swimming larvae. After a number of generations, the number varying with the species, and as the pond begins to dry up in the summer or winter, conditions reach a point where there is a crowding of females, an accumulation of excretory products, and a decrease in available food. Parthenogenetic male as well as female eggs are then produced. The resulting males are usually smaller than the females, but, subsequent eggs are fertilized by them and a thick shell is formed around them. These ephippial eggs are produced in smaller numbers and are very resistant to drying and freezing. When the pond again becomes filled with water, the ephippial eggs develop into reproducing females to start the cycle over again (Pennak 1953).

The life-cycle of the *rotifers* bears some resemblance to that of cladocerans. A few species are viviparous, but in most forms development of the egg takes place outside the body and is direct into the adult form. Two kinds of females are not distinguishable by external characters. One kind, amictic, produces large diploid eggs that are never fertilized and only develop parthenogenetically into more females. The other kind of female, mictic, occurs only at critical times of the year and produces smaller haploid eggs. If not fertilized, these small eggs develop into males; if fertilized, they form the thick-walled winter eggs which, under subsequent favorable conditions, develop into females. The males are usually small compared with the females; they lack an alimentary tract, and consequently live only two or three days. Females live one to three weeks or longer. The production of males appears to be periodic and is often correlated with a change in type or amount of food, or degree of crowding. Males have never been seen, and may not occur in, some groups (Pennak 1953).

The amphipod *Hyalella azteca* breeds only during the warmer months of the year. The male carries the female on his back for 1 to 7 days before copulation occurs. Oviposition follows copulation by 12 to 24 hours. The incubation period is 21 days, and the female may carry the young another 1 to 3 days in her brood pouch. A period of 24 to 36 days elapses between successive broods, and each brood is larger than the last. The females may live into a second summer and reproduce again. The young on hatching in the spring have all the adult appendages and can reproduce later in the summer (Gaylor 1921).

In the spring, aquatic Hemiptera commonly glue their eggs to submerged vegetation. Some species insert their eggs into incisions made in leaves or stems. The young emerge directly into the water and resemble the adults except that they do not acquire wings until after several molts. In the Sialidae of the Megaloptera, eggs are deposited in masses on leaves

TABLE 7-5 Monthly changes in the ostracod fauna of temporary ponds in central Illinois. The ponds dried up in mid-July (after Hoff 1943).

Ostracod species	March 9	March 17-20	April 1	April 15	May 4	May 18	June 9	June 22	July 10
Cypricercus reticulatus	+	+	+	+	+	+	+		
Cypria turneri		+	-	-	+	+	+	+	+
Candona simpsoni		+	+	-	+	+	+	+	
Candona fossulensis			+						
Candona distincta			+	-	+				
Candona indigena				+					
Candona biangulata				+					
Cypria maculata					+	+			
Cypria opthalmica					+	+	+		
Cypridopsis vidua					+	+	+	+	+
Candona suburbana						+	+		
Cypria obesa							+		

or bare ground near water; on hatching, the larvae proceed into the water. Here they stay for a full year, after which they leave the water and pupate for several months in a hollow that they scoop out of moist earth. The adult does not live over winter. Dragonflies may fasten their eggs to plants below or above the water surface, puncture leaves or stems for egg insertion, oviposit eggs in the bottom, or may scatter them through the water and over the bottom. The naiads hatch out in about three weeks and are of varied forms and sizes. Dragonfly naiads may be divided into three groups on the basis of their habits: the climbers that crawl through the vegetation; the sprawlers that lie half buried in the mud with legs extended and backs covered with silt; and the burrowers. They all undergo several molts under water, some forms living 11 months in this stage. For their last molt they crawl up the stem of some plant or onto a rock on the shore, molt, and emerge as adults. They live for a few weeks only. Adult dragonflies commonly feed on adult mosquitoes, and the naiads feed to some extent on the mosquito larvae (Needham and Westfall 1955).

Aquatic beetles commonly attach their eggs to water plants or bore holes into plant tissues to hold them. Some hydrophilid beetles make floating silk cocoons containing many eggs, anchoring these cocoons to surface plants. Beetle larvae live only a few weeks before they leave the water and pupate in characteristic mud cells that they build for themselves. Pupation varies from a few weeks to several months, depending on the temperature, before emergence of the adult occurs. The adults are the chief survivors of the winter but sometimes eggs or larvae live through it, too (Miall 1934, Balduf 1935, Rice 1954).

Mosquitoes reproduce abundantly in marshes, ponds, or even in small pools, tree holes, or other water-holding depressions. Some species of mosquitoes lay hard-shelled chitinous-covered eggs on the ground which are capable of withstanding freezing, extreme heat, and drought but hatch very quickly after being covered with warm water. In water, eggs may be laid singly or in rafts. The adult female *Culex vexans* stands at the margin of the pool or on some floating object and deposits as many as 300 eggs. The individual eggs are cigar-shaped and are placed vertically to form a floating raft. They fit together so snugly that the surface film of water does not penetrate between the eggs, and the surface of the raft is dry. The larvae hatch in 12 to 28 hours and hang head down from the surface film. Vibrating vibrissae continually sweep food particles into the larval mouth. The respiratory tube at the posterior end of the body penetrates the surface film and also prevents the body from sinking. At other times the larvae may suspend themselves from the surface film, dorsal side uppermost, and feed on floating materials (Renn 1941). After 3 or 4 molts (5 to 8 days), the larva changes into a quite differently-shaped pupa, which hangs from the surface film by two respiratory tubes proceeding from the thorax. The winged adult may emerge in 2 days. Some species may have seven broods per year.

Sexual and other behavior of mosquitoes varies considerably among species (Horsfall 1955). Ordinarily only the female mosquito bites, this to obtain the blood nourishment necessary for egg-laying. The male feeds only on plant juices. Studies made on marked individuals of *Aedes vexans* showed that 73 per cent of the individuals confined their activities to within a radius of 5 miles (8 km), but that 19 per cent traveled 5 to 10 miles (8–16 km) and some even to 16 miles (26 km) away from the point of marking (Clarke 1937). Other species, however, appear not to have such wide ranges.

The pulmonate snail *Physa gyrina* lays its eggs in the spring when water temperatures reach 10°–

12°C; thereafter the adult population dies. Snails born in the spring may reach sexual maturity by autumn but oviposition is normally delayed until spring because of cold weather. The life span is usually 12–13 months, but may be prolonged if development is interrupted by aestivation resulting from the drying up of the pond during the summer (DeWitt 1955).

Many warm-water pond fish, such as the black bass and sunfish (Breder 1936), spawn in nests or redds prepared in shallow water by removing all debris and vegetation over circular areas of one-half to one meter diameter. There is some preference for gravel and sand bottoms when they are available. The male remains to guard the several thousand eggs during the few days required for their hatching, and the fanning movements of his tail and fins doubtless help to aerate them. He may also guard the young until they can take care of themselves. Both bullhead parents guard the egg masses and keep them continually agitated for aeration; they may even suck the eggs into their mouths and expel them forcibly. The adults keep the young in compact groups by swimming about them. The European carp may spawn promiscuously a half-million or a million eggs during the early spring. The eggs settle in the water and adhere to the roots and stems of vegetation there. The eggs are not guarded, and the young are left to care for themselves.

Salamanders commonly hibernate in humus, under logs, or in other nooks or crevices on land. They usually emerge during the first warm rains of early spring and proceed to the nearest pond, there to lay their eggs. The males deposit their spermatophores on submerged leaves or twigs from whence the female picks them up for fertilizing the eggs. The eggs are laid in jelly-like masses and require several days to hatch if the temperature is low. The eggs of *Ambystoma maculatum* (Gilbert 1944) and *A. texanum* (Burger 1950) hatch more successfully and at a faster rate if they contain unicellular green algae within the capsule. These algae apparently create a symbiotic relationship for oxygen and carbon dioxide. Larval salamanders possess gills, but in all but a few forms these are later absorbed and the adult returns to land. *A. tigrinum* sometimes breeds while still retaining the larval gills, and never leaving the water.

Frogs commonly hibernate in the mud at the bottom of ponds, although some forms, including toads, hibernate in the soil on land. In the spring the males go to small bodies of water where their loud choruses attract the females for mating purposes. The jelly-like masses or strings of eggs require only a few days to hatch, but the tadpole stage lasts longer. Metamorphosis in toads that lay their eggs in temporary ponds takes place rapidly, but in other species, such as the bullfrog, adults do not occur until two years after the eggs are laid (Wright and Wright 1933).

Practically all species of birds characteristic of northern latitudes that nest in the marsh are migratory, as the freezing of the water and drying of the vegetation eliminate their food supply. Nests are located in a variety of situations: on floating masses of plant debris built above the water level, typical of grebes, terns, gulls, black-necked stilt, and ducks; in plant material, placed in tufts of vegetation or formed into platforms, or nests attached to cattails and other emergent plants well above the water level, typical of cranes, gallinules, rails, avocets, snipes, bitterns, ibises, marsh wrens, swamp sparrows, and blackbirds; in swamp shrubs, typical of flycatchers and yellow warblers; in holes in trees, typical of tree swallow, prothonotary warbler, and wood duck; in the tops of trees in adjacent forests, typical of herons, cormorants, egrets, and wood ibis.

The muskrat is one of the most conspicuous and important mammals of both salt and fresh-water marshes as well as river banks. Along rivers, the animal lives in burrows that it excavates well back in the bank. In marshes, it constructs a dome-shaped lodge, as high as one meter, by heaping up freshly-cut marsh vegetation. The lodge is hollow and dry within, the floor is placed well above the water level. The lodge has several underwater entrances and exits. In it the animal cares for its young and finds protection from enemies and weather in both winter and summer. In addition to lodges, the muskrat constructs shelters, where it may feed out of sight of enemies, and breathing holes, called push-ups, through the winter ice.

BIOMASS AND PRODUCTIVITY

In a pond in Iowa, the average summer population of bottom invertebrates in water 0.5 m deep averaged 3819 individuals, 1334 mg/m²; in water 1.5 m deep, 1540 individuals, 1370 mg/m². In the shallow water the most important components of the biomass were, in descending order: snails (shells removed), midge fly larvae, annelid worms, and the amphipod *Hyalella*. In the deeper water the biomass was mostly midge fly larvae (Tebo 1955). Productivity of the midge fly *Tanytarsus,* one generation per year, averaged 7.5 g/m² in a Michigan lake (Anderson and Hooper 1956). By mooring a floating cage over open water throughout the season in an English pond, a total of 8988 midge flies and other insects per square meter were caught as they emerged from the bottom mud. In shallow water, where the vegetation was thicker, a total of 5979 individuals per square meter were captured, a total which included fewer midge flies and more dragonflies and caddisflies (Macan and Worthington 1951).

Average standing crops of fish in backwaters and oxbows may be almost 500 lbs/acre (57 mg/m²), in midwestern North American reservoirs almost 400 lbs/acre (45 mg/m^2), in other reservoirs and ponds 200–300 lbs/acre (23–24 mg/m^2), in warm-water lakes 125–150 lbs/acre (14–17 mg/m^2), and in trout lakes less than 50 lb/acre (5.7 mg/m^2). There is no tendency for the standing crop to decrease with increase in size of the body of water (Carlander 1955). Biomass varies with the fertility of the pond and the food supply. Ponds and lakes receiving water that drains over fertile soil will have more basic food substances than drainage from poor soils brings. The presence of certain species depends also on suitable breeding sites (Shelford 1911).

Biomass is further affected by the food habits of the fish species present. In fertile ponds in Alabama containing species feeding largely on phytoplankton, the median biomass of fish was 925 lbs/acre (105 mg/m^2); in ponds with fish feeding largely on insects, 550 lbs/acre (62 mg/m^2); and in ponds with fish feeding largely on other fish, 175 lb/acre (20 mg/m^2) (Swingle and Smith 1941). It was estimated that about five pounds of food (2.26 kg) are required to produce one pound of fish (0.45 kg). The same ratio has been found characteristic of ponds in Michigan, (Hayne and Ball 1956). Hence, the biomass of animal life decreases with each additional link in the food chain.

In two small Michigan ponds where it was possible to tabulate the entire fish population, the benthic production (at least, that portion used as fish food) during one growing season was calculated at about 17 times the standing crop when fish were present. This equalled 811 lbs/acre (92.0 g/m^2). The productivity of the fish during the same period was 181 lbs/acre (20.5 g/m^2), giving a ratio of 4.5:1 (Hayne and Ball 1956).

When the standing crop of fish remains the same year after year, its productivity is indicated by the number or biomass harvested. In northern Wisconsin the maximum annual yield of desirable food fishes is about 21 per cent of the mean standing crop; in central Illinois it is about 50 per cent; in southern Louisiana, 118 per cent (Thompson 1941).

The productivity of ponds and marshes for vertebrates other than fish has been measured in a few localities. In northwest Iowa, redhead ducks annually produce about 1.4 young per hectare (56/100acre); ruddy ducks, 0.6 young (24/100acre); (Low 1941, 1945). Nine species of ducks in the Bear River marshes of Utah average 16 young per hectare (640/100acre) (Williams and Marshall 1938). In Idaho, nine species of ducks produce over 22 young per hectare (880/100acre) and Canada geese about 0.1 young (Steel *et al.* 1956, 1957). On a well-developed marsh, it is generally possible to remove two-thirds of the muskrats each year and still reserve sufficient brood stock for a sustained annual crop. This is about 2.5 muskrats per lodge (Dozier 1953).

POND AND MARSH MANAGEMENT

The maintenance and control, throughout the year, of the water level of ponds and marshes is important for increased productivity. This may often be accomplished by damming the outlet. It is also important to retard the plant succession which, if left alone, will eventually bring about the total disappearance of the habitat. This may be done by cutting, burning, use of chemical sprays, flooding, and ditching. Small ponds, called pot holes, with a good margin of marsh vegetation, or a marsh interspersed with numerous small areas of open water, give the highest yield of waterfowl and other birds, and muskrats. The abundance of waterfowl is often proportional to the extent of the pond margin rather than the acreage of emergent vegetation. In the Louisiana coastal marshes, the highest sustained yield of muskrats (14.5/hectare/yr or 580/100acre/yr) is in areas with *Scirpus americanus* (O'Neil 1949).

Artificial ponds are easily constructed (Anderson 1950, Musser 1948) and are an asset to farms as a source of food and recreation as well as water for domestic animals. Such ponds are commonly stocked with bluegill and largemouth bass, although other combinations may be used. High rates of reproduction bring the fish population up to full carrying capacity within one or two years. If the pond were stocked with an herbivorous fish only, such as bluegills, normal reproduction would soon become so excessive that a dense population of stunted fish would be present. Using a prey-predator combination in proper proportions, the predator (largemouth bass, for instance) will consume the excessive offspring of the prey species, and the average size of the remaining fish will be increased. The development of aquatic vegetation in these farm ponds is discouraged since it allows too many prey individuals to escape the predator. The fertility of poor ponds can be increased by applying fertilizer encouraging the abundant growth of bacteria, plankton, and bottom organisms providing fish food (Howell 1941). The control of turbidity is also important. Clear ponds with less than 25 ppm turbidity may have 12.8 times more plankton and 5.5 times more fish than ponds with a turbidity exceeding 100 ppm (Buck 1956).

Repeated stocking of ponds with artificially propagated fish is undesirable as there is more trouble in controlling overpopulation than underpopulation. The productivity of a pond is determined not by the number of fish introduced but by available food supply. The available food supply is divided between the individuals present. One study showed that 6500 bluegills per acre (16,250 per hectare) averaged 25.5 grams each, 3200 per acre (8000 per hectare) averaged 51.0 grams each, and 1300 per acre (3250 per hectare) averaged 104.9 grams each (Swingle and

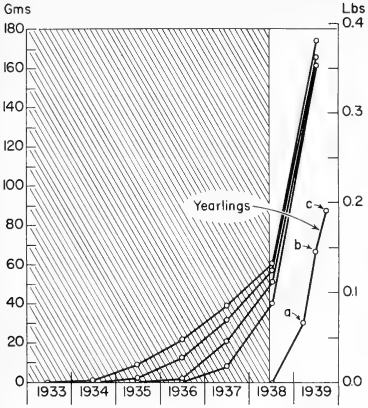


FIG. 7-4 **Increase in weight of bluegills upon removal from an overpopulated pond to a pond of lower fish populations (from Bennett, Thompson, and Parr 1940). The cross-hatched portion represents the circumstance of overpopulation; a = autumn, b = summer, c = spring.**

Smith 1942). When the available food supply must be apportioned to a relatively large population, growth of individuals is retarded, but with small populations there is more food available per individual, and growth is surprisingly rapid (Fig. 7–4). In Europe, fish, chiefly carp, are raised for food in small artificial ponds and are handled in much the same manner as other domestic animals (Snieszko 1941). Problems involved in stocking and maintaining suitable fish populations in small artificial ponds in various parts of North America are summarized in the *Journal of Wildlife Management* (16, 1952, 233–288).

A problem involved in the management of ponds and marshes is the control of mosquitoes. Oiling the water surface will kill mosquitoes, but also renders the habitat unsuitable for other organisms. Mosquito larvae and pupae are good food for such minnows as *Fundulus* and *Gambusia* that regularly feed at the surface. Stocking of these fish species will often keep mosquitoes under control. Elimination of aquatic vegetation in the shallow marginal areas will do away with hiding places and leave the larvae more exposed to fish predators.

Because ponds and marshes produce great numbers of fish, muskrats, and waterfowl, and are a source of recreation for hunting, fishing, boating, and swimming as well, the actual economic value of maintaining such areas is often greater than it would be if they were drained and planted to crops (Bellrose and Rollings 1949). Proper management of them is therefore a challenge to applied ecologists.

BOGS

Characteristics

Bogs or moors typically develop in the hydroseres of cold northern regions; while marshes and swamps, which are markedly different than bogs (Dansereau and Segadas-Vianna 1952), are characteristically southern in their location. Bogs commonly develop into a coniferous forest climax; swamps succeed to deciduous forest or other southern climax types. Several thousand years ago, when glacial climates gripped the northern states, extensive bogs developed and have persisted as relic communities in spite of the warming of the climate. These bogs are slowly being replaced by pond-marsh species at equivalent seral stages by cliseral succession (Table 7–6).

Bogs occurring in the Great Lakes region are ordinarily small in area and have little or no drainage. There may be oxygen present in the open water of the larger bogs, but it is characteristically in very low concentration, at most, in small bogs or in the marginal zones. Bog water has a distinct brown color; a low nitrogen content; a low temperature beneath the surface; a low pH, at least in the marginal vegetated zones; and a low dissolved salt content.

A false bottom is characteristic of bogs. It consists of finely divided plant material of a light brown color, held suspended in the water at varying depths below the surface. This false bottom may extend downward several meters before a true solid bottom is reached. The material disperses on slight disturbance and may render all the open water turbid. Ordinarily, the surface waters are quiet and clear. Dead vegetation does not completely decompose; as it accumulates, it becomes compressed to form peat.

The plant bog sere

In the early stages of development of the bog, organic detritus may accumulate mostly in the deepest portions (Potzger 1956). As time goes on, however, a definite concentric-circle zonation of vegetation is established around the margin. As peat accumulates, each zone encroaches on the next inner; the inmost shrinks until all open water disappears. The area becomes finally covered with climax forest (Dachnowski 1912).

TABLE 7-6 **Relation of biotic succession to climatic succession in ponds and bogs. Vertical succession from open water to climax forest is taking place in both the pond and the bog, but as the climate gets warmer, there is simultaneously a horizontal succession from the various stages in the bog sere to equivalent stages in the pond sere.**

		Clisere	
	Stage	Cold climate Bog	Warm climate Pond
Biosere	Floating vegetation	Pond and water lilies, or absent	Pond and water lilies
	Emergent vegetation	Sedge mat	Marsh: cattail, reeds, bulrushes
	Low shrubs or heath	Leatherleaf, labrador tea, bog rosemary	Absent
	High shrubs	Mountain holly, chokeberry	Buttonbush, alders
	Swamp or bog forest	Tamarack, black spruce	Soft maple, elm, ash
	Climax forest	Hemlock, pine, white cedar or spruce, fir	Oak, hickory or beech, sugar maple

In some bogs (Gates 1942, Dansereau and Segadas-Vianna 1952) the first plant stage may be composed of floating vegetation (*Nuphar, Nymphaea, Potamogeton, Sparganium*), but floating vegetation is often absent and the first stage is a *sedge-mat* composed of sedges, cottongrass, and buckbean. The rhizomes of the sedges grow out into the water and become so interlaced that they form a floating mat. At the water edge the mat may be very thin, but towards shore it may become as much as a meter thick. Since the mat floats on open water it jars easily, hence the name quaking bog—one must watch his step that he does not break through. *Sphagnum* moss is not essential for the formation of a mat, but it invades the mat quickly and helps bind it together. *Sphagnum* persists into the shrub and bog-forest stages following. Interesting insectivorous species such as the pitcher plant and sundew are common, as are various members of the orchid family.

The next plant stage is dominated by *low shrubs*, which encroach on the floating mat. The leatherleaf, bog rosemary, laurels, labrador tea, sweet gale, and cranberries are important species.

A *high shrub* stage commonly follows the low shrubs at such time as the mat becomes thicker or grounded. Common shrub species are holly, willow, chokeberry, alders, and dwarf birch.

The first tree of the *bog forest* to invade the shrubs is commonly the tamarack, but this species is now less common than formerly because of fire, logging, and the depredations of the sawfly larvae *Lygaeonematus erichsonii.* Black spruce may either invade the shrubs directly or follow the tamarack. Later, the northern white-cedar may become dominant and persist for a very long time, but the ultimate fate of the bog, upon addition of upland soil or lowering of the water table, is to be covered with the *climax* forest of the region.

Animal life

In bogs that have a large body of open water, or an inflow of water entraining oxygen, and in which the pH is not extreme, invertebrate life comparable to that found in ponds and marshes occurs. True bogs, however, have little oxygen and a low pH, and many pond species do not appear. Mollusks are characteristically absent; sphaeriids may persist but their shells become very thin. Bottom organisms in general are poorly represented because of the tenuous physical nature of the substratum.

Desmids predominate among the phytoplankton, although dinoflagellates, Chlorophyceae, and Myxophyceae are common. Rotifers and a variety of Protozoa are the principal zooplankters (Graaf 1957).

The chief fish found in acid waters in Michigan are the brown bullhead, northern pike, bluegill, yellow perch, and mudminnow (Jewell and Brown 1929). The mudminnow may be found in waters almost devoid of oxygen since it is one of the few species that can live indefinitely by gulping air at the surface.

Amphibians and reptiles are not characteristic of bogs, although the leopard frog is sometimes numerous on the sedge mat of bogs in Minnesota (Marshall and Buell 1955). Marsh birds are few in species and in no bogs do populations approach the magnitudes found in southern marshes. The muskrat and beaver persist into northern Canada.

In general, the productivity and economic value of bogs is very low compared with ponds and marshes. Liming experiments, calculated to improve productivity, are being made. Calcium combines with the humic colloids which then flocculate and fall to the bottom. This clears the water, light penetrates deeper, pH is raised, and greater algal, zooplankton, and fish growth is induced (Hasler *et al.* 1951). Peat is a special bogs product of importance in northern

FIG. 7-5 **Plant sere at Bryant's Bog, Michigan, from open water through a narrow broken mat stage of sedge, a low shrub stage of leatherleaf, a high shrub stage (in middle rear) of holly, to tamarack and black spruce (courtesy R.E. Rundus).**

Europe. It is cut out in blocks, dried, and used as fuel.

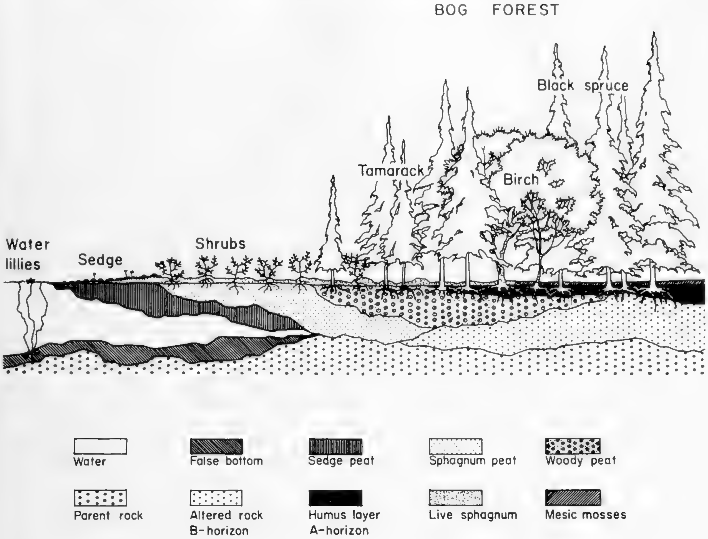
It is doubtful if the aquatic fauna of bogs is sufficiently distinct or unique to constitute more than a facies of the pond-marsh biocies. It is succeeded, however, by a distinct *shrub biocies* that differs from the deciduous forest-edge community. The shrub biocies is replaced by *coniferous forest biociations.*

SUMMARY

Ponds differ from lakes in that they are generally small and shallow, and, when mature, have rooted vegetation over most of the bottom. Bogs are limited to northern regions, contain a northern type of vegetation, and are generally acid and deficient in oxygen. As the climate of northern regions slowly warms, stages in the bog plant sere are replaced by corresponding stages in the pond plant sere. The pond sere consists of six or more plant stages but only three animal stages: pond-marsh biocies, deciduous forest-edge biocies, and deciduous forest biociation. These animal communities correspond with the *types of vegetation* in the plant sere, but not with the plant communities identified by *taxonomic composition* of the plant dominants. The animal community in bogs is an impoverished facies of the pond-marsh biocies.

The pond-marsh biocies contains plankton, ben-

FIG. 7-6 **Profile of a bog plant sere (from Dansereau and Segadas-Vianna 1952).**



thos, and nekton, as do lakes; in addition, neuston is present. Species that constitute these life-forms are mostly different from those in lakes. In ponds pulmonate snails replace the gilled snails of lakes, and clams are of lesser importance. Air-breathing adult beetles and bugs, mostly absent from the lake biocies, are often abundant. Adult stages of aquatic insects and terrestrial forms occur in the surrounding marsh. Fish spend most of their lives in the ponds, but go into the marshes to reproduce. Amphibians, reptiles, birds, and mammals are usually numerous.

Food-chains in ponds and marshes are based in part on detritus, bacteria, and phytoplankton, true also of lakes; and, in part, on rooted plants, the periphyton that covers them as well as other objects in the water, and filamentous algae. Biomass and productivity are usually greater in ponds than in lakes. Ponds, however, may become stagnant during dry periods, especially in late summer, with great adverse affect upon their carrying capacity. Pond and marsh management for high economic yield of fish, waterfowl, and muskrats requires control of the water level and control over plant succession; an incidental problem is mosquito control. The unique adaptations and behavioral adjustments of animals to meet the critical periods of summer stagnation and winter freezing, characteristic of ponds, are most interesting. Ponds and marshes are available to all ecologists for the study of the life-cycles and adjustments of animals in the pond-marsh biocies.

8

Rock, Sand, and Clay

The origin of life was undoubtedly in the sea. Physiological adjustments were necessary before organisms could occupy fresh water. Although some organisms may have become air-breathers and invaded land habitats directly from the sea, most evolution of terrestrial forms has doubtless come from fresh water. Relatively few major groups of animals have been successful in this invasion of land, the most notable being oligochaete worms; gastropod mollusks; many arthropods, especially the insects and spiders; reptiles; birds; and mammals.

ADJUSTMENTS TO THE TERRESTRIAL HABITAT

Living on land presents many problems. Our present concern is to analyze the ways in which animals have met these problems and to trace the succession of communities in the extreme terrestrial habitats of rock, sand, and clay.

Gravity

In water, organisms counteract gravity by means of various flotation and swimming mechanisms. Fluid buoyancy permits water-dwellers to attain huge size; consider the whale. A land animal, on the other hand, must support its entire weight. Some terrestrial animals gain a modicum of support by burrowing into the soil; others drag their bodies over the ground surface. But the supportive advantage they thus gain is costly in other directions, for they are slow moving and relatively helpless before predators. The animals best adapted to terrestrial life have evolved appendages in the form of legs or wings that not only raise the body above the ground but are also the means of more or less rapid locomotion and adroit movements over the surface or through the air. Terrestrial adaptation has involved the development of a tough body covering to hold fluids and internal organs in place; a skeletal framework to give permanent shape to the body and, as a system of levers, to furnish means of locomotion; and powerful muscles to lift and move the heavy body. Gravity thus limits the mass of land animals; dinosaurs, mastodons, and elephants approach the maximum practicable size.

Moisture

In sharp contrast to aquatic forms, terrestrial animals are not constantly enveloped with a continuous watery medium, with the limited exceptions of protozoans, nematodes, and other small organisms living in moist soil.

Land animals, lacking constant contact with the water medium, are faced with the problems of obtaining water and preventing excessive water losses from the body.

Water becomes available to animals in varying amounts in the forms of rain, snow, hail, frost, and fog. Whatever the form it arrives in, the significant things are the amount of free, liquid water added to the substratum, accessible to plants and animals, and the humidity of the air. Considerable amounts of moisture are lost to organisms as run-off water flowing into streams, by evaporation back into the air, and as water bound in snow and ice.

Evaporation of water from the earth's surface or from the bodies of organisms increases as temperature rises, air movement (wind) accelerates, and the amount of moisture already in the air decreases. When measured as grains per cubic foot or as millimeters mercury pressure, the actual amount of moisture vapor in the air is known as *absolute humidity.* This measurement is of less ecological importance than is *relative humidity,* the ratio of amount of water vapor actually in it to the quantity required to saturate the air at existing temperature and barometric pressure. Relative humidity is easily determined by means of sling or cog psychrometers, and may be continuously recorded with temperature by hygrothermographs.

The evaporation rate of water is more closely related to *saturation deficit* than it is to relative humidity. Saturation deficit is a quantity which cannot be directly measured, it must be calculated. It is that additional amount of moisture required to saturate air under prevailing temperature, relative humidity, and barometric pressure conditions, commonly expressed as grains per cubic foot or as millimeters of mercury pressure.

The most exact and desirable measurement of water evaporation is the *vapor pressure gradient* obtaining between the organism and the surrounding air. The gradient is positive if water molecules leave the organism at a rate faster than the rate at which the organism is absorbing them from the air, and negative if the reverse is true (Table 8–1). The determination of gradient magnitude involves the measurements of body temperature of the organism and air, permeability of body membranes, and rate of air movement over the body surface (Thornthwaite 1940).

Water is obtained by a land animal by various devices. There may be some direct *absorption* through body surfaces such as occurs in the toad in moist soil and in some beetle larvae in moist air; this device is important in only a few species. Large mammals frequently travel several miles each day to water holes to imbibe *drinking* water. Many, but not all, birds require drinking water; some species, for instances quail and partridge, get it as morning dew on vegetation. Butterflies may frequently be observed drinking water from small pools. An important source of water is the *free water in food,* particularly in succulent vegetation and in the blood and body fluids of animals. Desert animals depend almost entirely for water on that contained in their food and on *metabolic water,* liberated when fats and carbohydrates, and to a lesser extent, proteins, are oxidized in their bodies.

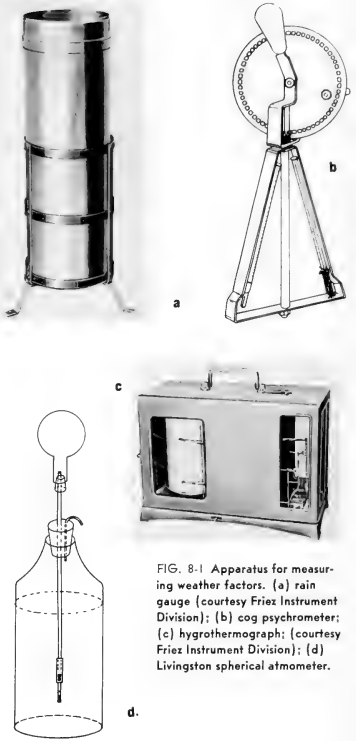


FIG. 8-1 **Apparatus for measuring weather factors. (a) rain gauge (courtesy Friez Instrument Division); (b) cog psychrometer; (c) hygrothermograph; (courtesy Friez Instrument Division); (d) Livingston spherical atmometer.**

Water is lost from the body through the skin and lungs as insensible moisture and perspiration. Rapid and largely uncontrolled loss of moisture through the skin of amphibians, snails, annelids, and insect larvae is a limiting factor confining these animals to moist

TABLE 8-1 Evaporation and condensation on a free water surface in relation to temperature, relative humidity, saturation deficit, and vapor pressure gradient (after Thornthwaite 1940).

Factor	Water evaporates	Water condenses
Water temperature	16°C	16°C
Air temperature	16°C	27°C
Relative humidity	70%	70%
Vapor pressure of saturated air	133 mm Hg	263 mm Hg
Vapor pressure of air 70% saturated	93 mm Hg	184 mm Hg
Saturation deficit	40 mm Hg	79 mm Hg
Vapor pressure of the water	133 mm Hg	133 mm Hg
Vapor pressure gradient	+40 mm Hg	-51 mm Hg

habitats or to activity only in times of high humidity. Adult insects and other arthropods, reptiles, birds, and mammals have evolved body surfaces of chitin and waxes, scales, or cornification of the surface layers of the skin that largely prevent uncontrolled loss of moisture. Moisture loss through the respiratory surfaces in these forms remains considerable, however. Water is also lost with the *feces,* although in some species much water is reabsorbed by the large intestine before the feces are ejected. The amount of water removed from the body by excretory organs, particularly the *kidneys,* varies directly with the amount of water intake and inversely with the amount lost through other devices. The kidneys are critical to maintenance of proper concentration of salts in the blood and body fluids. It is important that water intake balance water loss. Organisms are very sensitive to disturbances in body water balance, and this factor is very significant in determining the type of niche which a species comes to occupy.

In order that animals could exist in terrestrial habitats, they had to acquire the ability to carry on reproductive activities in the absence of water. The chief reproductive adaptations involve the following (Pearse 1950) : internal fertilization; a shell covering the egg to conserve moisture and salts; food provision to the embryo and young, by yolk in the egg cell, placenta in the uterus of the mother, or direct feeding by the adults; reduction in number of young with more efficient parental care; reduction or elimination of free-swimming larval stages; greater segregation of species into different niches to avoid interspecific disturbances.

Temperature

Aquatic animals are not ordinarily subjected to temperatures below freezing and are in a relatively stable temperature environment, but terrestrial species are exposed to highly variable temperatures that may reach extremes of about −68°C and +55°C. No single species is required to withstand such a wide range of temperatures, however. Optimum and tolerance limits vary from one species to another, inasmuch as each inherits a specific degree of acclimatization.

No aquatic species has evolved control over its body temperature. Aquatic warm-blooded mammals and birds are derived from terrestrial forms. An ability to maintain a constant body temperature has survival value in terrestrial habitats, however, and consequently physiological mechanisms for *homoiothermism* developed independently in birds and mammals. All other land organisms are *poikilothermal;* that is, they have no *physiological mechanism* for maintaining a constant body temperature. Some poikilotherms, such as bees, have developed *special behavior patterns,* that enable them to maintain fairly constant conditions in the hive by cooperative efforts; some lizards, snakes, and turtles are able to exert some control over their body temperatures by moving into and out of sunlit areas.

Rates of activity, food consumption, metabolism, growth, and other physiological functions increase, to a certain limit, with rise of body temperature. Homoiotherms maintain a continuous high rate of functioning because of their constant high body temperatures, but the rate at which poikilotherms function varies with the temperature of their habitats.

Latitudinal distribution of both poikilotherms and homoiotherms is often limited northward and southward by the extremes of temperature that they can tolerate. The rate of energy exchange in poikilotherms is so directly dependent on the amount of heat in the habitat that the total growth and reproduction of a species may be determined by the extent to which it can accumulate developmental heat units during the year (Shelford 1929: Chap. 7) ; the principle is similar to the principle of heat budgets in lakes. The closer a region lies towards either Pole, the shorter the growth season is, and distribution may be limited not by extreme low temperatures as such, but by accumulation of heat energy insufficient to permit completion of life cycles.

The relation of energy balance in homoiotherms to air temperature is even more complicated (Kendeigh 1949, Seibert 1949). In cold regions an animal may require all the energy its food provides it simply to maintain its own existence, no surplus available to meet the high demands of reproduction. Under such conditions, a species cannot become permanently established in a region. A warm-blooded animal requires a range of temperature that is comfortable and in which it can ingest and metabolize food at a rate sufficient to maintain normal body temperature, sustain physical existence, and carry on reproductive activities, too. We can thus speak of *existence energy* and *productive energy,* concepts essential to understanding the relation of an organism to the temperature of its environment.

All organisms outside the tropics must adjust to meet the critical winter season. In those species active throughout the year, there is an increase in resistance to cold, brought about, in part, by dehydration of body tissues (Payne 1927), or by increase in density of plumage (Kendeigh 1949) or fur (Sealander 1951). Those species incapable of maintaining activity *in situ* over winter either migrate to more favorable regions or hibernate, or the adults die. Many invertebrates survive the winter in resistant egg or larval stages.

Oxygen

Dry air at 760 mm Hg pressure contains approximately 21 per cent oxygen, 0.03 per cent carbon dioxide, 78 per cent nitrogen, and traces of other gases. Oxygen is thus much more abundant, constant, and available at all times in air than it is in water. Oxygen availability seldom becomes a critical factor for land animals, with the occasional exception of forms that live in the soil or invade high altitudes.

Although terrestrial organisms have evolved simple moist chambers, branched tracheal systems, or complicated lungs to replace the gills found in many aquatic forms, the fundamental requirement of moist membranes for the exchange of oxygen and carbon dioxide between body fluids, tissues, and the surrounding medium remains the same. The skin still serves this purpose in some terrestrial forms—annelids and some amphibians—but in most forms the moist membranes are within the body. Internal placement decreases the loss of water through evaporation. The evolution of an ability to take oxygen directly out of the air apparently preceded the actual invasion of land, and may have been induced in the pond and marsh habitat when oxygen dissolved in the water became reduced or absent during summer stagnant periods (Pearse 1950). The evolution of internal air-breathing organs was probably concurrent with the evolution of mechanisms to prevent excessive water loss from the exposed surfaces of the body.

Solar radiation

Solar radiation takes the form of an endless procession of waves. The length of a light wave from crest to crest, or trough to trough, determines its character in respect to energy and color; the height of the wave determines its intensity. Wavelength is commonly expressed in millimicrons (lmμ = 0.000001 mm = 10 Ångstrom units, Å). All wavelengths have a velocity of 299,340 kilometers per second. The solar spectrum varies from 51 mμ, which is the shortest ultraviolet radiation, to 5300 mμ, which is the longest infrared radiation. The spectrum visible to man is between 390 mμ and 810 mμ. Considerable ultraviolet is absorbed by the atmosphere, and the ultraviolet wavelengths reaching the earth's surface are mostly between 292 mμ and 390 mμ. Color perception by man is as follows: violet, 390–422 mμ; blue, 422–492 mμ; green, 492–535 mμ; yellow, 535–586 mμ; orange, 586–647 mμ; and red, 647–810 mμ. The longer waves are rich in heat energy; the shorter, in actinic energy.

Solar radiation may be measured with a pyrheliometer, by which readings are given in terms of heat energy (g-cal/cm^2/sec). Results are not accurate for the shorter wavelengths. Photoelectric cells accurately measure intensities in the shorter wavelengths; readings are given in foot-candles. The Macbeth illuminometer measures total sunlight in foot-candles by visual comparison of observed intensity with a standardized and calibrated light source set within the instrument; accuracy is limited by sensitivity of the human eye. With any photometric instrument, the measurement of intensity of any portion of the spectrum requires the use of calibrated color filters that screen out everything but the desired wavelengths.

Different wavelengths have different effects on organisms. Green light is reflected by plants; little is used in photosynthesis. Some early experiments on tadpoles, fish, snails, and other forms (Davenport 1908) indicate that there is an increasing growth rate in different wavelengths, in the following order: green, red, white, yellow, blue, violet. The physiological basis of this phenomenon is not known. An excess of infrared may produce overheating of the animal. Ultraviolet in large concentrations is harmful to most animals, but in lower intensities is beneficial to elaboration of vitamin D. Evidence indicates that ultraviolet combined with rainfall is important in controlling numbers of some mammals, forest-edge birds, and insects. In general, terrestrial organisms are exposed to much higher intensities of solar radiation than are aquatic organisms and have evolved horny or chitinous body coverings, hair, or feathers, that function in part to protect internal structures from lethal concentrations. Long-range vision has developed only in land animals and is correlated with the high light intensities characteristic of terrestrial habitats.

Diurnation

Animals may be divided into *diurnal* (daytime), *crepuscular* (late evening and early morning), *nocturnal* (night), and *arhythmic* (irregular) species. Animals that occupy microhabitats where temperature and light changes are negligible at most tend to

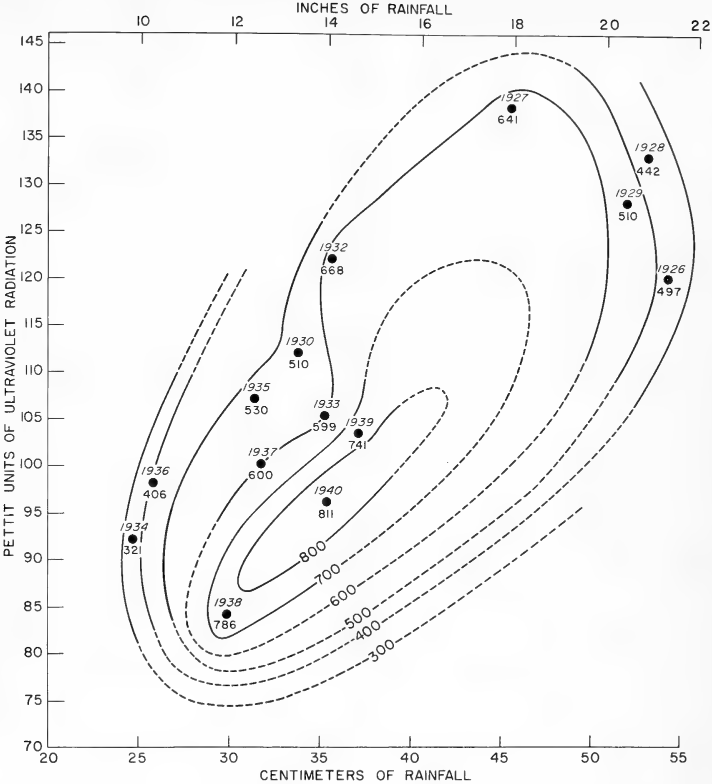


FIG. 8-2 **An ultraviolet-hydrogram for February populations of pronghorn antelope in Yellowstone Park for the years indicated in italic numerals. It appears that the number of young produced in any year has been determined in a sensitive period two Septembers earlier; hence, the ultraviolet data given for each year is for the second preceding September, and rainfall is for that September through the August following, inclusive (modified from Shelford 1954).**

be arhythmic; cave crayfish, log-inhabiting beetles, moles, shrews, and some ants, for instances. The microfauna of the soil is probably arhythmic. About two-thirds of the mammal species occurring in both temperate deciduous and tropical rain forests are nocturnal. Birds are predominantly diurnal, except that owls are nocturnal and goatsuckers crepuscular. The majority of amphibian and reptile species are nocturnal; some frogs and lizards are diurnal.

Among invertebrates, there is considerable variation. The drosophilid flies are crepuscular, having pronounced peaks of activity at dawn and dusk (Taylor and Kalmus 1954). The major period of activity of many nocturnal animals occurs during the first half of the night period, although they often possess a secondary pre-dawn period of activity. With diurnal animals, the major period of activity usually comes during the first portion of the day, although there may be a secondary pre-dusk period of activity (Calhoun 1944–46).

A classification of the diel activities of animals in respect to controlling influences can be made (O. Park in Allee *et al.* 1949: 558):

I. **Periodic activity.** Regularly most active for a specific period in the diel cycle.

1. **Exogenous type.** Activity rhythm directly induced and controlled by periodically recurrent environmental conditions.

2. **Endogenous type.** Activity rhythm more or less independent of obvious factors in the environment; persists even under controlled, apparently uniform environmental conditions. It is possible, however, that obscure environmental factors may still be regulative (Brown 1959).

a. **Habitual activity.** An endogenous rhythm that has become established as the result of previous experience of the individual.

b. **Inherent activity.** An endogenous rhythm that is inherited.

3. **Composite type.** A rhythm pattern that is partly endogenous but is accentuated when the animal is exposed to environmental conditions periodically recurrent.

II. **Aperiodic (arhythmic) activity.** No consistency between individuals of a species in exhibiting an activity pattern relating to a specific time of day or night.

Endogenous diel rhythms have been demonstrated in Coelenterata, Platyhelminthes, Echinodermata, Crustacea, Insecta, Cyclostomata, Pisces, Amphibia, Reptilia, Aves, and Mammalia, although they are not often inherent. Probably the great majority of species have rhythms of the composite type. Periods of rest or sleep alternating with activity seems to be a fundamental protoplasmic requirement (Park 1940).

Carnivorous, herbivorous, and omnivorous nocturnal animals occur throughout the metazoans. It is of interest that nocturnal animals are less frequently gregarious and social than are diurnal forms. Adjustments for night activity involve development of luminescent organs such as fireflies (Lampyridae) possess; infrared-sensitive vision, suggested for some insects and birds but not proven for owls (Dice 1945); increase in visual acuity by modification of eye structures (Walls 1942); keenness of smell displayed by some mammals; and increased sensitivity to sound, remarkably developed in bats. Bats have evolved a radar system, called *echolocation,* whereby the animals emit ultra high frequency sound waves, which are reflected from objects back to the ears (Griffin 1953). Color vision, well developed in some diurnal insects, fish, reptiles, amphibians, birds, and mammals, is largely lost in those nocturnal species active at such low intensities of light that colors would be indistinguishable anyway. Correlated with loss of color vision is restriction of body coloration to blacks and whites or intermediate shades. Nocturnal animals escape such diurnal predators as reptiles, birds, and hymenopterous insects. There are nocturnal predators, to be sure, but predation pressure at night appears to be less intense than during the day.

There is decreased competition for food and shelter when some species are active by night, others by day, over the same range. Butterflies are predominantly diurnal; moths, nocturnal. Animals with moist skin, like snails and amphibians, suffer less evaporation of water from their bodies at night, when the relative humidity is higher and the temperature is lower. There is some belief (Clark 1914) that nocturnal forms are derived from originally diurnal forms; an adjustment, perhaps, to avoid competition from aggressive diurnal species occupying the same niches.

Seasonal variations (aspection)

In tropical rain forests there is very little seasonal variation in the number of species active and size of populations attributable to length of day, temperature, and humidity, for these factors are nearly uniform throughout the year. In other parts of the tropics, however, there are definite wet and dry seasons, and a considerable change in numbers and activities of animals correlates with the seasonal variations in vegetation and food supply. In temperate

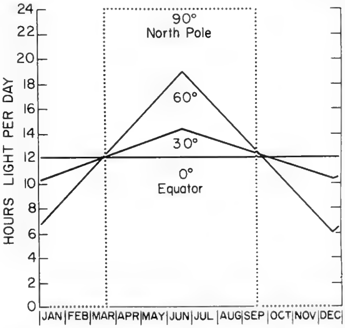


FIG. 8-3 **Monthly variation in daily photoperiods at cardinal latitudes of the Northern Hemisphere (after Boggs 1931).**

TABLE 8-2 **Ecological seasons (Macnab 1958).**

Aspect	Sector	Characteristics
Hiemal		Early November to late March.
	Hiemine	Deciduous trees nearly bare, herbs mostly dead except for winter-green species (Beatley 1956); insects, other invertebrates, some mammals, going into hibernation or dormancy; last migrant birds disappear.
	Hibernine	Deep winter condition, little animal activity evident except winter resident birds in sheltered locations and a few mammals.
	Emerginine	Some buds swell and subterranean sprouts begin to appear above ground, earliest migrant birds appear, animals beginning to emerge from hibernation.
Vernal		Early April to late May.
	Prevernine	First appearance of flowers both of herbaceous and tree species; mammals and permanent resident birds begin reproductive activities; salamanders go to ponds and lay their eggs; all insects, snails, and other invertebrates come out of hibernation.
	Vernine	Deciduous trees now fully foliated, early spring flowers replaced by species that tolerate shading; bird migration reaches its peak; insects and invertebrates become abundant in all strata.
Aestival		Early June to middle August.
	Cisaestine	Reduced number of flowering herbs but vegetative growth at maximum, birds at height of nesting.
	Aestine	Deciduous forest becomes hot and dry, many ground plants dry up; birds quiet and entering molt, molluscs aestivate, foliage insects attain maximum populations.
Autumnal		Middle August to early November.
	Serotinine	Fruits and nuts ripen, autumn flowers come into bloom, birds at height of southward migration, mammals reach maximum populations but invertebrates decreasing.
	Autumnine	Foliage of deciduous trees changes color and falls, insect and spider populations shift from higher strata to the ground.

and arctic regions, seasonal differences in length of day and temperature become increasingly great the closer the region lies toward a pole.

Correlated with seasonal changes in climate are adaptive adjustments of metabolism and energy balances, regulation of breeding time, change in food habits, and migration or hibernation. Birds breed in the spring and early summer, since lengthening daily photoperiods stimulate maturing of the gonads (Burger 1949). *Photoperiodism* also controls the breeding time of some mammals, fish, and invertebrates as well as plants. However, in some species, say trout and deer, shortening rather than lengthening photoperiods are stimulating, and such species regularly breed during the autumn.

In deciduous forests, seasonal differences in the development of the foliage greatly affect animals. When trees are bare, sunlight penetrates to the forest floor more readily than when foliage is in full development. Foliage is important because it is protective cover from weather and offers refuge and concealment from predators; to many species it is a direct source of food.

Four main ecological seasons, or *aspects,* may be recognized; each aspect is divisible into secondary periods, or *sectors* (Table 8-2). These periods are best developed in the temperate deciduous forest but also occur in modified form in other communities as well. The beginning and end of any aspect cannot be set with exactness, since aspects vary from year to year, with latitude and type of community.

Substratum

The substratum greatly influences the kind of plants and animals that occur in the pioneer stages of succession. Bare rock presents one extreme physical habitat, sand another, and clay yet another. The substratum affects animals indirectly in terms of the kinds of plants it supports and the variety of niches it affords. Differences between early sere stages notwithstanding, later ones tend to be more and more alike so that *convergence* occurs. In temperate humid regions, where the seres pass through several stages, the climax communities of all seres are very much alike regardless of the type of bare area on which they originated.

ROCK SERE

Plant communities

Stages in the plant sere on bare rock are lichens, mosses, annual herbs and grasses, shrubs,

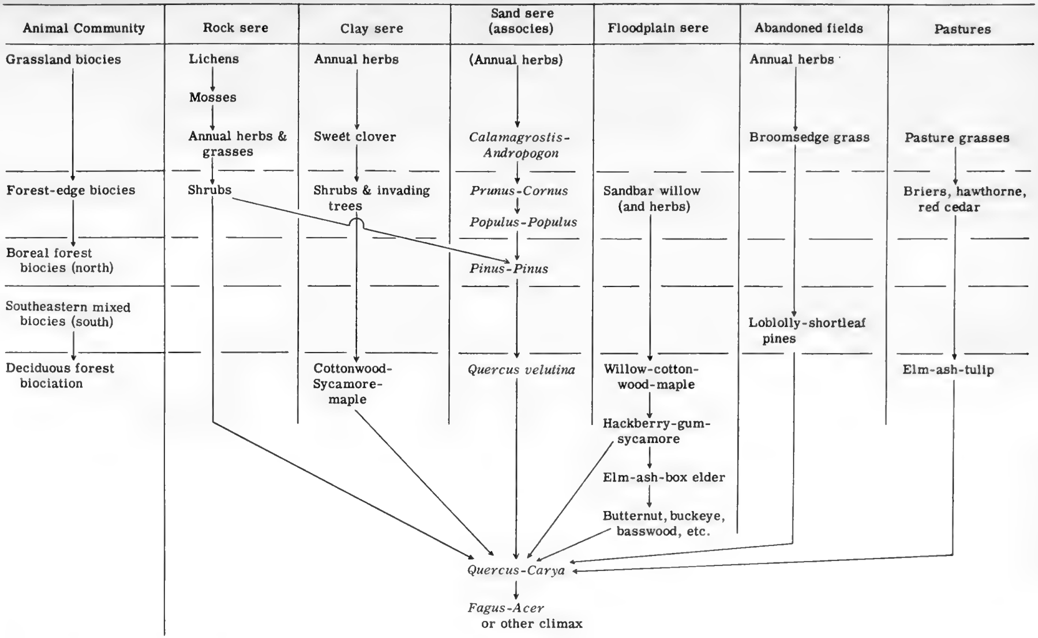


FIG. 8-4 Correlation of animal communities with converging stages of plant seres in Eastern United States.

FIG. 8-5 **Early crustose lichen, foliose lichen, and moss stages on rock, with ferns in a crevice (courtesy R.E. Rundus).**

and forest. The species composition of each stage varies with the chemical nature of the rock, the prevailing climate, and the locality.

In the first stage, various kinds of lichens compete for a foothold, but crustose types usually precede foliaceous types. Mosses and such fruticose lichens as *Cladonia* follow foliaceous lichens; or may initiate the sere, telescoping the earlier lichen stages (Keever, Oosting, and Anderson 1951).

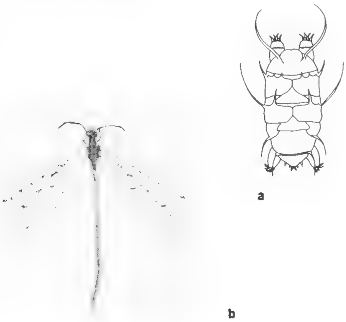


FIG. 8-6 **(a) a tardigrade, *Echiniscus oihounae*, occurring in moss, possessing long filaments (Heinis 1910). (b) ant-lion adult (Shelford 1913).**

Lichens and mosses soak up moisture in wet weather. They derive mineral nutrients from the underlying rock. Carbon dioxide secreted from the rhizoids forms a weak acid with water and dissolves the binding material of the small rock particles. Rhizoids may penetrate rock for several millimeters. These plants trap windblown dust and obtain nitrogen from organic compounds in it. When the plants die, they become an addition to the accumulation of organic matter. Herbs, grasses, ferns and later stages invade to continue the crumbling of the rock and buildup of soil. Freezing and thawing of water may crack the rock, and in these cracks wind- and water-borne soil lodges and supports plants. Once shrub and tree roots get started in crevices, their growth exerts a powerful force further splitting and crumbling the rock.

Animal life

Animal life in the pioneer plant stages on rock is scanty. Ants and spiders roam over the bare rock, and insects of various sorts may stop there, temporarily. Spiders may construct webs and nests in rock crannies or amongst the lichens. Some tardigrades find preferred niches in lichens. Mosses offer a somewhat more substantial microhabitat, but only those animals that can tolerate great extremes of flooding, dessication, heat, and cold can survive. Such forms are found in the rhizopod protozoans, nematodes, bdelloidid rotifers, tardigrades, copepods, small insects, and mites (Heinis 1910). They often have special means of attachment to keep them from being blown away by the wind, such as strong claws or cement glands on the feet, long bristle-like threads to entangle among the moss filaments; stickers or spines covering the eggs. Since wet periods are often too short to permit complete development, all stages must be tolerant of desiccation, at which time activities and growth are largely suspended.

Animal life in general and land snails in particular are usually more abundant in vegetation (grassland and forests) established on calcareous soils derived from limestone than in the vegetation established on soils derived from sandstone, granitic, or volcanic rock. Calcium carbonate is a mineral essential to the metabolism of most animals and for building such skeletal structures as bones and shells. Snails are less numerous in the grass stage than in the later, moister forest communities that develop in the succession.

SAND SERE

Plant communities

Sand is the product of mechanical pulverization of various rocks. It is deposited by wind and water. Where extensive areas of sand occur, strong winds pile the sand into shifting dunes. These dunes have a characteristic shape as the sand grains are blown up a long, rather gentle windward slope and swept over the crest onto a steep lee slope. Moving dunes may engulf whole forests; they eventually move on, leaving the denuded trunks of trees that they have smothered. The dunes continue to move until they reach the shelter of some other dune, get beyond the full force of the wind, or until invading vegetation covers the surface and anchors them down. The most successful sand-binding plants are the grasses *Ammophila, Calamovilfa,* and *Agropyron,* willows, sand cherry, and cottonwoods. Willows and cottonwoods will survive even when almost buried. Each succeeding stage ties the sand down more firmly, but any break in the vegetation occasioned by a blowdown of trees or disturbance by man may invite the wind to start moving the exposed sand, and change the partially anchored dune again into a moving one. Only when the pine stage or the black oak stage is reached does the dune become relatively secure from the wind.

The plant sere on the south shore of Lake Michigan consists essentially of the following stages (Cowles 1899):

Lower beach: Washed by summer storms and devoid of vegetation.

Middle beach: Washed only by severe winter storms; comparatively dry in summer; upper limit marked by driftwood and debris. Scattered annual plants present.

***Calamagrostis-Andropogon* associes** (upper beach): This is where the dunes begin to form. In this early developmental stage (associes) grasses are dominant, particularly *Calamagrostis longifolia, Andropogon scoparius, Agropyrum dasystachyum, Ammophila arenaria, Elymus canadensis;* various biennial and perennial herbs make their appearance. The sandbur grass occurs extensively in some areas.

***Prunus-Cornus* associes:** The commoner shrubs are sand cherry, chokecherry, red-osier dogwood, creeping juniper, and the frost grape vine. Shrubs may invade the grass directly but become more common in the following tree stages.

***Populus-Populus* associes:** The first tree stage in the southern portion is made up principally of the eastern cottonwood, and in the northern portion, of the balsam poplar. The trees commonly occur in open stands with grasses and shrubs forming the lower strata. The habitat is essentially forest-edge. The shrub and cottonwood stages are often missing so that the sere progresses from the grass directly to the pine or black oak stage.

***Pinus-Pinus* associes:** Jack pine, red pine, and eastern white pine may invade one after another, commonly forming mixed stands. Northern white-cedar and eastern redcedar also occur; the former, more commonly northward. Succession to this stage is mainly contingent on stabilization of sand in dunes, and more efficient utilization of water resources. For succeeding stages to emerge, soil must develop by deposition of humus. The floor of pine forest is covered with a carpet of needles, although patches of bare sand still occur. As the sere advances, all bare areas become covered with a layer of humus.

***Quercus velutina* consocies:** Black oak often forms a nearly homogeneous stand that may persist for a long time.

***Quercus-Carya* associes:** Black, white, and, to a lesser extent, red oaks are commonly mixed with shagbark and bitternut hickories and, in moist habitats, American basswood.

***Fagus-Acer* association:** When soil humus and moisture become sufficient, American beech and sugar maple invade the sand to form the final climax stage.

In other localities, the taxonomic composition of the communities, especially the later stages, differs considerably. The character of the climax varies according as climate and geography, but perhaps the

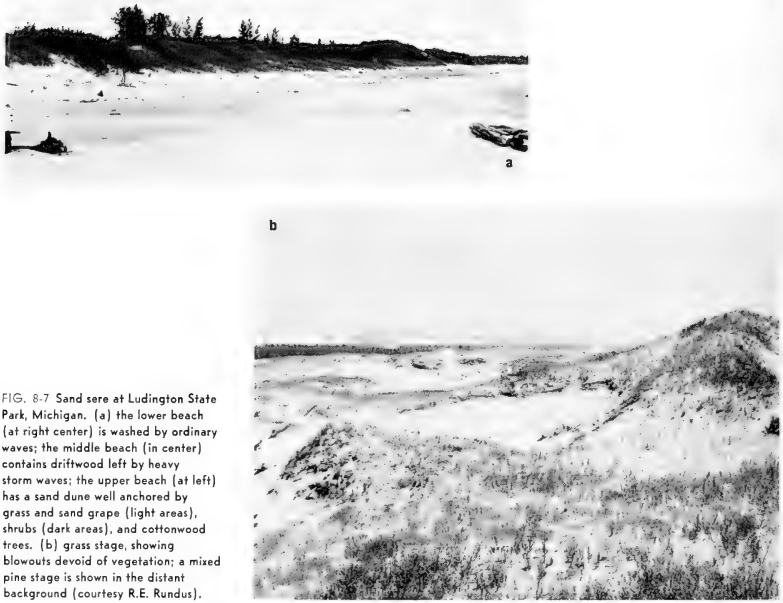


FIG. 8-7 **Sand sere at Ludington State Park, Michigan. (a) the lower beach (at right center) is washed by ordinary waves; the middle beach (in center) contains driftwood left by heavy storm waves; the upper beach (at left) has a sand dune well anchored by grass and sand grape (light areas), shrubs (dark areas), and cottonwood trees. (b) grass stage, showing blowouts devoid of vegetation; a mixed pine stage is shown in the distant background (courtesy R.E. Rundus).**

sere is as complete and as complex in the Lake Michigan region as it would be anywhere.

Habitat

The sand dune habitat is characterized by extreme fluctuations in physical conditions, generally resembling those of a desert (Chapman *et al.* 1926). Temperatures, especially at the ground surface, are very high during bright sunny days; relative humidity is very low. Evaporation from spherical atmometers is 2.5–3 times higher than in forest habitats at the same time of day. At night the ground surface temperature may be even lower than that of the air since there is little or no surface covering to prevent rapid heat radiation.

Correlated with the diurnal changes of temperature, relative humidity, and light, the kinds of animal active on the sand during sunny days are quite different from those active on cloudy or rainy days and at night. When the temperature of the sand nears 50°C, all insects leave the surface. Some climb grasses to get off the ground, others enter their burrows. Insects flying above the sand can select an optimum temperature from widely different temperatures merely by changing their elevation only a few inches. They make hurried landings when entering their ground burrows. The female velvet-ants are usually among the last to retreat into their burrows in the morning and the first to leave them in the evening. Experiments show that they of all insects in this habitat are the most tolerant of the high temperatures. Animals living here must either be physiologically tolerant of extreme heat or possess behavior patterns that enable them to avoid it.

Grasshoppers and other Orthoptera

There have been detailed studies of a few special groups of animals occupying the Lake Michigan sand dunes. Three species of wood roach, 2 species of walking-stick, 20 species of short-horned grasshopper, 13 species of long-horned grasshopper, and 6 species of field cricket occur in various stages of the sand sere in the Chicago area (Strohecker 1937). A breakdown of this list shows that 7 species, all short-horned grasshoppers, occur in the grass and cottonwood stages; of these, one species is not found in the pine stage, and the other 6 species disappear by the time the black oak stage is reached. Eight new species of orthopterans, including 4 short-horned grasshoppers, enter the sere at the pine stage, but only 5 species persist into the black oak stage. Altogether there are 23 species of orthopterans listed for the black oak forest, an increase of 18 new species. There are only 25 species of orthopterans listed for the climax, but this includes 4 species of camel crickets which for the first time can find their proper niches under logs, and a katydid that appears in the trees. The greatest change in species composition within the sere occurs at the black oak stage upon the disappearance of 67 per cent of the species present in the earlier stages and the appearance of 78 per cent of the species as new forms. Of that 78 per cent, 61 per cent persist through all later stages. The change in species composition at this stage can be correlated with the development of a canopy of foliage and the resulting reduction in light intensity and soil temperatures.

The community or niche restriction of the short-horned grasshoppers appears to be determined either by soil conditions or by the vegetation (Isely 1938a). Before short-horned grasshoppers lay their eggs in the ground, the female tests the soil with her ovipositors until she finds soil of proper conditions. Experimental studies show that in certain cases soil texture is the critical factor in the choice of the egg-laying site, while in other cases soil structure or degree of compaction is most important. Soil conditions appear particularly important for the sub-family of band-winged grasshoppers; for other groups, vegetation is of greater significance.

In an experimental study of how an available choice between foods may affect distribution (Isely 1938a), one-half of 40 species of short-horned grasshoppers showed a feeding preference for grasses and one-half for broad-leaved herbs. The latter group included the spur-throated grasshoppers. Four species were restricted to feeding on a single plant species; 30 species confined themselves to a few plant species only, and usually of a single plant family at that; only 2 species fed on a wide variety of plants. In several instances grasshoppers starved in cages, when there was an abundance of fresh plant materials present that were palatable for other species, because their own preferred food species were absent.

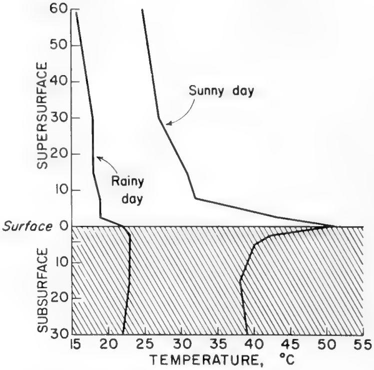


FIG. 8-8 **Temperature gradient on a sand dune, on a rainy day and on a sunny day (after Chapman *et al.* 1926).**

All five species of false katydids studied in Texas (Isely 1941) confined their choice of food to related species of broad-leaved herbs or forbs, refusing grasses; adults showed a marked preference for the flower parts and tender fruit pods. Two species of shield-backed grasshoppers were wholly carnivorous. The flower-feeding false katydids disappeared from the prairie in late spring and early summer as the flowering plants passed their peak, but the insect-feeding grasshoppers persisted to the end of July or until temperatures became too high for their comfort.

Ants

Ants cannot get established on the beach because of its unstable character and are scarce even in the grass and cottonwood stages because of the shifting character of the dunes (Talbot 1934). Species found are crater-formers *Lasius niger neoniger* and *Pheidole bicarinata,* and two species of *Camponotus* that find protection under the occasional log

TABLE 8-3 Number of species of each spider family found in each sand sere plant stage except the oak-hickory (after Lowrie 1948)

Spider family	Middle beach	Grass stage	Cottonwood	Pine	Black oak	Beech-maple
			Web-builders			
Ariopidae	2	5	3	5	26	20
Micryphantidae	2	2	0	2	8	3
Theridiidae	1	1	2	5	10	13
Dictynidae		1	1	4	3	2
Linyphiidae		2	0	0	5	7
Agelenidae				1	3	8
Ciniflonidae					1	1
Hahniidae					2	1
Mimetidae					1	1
Uloboridae						2
Total	5	11	6	17	59	58
Per cent all species in stage	29	35	34	40	35	48
			Non-web-builders			
Lycosidae	9	4	2	1	24	11
Gnaphosidae	2	1	0	3	11	6
Salticidae	1	7	5	10	29	17
Thomisidae		7	4	10	22	14
Clubionidae		1	1	1	14	7
Anyphaenidae				1	1	3
Dysderidae					1	0
Oxyopidae					1	1
Pisauridae					6	4
Total	12	20	12	26	109	63
Per cent all species in stage	71	65	66	60	65	52
Number individuals of all species in herb stratum per 50 sweeps		8	6	10	18	24

that occurs. On hot dry days these ants withdraw to several inches below the surface and emerge only in the cool of the evening.

In the pine stage, the slight mixture of humus in the sand is decidedly favorable, food is more abundant and varied. Of 18 ant species found, 9 live in patches of open sand with no shelter, 6 require sand with some protection above it (logs, bark, needles), and 3 are strictly log-inhabiting forms. *Monomorium minimum* and *Paretrechina parvula* are characteristic species.

In the black oak community, 29 species occur of which only 6 live in scattered open areas of sand. These 6 species are quickly crowded out when there is development of a complete leaf covering over the ground. *Formica pallide-fulva,* which was becoming important in the pine community, is the predominant ant in the black oak stage. Its nests are invariably found under pieces of bark or branches lying on rather open ground.

As the sere advances into the white and red oaks stage, open areas of sand disappear, humus and moisture increase, logs in all stages of decay occur, the whole area becomes shaded, and the daily extremes in temperature and humidity typical of the open dunes are considerably curtailed. Species of ants characteristic of the early stages disappear, and forms that are found in mesic deciduous forests generally predominate, although there are only six species found here that do not also occur in the black oak community. *Formica truncicola obscuriventris* is the most numerous species. The number of colonies and variety of species reach maximum in the oak stages.

In the climax beech-maple community, the number of soil-dwelling forms is reduced, perhaps because of the thick rich humus, although log-inhabiting forms are numerous. *Lasius niger alienus americanus* and *Aphoenogaster fulva aquia picea* are the only ants abundant in the deep woods; ants are more numerous in the forest-edge than in the forest-interior.

Although different species reach peaks of abundance at different points in the habitat gradient proceeding from open sand to dense forest, the nature of the substratum divides the species into two major groups: those that tolerate and reach their greatest abundance in the sandy areas where vegetation is scattered, and those that are limited by sand and require humus in the soil or the microhabitat of decaying logs. The transition or ecotone between these two ant communities comes at the pine and black oak stages. Experimental studies of six species in the genus *Formica* indicate that physiological differences occur, and that some species are able to invade places of low relative humidity that others cannot.

Spiders

In the sand dunes on the south shore of Lake Michigan and in adjacent areas, 228 species of spiders are to be found (Lowrie 1948). The number of families represented, the number of species involved, and the abundance of individuals per unit area increase as plant stages in the sere succeed one another (Table 8.3). Probably because of the greater diversification of the vegetation, the availability of logs, the increase in number of strata, and the consequent greater variety of niches, spiders, like ants, are represented by a larger number of species in the oak communities than in the earlier stages of the sere or in the climax. It is of significance that up through the black oak stage new species appear in each succeeding stage with very few dropping out. In the beech-maple climax, however, 51 per cent of the spider fauna occurring in preceding stages are no longer found, while 79 per cent of the species are either new with this stage or came in at the black oak stage and remained. Up to the black oak stage the species composition of the spider population shows ecesis, but with the advent of deciduous forest, the change in the fauna composition is sufficiently extensive to indicate succession of distinct communities.

There is also a change in the mores of spiders as the sere advances. Small lycosids that hide during the day under driftwood or other debris and run over the sand at night hunting for insect prey washed up by the waves are most characteristic of the beach. The permanent population is small. A burrowing spider, *Geolycosa wrightii,* is usually common. The burrows in which the spiders stay during the day may be easily spotted on the beach and through the grass and cottonwood stages. Web-building species are at a disadvantage in the early stages of the sere, however, because of the general lack of vegetation to which their webs may be anchored and because of the destructive effect of unchecked wind. With the appearance of grasses, a substratum in which spiders can build webs becomes available. In later stages, the percentage of web-builders increases considerably as stratification progresses and the forest furnishes a scaffold.

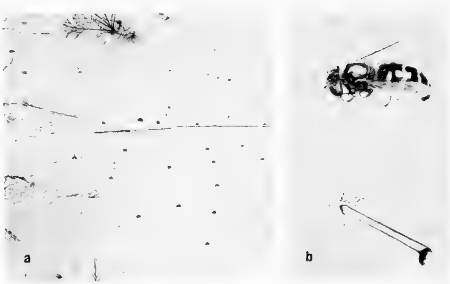
Other animal life

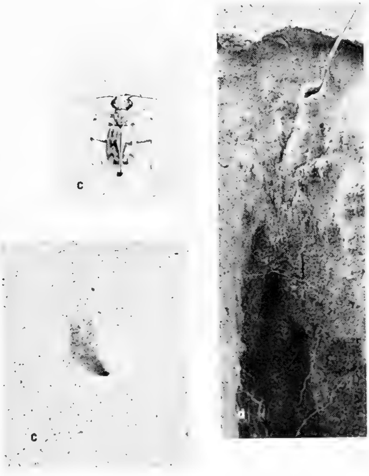
Strong offshore winds often blow insects out over the water where they are forced down onto the surface and washed ashore. Windrows of such insects many thousands of individuals representing a wide variety of species, are sometimes to be seen. Dead fish washed up on shore are fed upon by flesh-flies and histerid, dermestid, and rove beetles. The tiger beetles *Cicindela hirticollis,* and *C. cuprascens,* a white ground beetle and other carabids, shore bugs, digger-wasps, robber flies, and other insects and spiders come down from higher ground to feed on the scavenger species and those washed up by the waves (Shelford 1913, Park 1930). The tiger beetles, ground beetles, digger-wasps, and sand spiders build their burrows and larval stages far enough back to escape the summer waves. Termites feed on buried wood that is decaying or on the undersides of logs that have drifted ashore. The piping plover and spotted sandpiper place their nests in the middle and upper beaches. At night, the toad, opossum, raccoon, and the deer mouse come down to scavenge whatever is available. The light coloration of many of the insects and spiders that occur on sand is doubtless an adaptation for concealment (Hart 1907).

The kinds of animals occurring in the grass, shrub, and cottonwood communities are similar except that new species invade with each successive plant stage. The white tiger beetle *Cicindela lepida* first appears on the upper beach and reaches maximum populations in the cottonwood stage, as do the digger-wasps, robber flies, and sand spiders. Another tiger beetle, *Cicindela formosa*, occurs in the ecotone between the cottonwood and the pine stages. Snout beetles, spittle bugs, and miscellaneous other insects are occasionally very numerous. Some 592 species and varieties of beetles have been taken from various stages of this sere (Park 1930). Fifty species were found to occur in the cottonwood stage, 23 in the conifer stage, and about 200 in each succeeding forest stage. The occurrence of bees is dependent to a large extent on the variety and abundance of flowers, but the number of species in each plant stage increases up to the black oak and then declines to the climax (Pearson 1933).

Vertebrates are not usually numerous on sandy flats or dunes away from the water's edge. The vesper and lark sparrows occur among the grasses, the prairie warbler and chipping sparrow are found among the shrubs, and the kingbird is conspicuous

FIG. 8-9 **Burrows made in sand by arthropods. (a) burrows of a digger wasp, *Microbembex monodonta*. (b) a digger wasp, *Bembex spinolae*, and a cross-section sketch of its burrow (Shelford 1913). (c) the white tiger beetle and its burrow (Shelford 1913). (d) excavated burrow of a sand spider (courtesy R.E. Rundus). The upper portion, shown with a stick in it, is intact; the lower portion, in the shadow, is broken open.**





in the trees. Tracks of the prairie deer mouse are frequently to be seen on the sand. Fowler's toad and the hognose snake are the only amphibian and reptile that regularly occur. The grass, shrub, and cottonwood stages ordinarily occupy relatively narrow belts parallel to the lake shore. Extensive sandy areas inland may have a larger variety of species present (Vestal 1913).

The pine community in the sere is not so well developed around the south end of Lake Michigan as it is northward. The coniferous forest penetrates southward from the north, and some northern animals move with it. Nesting birds are represented by the slate-colored junco, red-breasted nuthatch, black-throated green warbler, blackburnian warbler, and myrtle warbler, all belonging to the boreal forest biociation. Forest-edge and deciduous forest birds also occur. The red squirrel is a characteristic boreal mammal that occupies this stage, and the white-tailed deer browses on conifer foliage, especially the white cedar. The six-lined racerunner and blue racer snake appear. Among the invertebrates are the bronze tiger beetle *C. scutellaris* and the ant-lion.

With the advent of the black oak and later forest stages, most species requiring open areas or depending on patches of bare sand disappear. Although the bronze tiger beetle remains abundant in the black oak community, it, as well as the other tiger beetles, disappear in the higher plant stages. Only the green tiger beetle *C. sexguttata* is in the climax, a species that requires bare spots on the forest floor, but not sand.

Reptiles are not common in the sand sere around Lake Michigan, but elsewhere around the world lizards and snakes are quite characteristic of sandy habitats. They are remarkable in showing a variety of structural and behavioral adaptations specific to locomotion in sand and for protection of their sense organs and body openings from sand (Mosauer 1932). The sidewinder rattlesnake, for instance, has evolved, in addition to the usual undulatory lateral movement of snakes, a rolling sidewise movement that involves spiral contractions of the body and applies vertical rather than lateral pressure to the sand. Sand offers the snake an unstable footing—lateral undulations alone do less to propel the snake forward than to merely push sand aside. Sand provides firm footing only if it is pushed down upon, hence the effective, if singular, action of the sidewinder.

TABLE 8-4 **Percentage location of ovipositor holes and larvae in different soils, experimental conditions (from Shelford 1911, 1915).**

Tiger beetle species	Holes or Larvae	Number	Sand	Sand and humus	Humus	Clay	Niche under natural conditions
Cincindella hirticollis	Holes	69	40%	50%	7%	3%	Wet sandy beaches
	Larvae	50	56	42	2	0	
Cincindella tranquebarica	Holes	141	34	48	2	16	Adults on sandy ridges covered with vegetation, larvae on sand or clay
	Larvae	129	7	75	2	16	
Cincindella sexguttata	Holes	117	8	22	0	70	Clay soils, oak-hickory forests, prefer leaves on ground
	Larvae	93	15	53	0	32	
Cincindella purpurea limbalis	Holes	51	0	2	0	On level 23 On slope 75	Adults on sand or clay, larvae entirely on clay banks
	Larvae	47	0	2	0	On level 23 On slope 74	

FIG. 8-10 **The sidewinder rattlesnake and the track it makes (Mosauer 1935).**

Life history of tiger beetles, Cicindelidae

The intimate adjustments of a species to its habitat and the manner in which it selects a particular stage in the sere may be illustrated by briefly describing the life-histories of tiger beetles.

Adult tiger beetles are bright-colored, alert, swift fliers. They are frequenters of bare ground. Both adults and larvae feed predatorily on ants, sowbugs, centipedes, spiders, beetles, flies, dragonflies, butterflies, and larvae of various forms. Tiger beetles commonly dig shallow burrows in the soil for shelter. They reach sexual maturity after several warm days in spring or early summer after they have emerged from hibernation. They copulate on warm, humid days when there is an abundance of food and sunlight. After laying their eggs, they die.

The female deposits one egg at a time, and lays up to 50 in all, in small vertical holes, 7–10 mm deep, which she makes with her ovipositor. The female tests soil with her ovipositor until she locates soil of the required characteristics. Hatching occurs in about two weeks.

The larvae are elongated, yellowish, and grub-like. Anteriorly directed hooks, spines, and bristles on the dorsal side of the larval body prevent the larvae from being pulled out of their burrows by the larger prey on which they feed. At the site of the ovipositor hole the larva excavates a vertical cylindrical burrow 8–50 cm deep in temperate climates, much deeper in colder northern regions. Most of the time the larva stations itself at the top of its burrow with its mandibles extended, and with its head and prothorax just closing the round opening. It grabs passing prey and carries it off to the bottom of its burrow to devour it; larger prey are eaten at the entrance. Inedible parts are cast out on the surface of the ground around the burrow entrance. After feeding 3–4 weeks, the larva closes the mouth of its burrow with soil and goes to the bottom to molt. The second larval stage lasts five weeks or longer, after which there is another molt. The last of the larval stages closes the entrance to its burrow in late August or September and goes to the bottom to hibernate over winter (some species hibernate in the second larval stage). The larva comes out of hibernation in late spring and feeds until summer. Then it closes the entrance of its burrow and constructs a side chamber in which it pupates. The adult emerges in late summer and feeds until October. It then digs a hole in which to hibernate over winter. Two years are commonly required to complete a generation, although in various species the interval between successive generations may be one to four years, depending in part on regional temperatures.

The niche requirements or seral stage preferred by different species are rigid and appear determined, in large part, by the character of the type of soil a species finds suitable for deposition of eggs and larval growth. Studies performed under experimental conditions demonstrate the nature of these requirements (Table 8-4) but suggest no physiological explanation (Shelford 1908, 1911, 1915; Balduf 1935).

CLAY SERE

Plant communities

Erosion or calculated removal of overlying material may leave bare areas of clay exposed. In clay above pH 4.5 annual plants, of which smartweed is particularly important, appear within a few weeks to two years; the higher the clay pH, the quicker the appearance of vegetation. Within two to five years thereafter sweet clover invades and develops nearly complete dominance over large areas. Sweet clover is a biennial, and an exotic species unimportant in the sere in some parts of the country (Bramble and Ashley 1955). Prior to its introduction, this stage in the sere on bare clay may have consisted of the perennial grasses still found in small scattered patches, or it may not have been well developed. A shrub stage seldom takes dominance over extensive areas, but thickets of raspberries and blackberries, smooth sumac, trumpet creeper, and various other species succeed the sweet clover and grass stage. The first trees begin to invade early in the sere, but they are scattered and slow of growth, and do not attain dominance for 25 to 30 years. The tree stage is commonly made up of eastern cottonwood, American sycamore, silver maple, and American elm. Willows occur in wet spots. Herb species of the first two plant stages disappear, for the most part, in the shrub stage. The herb stratum now consists largely of wood nettle. Advanced forest stages of oaks, hickories, basswood, and sugar maple will likely invade in the future; as they occur now in adjacent areas.

Animal life

The number of invertebrate species tends to increase as the sere advances, although not always regularly. In a study of a formerly strip-mined area (Smith 1928), 18 species were found to be important in the annual stage, 41 species in sweet clover, 40 species in shrubs, 32 species in the early forest stage, and 67 species in the upland climax. More species would be found in advanced stages because of the greater variety of niches then available. Thus, in the initial bare area there is only the ground stratum; in the annuals and sweet clover stages there are the ground and herb strata; in the shrub stage there are ground and shrub strata. The herb stratum is poorly developed or absent altogether. In the forest there are the ground, herb, shrub, and tree strata. Since the early forest is on a floodplain, the ground is frequently swept by floods, and the shrub stratum is poorly represented. The climax forest has all strata, richly developed, and possesses the greatest number of animal species. There is an increase in the abundance of individuals per square meter with the progression of the sere: annuals, 268; clover, 531; shrubs, 532; early forest, 748; climax, 2445 (Davidson 1932).

Beetles, spiders, ants, and mites are the most abundant animals in the annuals stage, and along with aphids remain most abundant also in the sweet clover community. Grasshoppers are fewer in number but especially characteristic of the first three stages; they practically disappear in the forest. Earthworms are absent in the annuals and scarce in the sweet clover, as are the springtails; as the amount of soil humus increases with the development of the sere, both groups become more and more numerous. Snails first appear in the sweet clover stage and increase in importance in the forest stages.

The first two stages are not sufficiently extensive to support a distinct bird fauna, but they are quickly invaded by scattered shrubs and trees. A forest-edge habitat is thus established and is occupied by forest-edge birds (Brewer 1958). Beginning with the early forest stage, these forest-edge species are replaced by the forest bird community. The composition and stucture of these two communities will be discussed in Chapter 9.

The first small mammal (Wetzel 1958) to invade the annuals and sweet clover stages is the prairie deer mouse. It attains populations as high as 22 per hectare (9/acre). It persits until the shrubs and trees have become well established. Its place is taken in advanced stages by the woodland white-footed mouse. The prairie vole prefers the grassy areas and is found under briars and other shrubs. Peak populations are about 18 per hectare (7/acre). The short-tailed shrew invades the sweet clover stage but does not establish a stable population until the shrubs come in; it persists into the climax forest. Woodchucks commonly occur throughout the early stages of the sere, but mostly disappear in the forest. The cottontail rabbit is common in the early stages, and the fox squirrel invades with the first trees.

FLOODPLAIN SERE

A stream continuously deepens its channel, thus lowering the water table of the surrounding land. At times of flood, the stream overflows its banks. The flow rate of water declines as the water passes over vegetated areas, and there is a deposition of silt which may sometimes amount to several inches. In a valley, the lowland area between the river and the bluffs on each side is called the *floodplain.* In the course of time, the river meanders back and forth across the floodplain, cutting new channels and abandoning old ones, and frequently leaving a sequence of terraces between its present channel and the surrounding upland. A study of these terraces commonly shows a variety of plant communities that constitutes the plant sere.

Plant communities

Gravel, sand, or silt is deposited on the inner side of river bends. Attached aquatic vegetation may occur in the water. On land, such herbs as smartweed, cocklebur, ragweed, beggar's ticks occur. At some bends small sand dunes may occur, displaying their characteristic plants and animals; usually this stage is narrow at most, and may be entirely absent. On sandy islands in the river or on sandy shores, the sandbar willow often forms dense, shrubby thickets. The first tree stage is ordinarily black willow mixed with eastern cottonwood, and sometimes silver maple. On the floodplain of the Canadian River in Oklahoma (Hefley 1937), the sere proceeds next to an edaphic subclimax of either tall grass prairie or elm-oak. The climatic climax on the surrounding upland is mixed prairie. The normal sequence of stages in this region has become considerably modified by the extensive ecesis of the exotic tamarisk tree, introduced from Asia.

On the Mississippi floodplain in western Tennessee (Shelford 1954b) the mature cottonwood-willow associes contains an abundance of vines of several species that form such tangled masses as to be almost impenetrable. The next stage is one in which sugarberry, sweetgum, American elm, and American sycamore predominate; several other species are present in small numbers. This leads to an oak-hickory stage that includes a complex variety of species, and eventually to the regional climax of western mesophytic forest. Cypress becomes part of the composition of the early floodplain forest around the edge of small oxbow ponds or other standing water. The schedule for this sere, the time from the start to the beginning of dominance by each successive plant community, has been estimated as follows: sandbar willow, 3 years; cottonwood-willow, 35 years; sugarberry-sweetgum, 82 years; early species of oaks and hickories, 260 years; intermediate species of oaks and hickories, 350 years; early climax of oaks and tuliptree, 440 years; full development of the climax, 600 years.

Elsewhere in the eastern United States, the cottonwood-willow stage gives way to a narrow zone of sycamore. Two or three species of elm ,white ash,

TABLE 8-5 Distribution of annelid worm species in the Sangamon River floodplain forest of central Illinois (Goff 1952). Original nomenclature revised by W. J. Harman.

Annelid species	Family	Ruderals	Willow-silver maple	Silver maple-elm	Elm-bur oak	Elm-shingle oak	Oak-hickory upland
Lumbricus terrestris	Lumbricidae	++	++	++	++	++	
Allolobophora iowana	Lumbricidae	+	++	++	++	+	
Bimastos tumidus	Lumbricidae		++				
Octolasium lacteum	Lumbricidae			++			
Henlea urbanensis	Enchytraeidae				++	+	
Henlea moderata	Enchytraeidae				+	++	
Diplocardia singularis	Megascolecidae					+	
Fridericia agilis	Enchytraeidae					++	
Fridericia sima	Enchytraeidae					+	++
Friderica tenera	Enchytraeidae						++

and boxelder follow; then a mixed forest that includes black walnut, butternut, black maple, Ohio buckeye, red mulberry, American basswood, tuliptree, and hackberry; next an oak-hickory stage; and finally the beech-sugar maple climax. The herb and shrub strata are usually well developed in mature floodplain forests. Telescoping or skipping of stages is not uncommon in this sere, since variation in ground level or in height of terraces is considerable and the transition between heights is often abrupt. The later stages occur only on the very oldest terraces and may be hard to find at all.

Animal life

In the bare areas, in the herbs, and among the invading trees occur such beetles as *Heterocerus pallidus* and *Bembidion laevigatum* that feed on the algae and detritus present on the shore. They make their burrows in sand. Fly larvae, a cocklebur weevil, a cocklebur mirid, and a cocklebur fly also occur. The tiger beetles *Cicindela hirticollis, C. cuprascens,* and on slightly higher ground *C. punctulata,* prey on the ground species and may even dig them out of their burrows. Spiders, ground beetles, and rove beetles invade from higher stages. In the herb stratum and in the shrubby growth of willows, adult midge flies and other flies are sometimes very abundant. Tarnished plant bugs, 12-spotted cucumber beetles, and other insects of open area habitats are present, and there is invasion of various species from the forest itself (Hefley 1937, Shelford 1954b).

The animal life of the floodplain forest is much the same as that of the deciduous forest in general (Chapter 9) and does not need to be discussed here except for its unique features. Annelid worms make their appearance in the ruderal stage, become very abundant in the moist soils of the elm-ash and mixed floodplain forests, then decrease in numbers in the drier soils of the late seral stages. They occur mostly in the first 5 to 10 cms below the surface in moist soil, but up to 30 cms or more in dry soil. During the winter they keep below the frostline, and in very dry weather they roll up in small knots and aestivate. Ten species occur in the floodplain of the Sangamon River in central Illinois, and each species has its particular range of moisture requirements between the river's edge and the upland forest (Table 8.5).

Snails and slugs are moisture-loving animals and occur in large numbers and great variety in floodplain forests; it is not hard to find 15 to 20 species with a little searching. *Mesodon thyroidus* is a common snail, and on a floodplain in central Illinois an average population of 6.3 individuals per m^2 was found during the autumn (Foster 1937). This amounts to a biomass of living flesh (shell excluded) of 15.8 g/m^2 (141 lbs/acre). *Succinea ovalis* on another old Illinois floodplain (Strandine 1941) averaged 6.5 individuals per m^2 in September with a biomass of only 0.878 g/m^2 (7.84 lbs/acre). Snail flesh is an important source of food for such small mammals as the short-tailed shrew.

Effects of flooding

Animals living on floodplains must usually tolerate flooding of their habitats almost yearly, and in years with heavy precipitation, often several times annually. All land except the surrounding bluffs may be flooded. Leaves are swept up from the forest floor and piled with other debris against shrubs and the bases of trees. Herbs and shrubs may be damaged, sometimes killed.

Observations during time of flood (Stickel 1948) showed that emergent brush, the bases of trees, and debris rafts supported masses of insects, spiders, millipedes, snails, and amphibians. Debris rafts were refuges for box turtles and pine-mice as well. Snakes, turtles, and amphibians were also seen swimming or floating in the water. No white-footed mice were found in the flood, but the size of the population per unit area, determined by live-trapping immediately after the flood, was the same as it was immediately before the flood, and a number of tagged individuals were found surviving. This species readily climbs trees and may well have passed the danger period arboreally. Tagged box turtles were found on the identical home ranges they had occupied before the flood. This flood lasted only a few days. Severe flooding persisting for long periods is known to have virtually exterminated species of small mammals from wooded floodplains in grassland areas (Blair 1939). Larger mammals, such as rabbits, opossums, and foxes, quickly leave flooded areas and may be temporarily concentrated around their margins. Squirrels and raccoons easily obtain refuge in the trees, but if the flood persists for some time, they may have trouble finding food. Woodchucks normally spend considerable time in underground burrows and may be trapped there by floodwaters (Yeager and Anderson 1944).

Invertebrates in the soil are also affected by flooding. A gradually rising water-table may eventually displace all the air from a soil, and the arthropods are killed. Many earthworms leave their tunnels when these are inundated and are killed. Some species that regularly exist in areas subjected to frequent flooding, however, are not injured. Crane fly larvae are flood-resisting. In normal flooding, bubbles of air trapped in the soil provide sufficient oxygen for at least the smaller arthropods (Kevan 1956). The eggs of some floodplain mosquitoes are laid just above the water level of pools during late summer or autumn and must be flooded the following spring before they will hatch.

SUBSERES

Abandoned fields

When farmland is abandoned, succession back to natural vegetation and ultimately to the climax is rapid, since the soil is already relatively fertile and does not need a great deal of conditioning. On the Great Plains the subsere proceeds rapidly through stages of annual herbs, several of which may be exotics naturalized from other continents; mixed annual and perennial herbs; a short-lived perennial grass; dense stands of triple-awned grass; finally, the climax of short grasses. This last stage may be attained in 10 to 20 years.

Small mammals and grazing domestic animals retard the succession by feeding on grasses while avoiding the herbs. Sheep have the opposite effect, preferring the herbs. Harvester ants denude the vegetation in a circle around their mounds and consume a considerable amount of the available seed supply. Ant coactions may be of very great importance when we consider that the population of a mound may average 10,000 individuals and the number of mounds per hectare range from 0 to 10 (0 to 4/acre) in the annuals stage, 7 to 28 (3 to 11/acre) in the mixed annual and perennial herbs, 12 to 52 (5 to 21/acre) in the first grass stage, 40 to 142 (16 to 57/acre) in the triple-awned grass, and 0 to 32 (0 to 13/acre) in the final stage (Costello 1944).

Six plant stages are recognized in the sere that develops in the mixed prairie region of Oklahoma: an initial stage of mixed herbs; three intermediate stages involving different proportions of triple-awned grass; a subclimax; and the climax of *Andropogon* and *Bouteloua* grasses. The insect population consists of 293 species representing the following orders, ranked in decreasing abundance: Coleoptera, Hemiptera, Homoptera, Diptera, and Orthoptera. There was a greater variety of species and a greater abundance of individuals in the intermediate stages than in either the early or the climax stages, probably because of the greater variety of plant species present in the intermediate stages. Of the 144 species of insects in the climax, 58 per cent entered the sere in its initial stage, 15 per cent in the second stage, 12 in the third, 5 in the fourth, 2 in the fifth, and only 8 per cent were limited to the climax itself. The ecesis of the mature animal community was therefore a gradual and progressive one. On the other hand, many species that were present in the early stages did not persist into the climax community (Smith 1940).

Succession in abandoned fields of the southern Atlantic and Gulf states is of special interest. During the first year, crabgrass and horse-weed, annuals, predominate. During the second year an aster and a ragweed, and in the third year the perennial broomsedge grass, become dominant. The grass is invaded quickly by loblolly and shortleaf pines which form closed stands in some areas in as little as 10 to 15 years. These pines do not reproduce in their own shade. They mature in 70 to 80 years, and are replaced by the climax oaks, hickories, beech, and sugar maple which take complete dominance by the time the area is 150 to 200 years old (Oosting 1942).

The bird succession (Table 8-6) shows a change from grassland to forest-edge to forest species with an increase of both species and number of pairs as the sere progresses. A great diversity of species inhabits the pine forest since several forest-edge species persist, while pine warbler, brown-headed nuthatch, solitary vireo, and yellow-throated warbler are particularly characteristic of it. Pine-mice and meadow voles are common in the grassy stages and pine-mice, cotton-mice and golden mice in the forested stages.

In Michigan, the sere in abandoned fields passes through the following stages: annuals-biennials;

FIG. 8-11 Stages in the strip-mine plant sere in east central Illinois. (a) sweet clover, aster, ragweed, after 7 years. (b) same area 10 years later, trees invading. (c) silver maple-cottonwood-sycamore floodplain forest after about 40 years (Wetzel 1958).

perennial grasses; mixed herbaceous perennials; shrubs; and finally three tree stages, the first reached in 21 to 25 years. Prairie deer mice are at their most abundance during the early stages, meadow voles in the intermediate grassy stages, and the woodland white-footed mouse and short-tailed shrew in the shrub and tree stages. Such game species as ring-necked pheasants, bobwhite, and cottontail rabbits are common on abandoned farmlands but give way to another group of game species, including white-tailed deer, ruffed grouse, and gray squirrels, when the forest stages become established (Beckwith 1954).

Pastures

Pastures in northern Ohio contain a sod principally of blue grass. With light grazing, this sod will resist invasion of other species for a long time, but with heavy grazing, resistance is weakened and unpalatable herbs, briars, and hawthorne come in. The latter two species are armed with prickles or thorns discouraging animal browsing. When they become dense enough they kill the grass beneath them. Eastern redcedar may establish itself in horse pastures, but not in cattle pastures; cattle browse it but horses will not. In the middle of protecting thickets of briars, hawthorns, and redcedar such deciduous trees as elm, ash, tuliptree, sycamore, and oak come in. After a few years they grow beyond the reach of animals, shade out the briars, hawthorns, and red cedar, and establish a forest dominance. Where left undisturbed by man, the succession of native vegetation will thus bring about the elimination of domestic animals from the area and replacement with the biotic climax natural for the region.

In western areas too dry for deciduous forest, overgrazing reduces the vigor and abundance of the taller climax grasses, and the short grasses that are less easily grazed are favored. Unpalatable herbs, sagebrush, cacti, and mesquite may also replace grasses over extensive areas. Although native animals such as the bison and pronghorn may have heavily grazed the original prairie in locally arid regions, the result was less drastic than that produced by the heavy concentrations of grazing stock on our farms and ranches at the present time. When the most favored vegetation was reduced, native animals commonly dispersed into other areas so that the carrying capacity of the land was not critically reduced.

Burns

Prairie fires, frequently started by lightning or by Indians, were doubtless important in preventing deciduous forest from succeeding grassland in parts of the middlewest. More lately, fires are started by careless campers or travelers. Fires are especially destructive in coniferous forests, as the clinging dry needles encourage crown as well as ground fires to develop. Many thousands of square miles of forests are burned over annually.

The extensive pure stands of longleaf pine on the coastal plain of the southeastern states are probably a consequence of ground fires that regularly occurred at intervals of 3 to 10 years before white men came. The terminal bud of the longleaf pine is well protected by a thick covering of green leaves, one of several characteristics that make the species extremely fire resistant (Chapman 1932). Fire destroys all seedling hardwood trees as well as other species of conifers.

When coniferous forest is destroyed by fire, the first trees to invade are usually quaking aspen, paper birch, and sometimes balsam poplar. These forests cover extensive areas in Canada and southward on the Rocky Mountains. Jack pine in the north and lodgepole pine in the western mountains either come in with the deciduous trees or succeed them. The cones of these two trees take several years to open and shed the seeds held within, and may not do so at all unless heated by forest fires. Aspen and pine are eventually replaced by the climax forest. In many

TABLE 8-6 **Breeding bird pairs per 40 hectares (100 acres) in sere developing on abandoned fields, Georgia Piedmont region, averaged from two stations in herb-shrub (1, 3 years old), three stations in grass-shrub-tree (15, 20,25 years old), four stations in pine forest (25, 35, 60, 100 years old), and one station in oak-hickory (over 150 years old) (condensed from Johnston and Odum 1956).**

Bird species	Herb-grass	Grass-shrub-tree (forest-edge)	Pine forest	Oak-hickory climax
Grasshopper sparrow	20	8		
Eastern meadowlark	8	6		
Yellowthroat		11		
Yellow-breasted chat		7		
Prairie warbler		4		
Catbird		1		
Indigo bunting		1		
American goldfinch		+		
Bobwhite		+		
Field sparrow		36	4	
Rufous-sided towhee		9	13	
Bachman's sparrow		5	1	
Pine warbler		5	43	
White-eyed vireo		3	3	
Mourning dove		+	+	
Cardinal		6	15	23
Summer tanager		2	14	10
Chuck-wills-widow		+	+	+
Brown-headed nuthatch			2	
Brown thrasher			1	
Solitary vireo			1	
Yellow-throated warbler			1	
Pileated woodpecker			+	
Hooded warbler			11	11
Carolina wren			10	10
Ruby-throated hummingbird			6	10
Blue-gray gnatcatcher			5	13
Tufted titmouse			5	15
Eastern wood pewee			4	3
Blue jay			4	5
Carolina chickadee			4	5
Crested flycatcher			4	6
Red-eyed vireo			4	43
Yellow-throated vireo			3	7
Wood thrush			2	23
Yellow-shafted flicker			1	3
Hairy woodpecker			1	5
Downy woodpecker			1	5
Yellow-billed cuckoo			+	9
Black and white warbler				8
Acadian flycatcher				5
Kentucky warbler				5
Total species	2	18	30	22
Total pairs	28	104	163	224

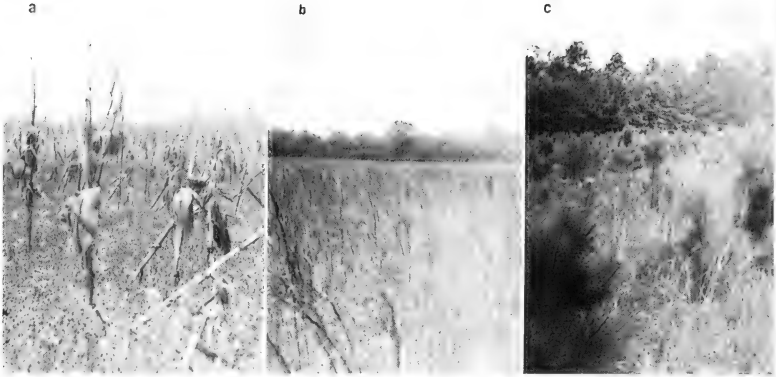


FIG. 8-12 **Plant succession in abandoned fields in Virginia. (a) annual herbs invading old cornfield. (b) broom-sedge grass. (c) invasion of young pine trees.**

FIG. 8-13 **The Tillamook Burn in coniferous forest in Oregon, 1944 (courtesy U.S. Forest Service).**

FIG. 8-14 **This aspen forest in New Mexico will be replaced by one of spruce as the young trees now forming in undergrowth reach maturity (courtesy U.S. Forest Service).**

western areas, particularly in the Sierra Nevada, chaparral may occur in dense stands after fires and persist for a long time.

Since the burn subsere in coniferous forest commonly includes the aspen-birch associes, many of the typical animals in this stage are deciduous forest and forest-edge species, although there is a penetration of coniferous forest species as well. The birds and mammals are not generally very numerous in the aspen-birch community, but ground invertebrates may be more abundant here than in the poorly decomposed acidic ground duff found in the coniferous climax.

ANIMAL COMMUNITIES

Although the plant communities that make up the stages of the different land seres and subseres we have described are numerous and varied, the number of distinct animal communities that can be clearly recognized are few. Actually, we can distinguish in eastern North America only the animal communities of *grassland, forest-edge, deciduous forest, southeastern evergreen forest* and *coniferous forest.* Each of these communities varies in the different habitats of rock, sand, and clay, and in the various subseres, but the variations are of minor significance and are best treated as facies of the larger communities.

SUMMARY

For terrestrial living, animals must actively support themselves against gravity, obtain water, and prevent excessive water losses from the body. They must be equipped to endure a wide range of fluctuating temperatures, to secure oxygen, to endure intense solar radiation, adjust to diurnation (day and night) and aspection (seasonal changes), and yet maintain close contact with the substratum.

Succession occurs on all primary bare areas, such as rock, sand, clay, and floodplains, and in such secondary bare areas as abandoned fields, pastures, and burns. In humid regions, all seres converge to the same climax community. There are normally more plant than animal stages in any sere. The succession program of animal communities correlates with the succession program of vegetation-types or life-form of the plant dominants, not with plant communities identified by the taxonomic composition of the plant dominants. In eastern North America, we can distinguish only the grassland, forest-edge, deciduous forest, southeastern evergreen forest, and coniferous forest terrestrial animal communities.

9

Grassland, Forests, and Forest-edges

We have seen that succession of animal communities in humid climates passes through three terrestrial stages before attaining climax: grass, shrubs and scattered trees (forest-edge), and forest. In arid climates, the climax may be reached at the first or second stage. It is important for us to examine each community in more detail, therefore, if we are to gain an understanding of the ecology of animals prevailing locally in different parts of the world.

VEGETATION

Grassland vegetation differs from forests in that the above-ground vegetation is completely renewed each year. Grasses may be divided into three categories on the basis of height: *tall grasses* (1.5–3 meters tall), such as big bluestem and slough grass; *mid grasses* (0.5–1.5 meters tall), such as little bluestem and needle grass; and *short grasses* (less than 0.5 meter tall), such as buffalo grass and grama grass. The taller grasses grow in wet habitats, the short grasses in arid habitats. Most native grasses are *bunch grasses* in that they grow in clumps with the areas between the clumps either bare ground or occupied by other species. Broad-leaved herbs occurring between the dominant grasses are called *forbs*. A few species are *sod formers* in that their growth is continuous over the ground surface. The leafy aerial parts of perennial grasses die in the winter or in dry season, leaving the underground stems or rhizomes to propagate the plant the following year (Weaver and Fitzpatrick 1934).

Forests are composed of trees growing sufficiently close together to dominate the entire area of ground surface. In cold climates, forests are needle-leaved evergreen; in intermittently warm, moist climates, they are broad-leaved deciduous; and in continuously warm, moist climates, they are broad-leaved evergreen. In spite of these secondary differences in life-form, the structure and internal dynamics of all forest communities are quite similar. Useful methods for measuring the density of trees per unit area are described by Cottam and Curtis (1956).

Between forests and open country, the trees are often widely spaced and do not completely dominate the area; open-country shrubs and grasses become interspersed. This transition area is usually narrow around the margins of a mature forest, but where succession is occurring, large areas of shrubs containing small or scattered trees are essentially forest-edge in character. Likewise, in agricultural areas, hedge and fence rows, or narrow strips of trees and shrubs along streams, are really edges without the adjacent forest. Essentially, forest-edges provide, in close proximity, forest, shrub, and open ground habitats which animals take advantage of in a variety of unique ways.

Deciduous trees shed their foliage in the autumn, are bare over winter, and obtain new foliage in the spring. Coniferous trees, on the other hand, retain their foliage throughout the year, although old dried leaves fall a few at a time at all seasons. Differences in the size, shape, and structure of the leaves are important to many animals. The lack of foliage in deciduous forests during the winter permits a greater light penetration to the forest floor, more wind circulation, and relatively lower temperatures than in coniferous forests. During the summer, deciduous forests generally have higher but more variable temperatures and lower relative humidities than do coniferous spruce and fir forests (Blake 1926, Dirks-Edmunds 1947). Pine forests, however, commonly develop in habitats that are warm and dry.

As shade producers, the deciduous and coniferous trees do not vary as groups, but only as individual species (Weaver and Clements 1938):

Deciduous trees	Coniferous trees
Heavy shade producers	
Sugar maple	Yew
Beech	Spruce
Basswood	Hemlock
	Firs
	Thujas
Medium shade producers	
Elms	Eastern white pine
White oak	Douglas-fir
Northern red oak	
Ash	
Black oak	
Light shade producers	
Silver maple	Ponderosa pine
Bur oak	Tamarack
Birches	Lodgepole pine
Poplars	
Willows	

It is interesting that light shade producers are species found in the early stages of succession while the heavy shade producers are mostly climax species.

There is an important difference between deciduous and coniferous forests in the nature of the decomposing dead leaves that fall from the trees. Decomposition of broad leaves is rapid and relatively complete to form a rich humus that mixes gradually with the mineral soil beneath. Needle leaves decompose slowly and form a somewhat acid humus sharply defined from the underlying mineral soil. Humus formed in humid grasslands is similar to but richer than that of deciduous forest; in arid grasslands it is poorly developed. The nature of the humus and litter affects the number and kinds of animals that occur in the soil.

In grassland there are three strata of vegetation: *subterranean*, composed of roots and other underground plant parts as well as bacteria, fungi, and algae, *ground*, including the surface litter, and *herb*, the stems and leaves of the grasses and forbs. The forest not only has these strata, but also one of *shrubs* and one or more of *trees*. Animals characteristically limit their major activity to one or more of these strata.

HABITAT

Grassland, forest-edge, and forest-interior compared

At the University of Illinois, no significant difference in mean monthly temperatures, calculated bihourly day and night, has been found between the interior of a virgin oak-maple forest and an adjacent open grassland. In the forest, however, the daily extremes are not so great; i.e., the maximum mid-afternoon temperature is not as high, nor the minimum night temperature so low, as in the grassland.

Relative humidity during a summer day in Iowa was found (Aikman and Smelser 1938) to average 20 per cent lower in grassland than in a shrubby forest-edge, and 5 to 8 per cent lower in the forest-edge than in the forest-interior. There is less difference between the three habitats, however, at night. Rate of evaporation, as measured with Livingston atmometers, is inversely correlated with humidity, being greatest in grassland and least in the forest-interior. Daily changes in relative humidity between day and night tend to vary inversely with the temperature, except when there is rain.

During four years at the University of Illinois woods, rain gauges recorded 88.8 cm (35.5 in.) per year in the adjacent grassland, upon which full precipitation fell, and 70.1 cm (28.0 in.) *throughfall* (the amount reaching the ground) under the tree canopy of the forest. There was variation of throughfall from spot to spot in the forest, depending on the location of openings in the canopy and drip-points from the leaves and stems. *Stem-flow* of water down the tree trunks was not measured. Throughfall and stem-flow together make up the *net rainfall*. In a shortleaf pine plantation in southern Illinois (Boggess 1956), the net rainfall over three years averaged 91.2 per cent of the total rainfall. *Interception,* the amount of rainfall presumably evaporated back into the air, was 100 per cent in very light rainfalls but less than 5 per cent of rainfalls exceeding 5 cm (2 in.).

In a beech-maple forest in northern Ohio, which bordered on an open field, wind velocity at a distance 245 meters (about 800 ft) inside the west margin

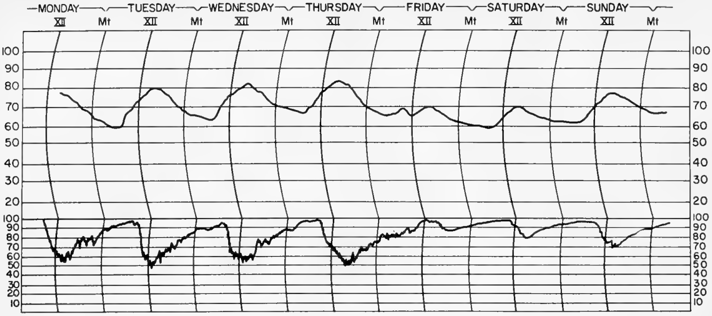


FIG. 9-1 **A weekly chart from a hygrothermograph placed at shrub level in a deciduous forest in central Illinois.**

was reduced to a minimum of 10 per cent when the trees were in leaf and 25 per cent when not (Williams 1936). With a protective edge of shrubs, the wind velocity would doubtless have been decelerated more quickly.

Summer light intensities are much less under foliage than out in the open. Noontime illumination under shrubs in Iowa averaged 26 per cent of full sunlight; within the forest interior, 6 per cent (Aikman and Smelser 1938). The forest floor is not uniformly illuminated because small openings in the canopy admit sun-flecks of varying intensity. In the cottonwood, pine, black oak, and sugar maple stages of the sand sere at the lower end of Lake Michigan, the percentages of the forest floor shaded during the midday hours were 68, 87, 75, and 90 per cent, respectively (Park 1931). There may be some change in the quality of light that filters through the forest canopy, as there is of intensity, as some wavelengths are used more than others in photosynthesis; green is transmitted or reflected and not absorbed. Where a stand of trees abruptly confronts an open field, light penetrates laterally under the forest canopy and, the typical edge configuration reversed, the light permits shrubs to extend 40 meters or more into the interior.

Vertical gradient

There is a gradient in microhabitat factors from above the grasses down to the ground. In one study of virgin prairie (Weaver and Flory 1934), light intensity varied from 100 per cent in full sunlight to 25 per cent at one-half the pile depth of the grasses to 5 per cent at the base of the stems, and, of course, zero per cent in the subterranean stratum. The relative humidity above the grass was 20 per cent; in the grass, 31 per cent. The wind velocity above the prairie grasses was 14.5 km/hr (9 mph); at the top level of the grasses, 6.0 km/hr (3.7 mph); at the soil surface, zero. The rate of water evaporation from white spherical atmometers was 55.3 cc/day above the grasses, 33.3 cc at top surface of the grasses, 15.1 cc at one-half the pile depth of the grasses, and only 13.4 cc just above the soil surface. The temperature gradient varies with the height of the grass and between day and night.

The vertical gradient of temperature in a deciduous forest in central Ohio varies with the season and with the height of macroclimatic temperature (Table 9-1). In the summer, the greatest extremes of temperature occur in the canopy, but at other levels, both above and below the ground, summer daily mean temperature is more stable than at any other season. Because the canopy largely controls the air temperature beneath it, there is little or no thermal stratification between it and the ground. Summer soil temperatures are always lower at 1.2 meters below the surface than at the surface. For comparison, air temperatures in a coniferous forest in Wyoming during July and August averaged 12.3°C at 0.1 meter above the ground and 7.6°C 0.1 meter below the surface litter (Fichter 1939).

During the winter, temperatures in deciduous forests are lowest near the ground and more uniform at all higher levels than during the summer, since the absence of a canopy permits greater turbulence, hence less stratification, of the air. Soil temperature at 1.2 meters depth is generally higher than surface tem-

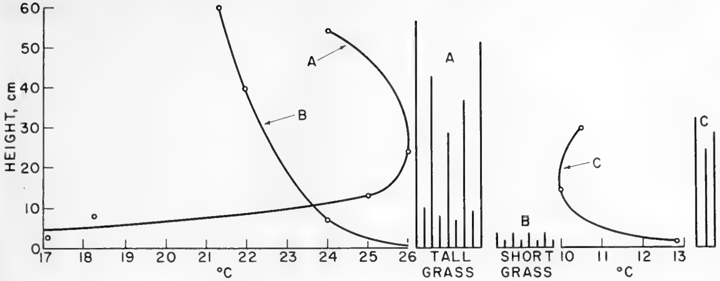


FIG. 9-2 **Gradient of air temperatures in and above (a) tall grass and (b) short grass on a sunny day, and (c) in grass of medium height at night (after Waterhouse 1955).**

perature; beneath the litter in the central Ohio area temperatures do not usually go below freezing (Christy 1952). A covering of snow gives added protection against freezing of the leaf litter. Another study (Wolfe *et al.* 1949) revealed differences between temperatures above and below a snow covering 2 to 10 cm deep during a period of two months averaged 8.9°C, and on one occasion reached 15.5°C.

Relative humidity decreases from the ground stratum upwards. In a young elm-maple forest in Tennessee, the relative humidity from mid-February to mid-August averaged 77.9 per cent at the surface of the leaf litter, 75.2 per cent in the herb stratum 0.5 meter above the ground, 72.5 per cent in the shrub stratum at 0.9 meter above ground, and 67.4 per cent in the trees at 7.6 meters above ground (Adams 1941). In this same forest, the rate of evaporation between May and November in the four strata respectively averaged 29.4, 60.7, 72.8, and 99.2 cc per week. In a spruce-fir forest in Wyoming, the average weekly evaporation at 0.1 meter was 50.5 cc, at 1 meter 75.2 cc, and at 3 meters 103.9 cc (Fichter 1939).

In the Tennessee elm-maple forest mentioned a moment ago (Adams 1941), the average daily midsummer light intensities measured with a MacBeth illuminometer for ground, herb, shrub, and tree (beneath the canopy) levels were respectively 52.3, 60.3, 60.4 to 76.2 foot-candles; in early May, before the foliage was fully developed, intensities of 65.8, 78.3, 104.4, 119.1 foot-candles were measured. Under the leaf litter and in the soil, the light intensity was, of course, zero. Above the trees it was doubtless several thousands of foot-candles. Maximum light intensities from the sun occasionally reach 15,000 foot-candles. There are, therefore, three distinct sections in the vertical gradient; below ground surface, between ground and tree canopy, and above the canopy.

Ground insects, millipedes and isopods, when placed in experimental gradients, show a preferendum for lower light intensity, higher humidity, and lower temperature than do insects taken from the herb or shrub startum (Table 9-2). In grassland, motile organisms can quickly vary the microhabitat to which they are exposed by changing their vertical position only a few centimeters, and they do shift in position as the gradient varies at different times of day or from day to day. To obtain an equivalent

TABLE 9-1 **Vertical gradient of temperature in a beech forest in central Ohio (Christy 1952).**

Elevation	May - September			November - December		
	Minimum	Maximum	Range	Minimum	Maximum	Range
Macroclimate	10.0°C	34.4°C	24.4°C	-19.4°C	18.3°C	37.7°C
+25.0 meters	7.8	31.7	23.9	-17.8	13.3	31.1
+18.9	8.9	30.0	21.1	-17.2	13.3	30.5
+6.1	8.9	30.0	21.1	-16.1	13.9	30.0
+1.5	8.9	28.9	20.0	-21.1	12.2	33.3
Surface of leaf litter	9.4	28.3	18.9	- 8.3	8.3	16.6
Under leaf litter	12.2	22.2	10.0	0	10.0	10.0
- 0.15	12.2	18.9	6.7	2.8	12.8	10.0
- 1.2	10.6	16.1	5.5	4.4	13.3	8.9

TABLE 9-2 Results of experiments conducted in the field to establish light orientation of arthropods taken from different strata.

		Light intensity gradient			Control (no gradient)		
Mixed species	**Number of experiments**	**Strong**	**Intermediate**	**Weak**	**Left**	**Middle**	**Right**
Grassland animals from herb stratum	5	47%	34%	19%	40%	31%	29%
Forest animals from herb and shrub strata	7	46	21	33	33	30	37
Grassland animals from ground stratum	5	24	27	49	34	23	42
Forest animals from ground stratum	8	18	23	59	34	29	37

change in microhabitat in the forest gradient requires a shift of several meters in vertical position. Experiments show, however, that each forest animal species occupies a stratum approximating its preferendum for a particular microhabitat, in response especially to the relative humidity factor (Todd 1949).

Slope exposure

Microclimatic differences between North- and South-facing slopes are great. South-facing slopes receive a greater amount of solar radiation and are commonly exposed to the prevailing winds. As a consequence, both air and soil temperatures are higher on South-facing slopes than on North-facing slopes; relative humidity is lower, soil moisture lower, and the rate of evaporation is higher. The differences between the two slopes are most marked close to the ground, increasingly less so at higher levels (Cantlon 1953).

The vegetation on the protected North-facing slopes is usually more mesic in type and more luxuriant than on the exposed South-facing slopes, and there is a deeper organic leaf litter on the ground. Types of vegetation characteristic of arid habitats penetrate humid climates on South-facing slopes; mesic vegetation penetrates the relatively arid climates obtaining on North-facing slopes. Southern types of vegetation invade boreal climates on the warm South-facing slopes, and boreal vegetation invades southward on North-facing slopes. In mountain areas, vegetation characteristic of lower altitudes penetrates higher on South-facing slopes, and vegetation of the upper altitudes penetrates farthest downward on North-facing slopes. Animals are locally distributed in a similar manner, partly as a direct response to the climate, partly to the differences in vegetation. Many other differences in microclimate occur in various parts of the forest and forest-edge (Wolfe *et al.* 1949), and in grassland.

In studying the distribution of animals in relation to climate, it is obviously not sufficient to consider only the macroclimate. Animals respond to the microclimate of their particular niches, and the relation between these microclimates and the prevailing macroclimates of the region must be demonstrated.

THE GRASSLAND COMMUNITY

Invertebrates

Snails, earthworms, and myriapods are not numerous in grassland because of the dry habitat. Insects, however, are abundant; some 1175 species and varieties have been listed for different grassland plant communities in Iowa (Hendrickson 1930). These belong principally to the orders Orthoptera, Hemiptera, Homoptera, Coleoptera, and Diptera. Ants, bees, and wasps (Hymenoptera) are also numerous.

Spiders make up about 7 per cent of the total arthropod population in grassland. In one study made in Nebraska (Muma 1949), 111 species were collected from 128 hectares (320 acres) of mixed high and low prairie containing some shrubs. Less than a dozen species were web-builders; there is a lack of suitable web-building sites in grasslands. The vast majority were wandering cursorial forms. In regard to strata in this prairie, 45 species were restricted to the soil and litter, 30 to the herbs, 1 to the shrubs. Thirty-five species occurred in two or more strata. The total population for the area was least in the spring and greatest in the autumn. Peak populations in the ground stratum were reached during the winter, however, because of the presence of many hibernating immature forms. Similar seasonal fluctuations occur with other invertebrates, although the peak populations of insects are usually attained during the summer (Shackleford 1939, Fichter 1954).

In grazed pastures and in grassy meadows in New York State, invertebrates average 777 individuals per square meter (Wolcott 1937). Of this population, ants make up 26 per cent, leafhoppers 15 per cent, other insects 34 per cent, spiders 9 per cent, millipedes 9 per cent, sowbugs 2 per cent, snails and slugs 2 per cent, earthworms 2 per cent, and large nematodes 1 per cent.

Some insects show structural adaptations for living in grassland (Hayes 1927). May beetles in forested regions commonly feed at night on the foliage of trees and have well developed wings, but closely related species in grassland areas feed on low growing plants during the day and are flightless. The development of pilosity and thick integuments in some insects appears to be an adaptation to prevent evaporation. Prairie May beetles pupate in the spring rather than autumn, probably in correlation with their change in food habits, and adults appear in midsummer rather than late spring.

An insect microhabitat of special interest is the dung of the larger mammals. Bison formerly occurred in frequency one to 10–20 hectares. Inasmuch as the output of each animal is about 25 droppings per day, the number of these microhabitats available was considerable. Some 83 species of arthropods have been collected from cow dung, mainly beetles and flies, but including annelids, nematodes, and protozoans. There is a regular succession of insect species breeding and maturing. The microsere is completed in about eight days, the length of time required for the droppings to dry. The first species that arrive are the obligatory breeders on dung. They have the shortest life-histories, and remain for the shortest time. Predatious and parasitoid species prey on the coprophagous ones. The greatest variety of species is present at the middle of the microsere, but the composition of species varies with the season. Species disappear as the dung disintegrates into the general surroundings (Mohr 1943, Laurence 1954). A comparable microhabitat and succession occurs in carcasses of dead animals (Chapman and Sankey 1955).

Vertebrates

Table 9-3 gives a representative sampling of small mammal populations found in grassland, although it is to be expected that the species composition and size of populations will vary locally and from year to year. The mores of grassland mammals, which show how they are adjusted in behavior to live in this community, are tabulated in Table 9-4.

Birds are not numerous in grassland. In northwestern Iowa (Kendeigh 1941b), grasshopper sparrows, western meadowlarks bobolinks, ring-necked pheasants, marsh hawks, and short-eared owls averaged less than one pair per hectare (2.5 acres). Prairie chickens and sharp-tailed grouse formerly occurred where now is to be found only the introduced pheasant. The eastern meadowlark predominates over the western meadowlark in the wetter and smaller pastures east of the Mississippi River. Vesper sparrows and horned larks occur in short grasses, but usually not in climax areas with dense tall grasses. Upland plovers, Henslow sparrows, lark buntings, and longspurs are common locally.

Some fourteen species of snakes are generally distributed over the prairies (Carpenter 1940). To the east, the blue racer, massasauga, bullsnake, and garter snakes are frequently found. The prairie rattlesnake is increasingly common westward. The lizards *Cnemidophorus sexlineatus, Sceloporus undulatus,* and *Holbrookia maculata,* commonly occur in grassy areas at forest-edges. The horned toad is found in arid habitats.

The most characteristic amphibian of grassy areas is the toad. All species breed in the ephemeral bodies of water resulting from the rains of spring and summer. One species, *Bufo cognatus,* will not breed unless it rains, even though bodies of water are present. During the hot, dry weather of later summer, the toads retreat to burrows in the earth or to other shelter until favorable conditions again return (Bragg and Smith 1943).

Grazing food coactions and range management

Since the vegetative productivity of grasses is very high, herbivorous animals, especially large mammals, are favored in the grassland community (Renner 1938). Unlike trees and shrubs, the terminal bud on grasses lies close to the ground and is not ordinarily injured by grazing. Meristematic tissue lies at the base of the leaves so that when the terminal portion of the leaf is eaten off, the leaf keeps on growing. Actually, lateral branching at the base of the grass stem is stimulated by grazing, and a thicker and more succulent growth with less fiber is produced. Productivity of grass is reduced if the herbage is removed more than two or three times during the growing season. However, total protein production is not diminished, for frequent clipping results in an increased ratio of leaves to stem, and leaves are much richer in protein content. Light to moderate grazing

TABLE 9-3 **Population of small mammals per hectare (2.5 acres) in mixed prairie of western Kansas (after Wooster 1939).**

Mammal species	Number
Prairie meadow-mouse	9.6
13-striped ground squirrel	7.6
Prairie white-footed mouse	6.8
Harvest mouse	2.8
Little shrew	2.4
Short-tailed shrew	1.3
Black-tailed jackrabbit	0.7
Cottontail rabbit	0.1
Total	31.3

TABLE 9-4 A tabulation of certain grassland mammal mores (Carpenter 1940).

Mammal species	Social life		Stratum			Food habits			Seasonal activity		Production of young		Daily period of activity			
	Solitary or family groups	Herds or packs	Fossorial, locally cursorial	Fossorial	Cursorial	Herbivorous	Omnivorous	Carnivorous	Migratory	Hibernating	2 litters / yr	1 litter / yr	Diurnal	All 24 hours	Crepuscular	Nocturnal
Bison		×			×	×			×			×	×			
Pronghorn antelope	×				×	×						×	×			
Wapiti		×			×	×						×		×		
White-tailed deer	×				×	×						×			×	×
Mule deer	×				×	×			×			×			×	
Cottontail	×				×	×					×			×		
White-tailed jackrabbit	×				×	×						×		×		
Prairie-dog		×	×			×				×		×	×		×	
Prairie white-footed mouse	×				×		×				×				×	×
Prairie meadow-mouse	×				×		×		?		×				×	×
Jumping mouse	×		×			×				×		×		×		
Pocket mouse	×				×		×				×				×	×
Harvest mouse	×				×		×				×				×	×
Franklin ground squirrel	×		×				×			×		×	×			
13-lined ground squirrel	×		×				×			×		×	×			
Pocket gopher	×			×		×						×			×	×
Richardson ground squirrel		×	×				×			×		×	×			
Wolf		×			×			×	×			×		×		
Coyote	×		×				×					×			×	×
Badger	×			×				×				×			×	×
Bobcat	×				×			×				×			×	×
Skunk	×		×					×				×			×	×
Weasel	×				×			×				×			×	×
Red fox	×		×				×					×		×		
Swift fox	×		×					×				×			×	×
Shrew	×				×			×			×				×	×

can, therefore, be carried with full or nearly full productivity. Heavy grazing, however, should not be permitted. In addition to reducing herbage production, heavy grazing may destroy seed stalks prior to the dropping of the seed or so weaken the plants physiologically that seed is not even produced. The growth of underground rhizomes and vegetative reproduction is retarded when photosynthetic activity is reduced. The best pastures are those in which grazing animals do not consume more than 70 to 80 per cent of the total herbage productivity of the grasses (Stoddart and Smith 1943). As a rule, not more than about 60 per cent of the current forage volume and 25 per cent of the flower stalks should be harvested by grazing animals. Overgrazing always brings about a reduction in abundance of the more palatable species and an increase in the less desirable ones with the consequent deterioration of the range and the productivity of the community (Weaver and Tomanek 1951, Kucera 1956). The carrying capacity of grassland or the largest number of animals that can be supported without deterioration of the range varies with the type of grasses involved, the climate, and the soil (Table 9-5).

Although often overlooked, invertebrates constitute one of the three important groups of grazing animals. Individually they may not consume appreciable amounts, but in the aggregate they produce a very significant effect. The total biomass of insects in a New York pasture amounted to 3.2 g dry weight per square meter. This is to be compared to 14.5 g for the dry weight of cows per square meter that the pasture was supporting. Feeding experiments showed that in one pasture where grazing by the cattle was moderate and the vegetation was ample, the insects ate more of the grasses and clovers than the cows did, but in another pasture which was being overgrazed and in which the vegetation was short, the cattle ate more than the insects did (Wolcott 1937). Grasshoppers and Mormon crickets are sometimes very destructive in the arid west. In one area in Montana, a population of 25 grasshoppers per square

FIG. 9-3 **Forest-edge at William Trelease Woods, University of Illinois: prairie grasses and herbs in foreground, briers and shrubs in middle, forest in background.**

meter destroyed enough forage on three acres during one month to support one cow for a month (Stoddart and Smith 1943).

Rodents and rabbits consume very considerable amounts of grasses and other herbs and cause great damage at times of high populations. In a study performed in Arizona (Taylor 1930), grazing by Gunnison's prairie dogs alone consumed 87 per cent of the total grass production and grazing by cattle and rodents combined, 95 per cent. In California, Beechey's ground squirrels eliminated 35 per cent of the green forage by the end of the season, pocket gophers 25 per cent, and kangaroo rats 16 per cent (Fitch and Bentley 1949). Since these various rodents have food preferences of grass species similar to those of cattle, there is obviously severe competition between them, especially in times of drought. When rodents are not overly abundant, they have some beneficial effects in fertilizing, aerating, and mixing the soil.

Among big-game mammals, bison and wapiti are largely grass-eaters, especially during the summer season. Food consumption of bison is about equal to that of cattle, but wapiti eat only about half as much per individual. In Yellowstone Park it has been estimated that wapiti may utilize 67 per cent of the avail-

TABLE 9-5 **Carrying capacity of natural grasslands for big game and livestock (from various sources, compiled by Petrides 1956).**

Location	Game or livestock	Number/mi^2 ($2.6\ km^2$)	Biomass/mi^2	
			Pounds	Kg
Oregon	Antelope (64%), mule deer (36%)	9	1,000	454
Tanganyika, Africa	Bush country game	10	3,300	1,498
Montana	Bison (50%), mule deer, elk, bighorn	21	14,000	6,356
Arizona	Bison	17	17,000	7,718
Western U.S.	Cattle, ave. all grassland types	20	20,000	9,080
Western U.S.	Cattle, tall grass prairie	28	28,000	12,712
Nairobi Nat. Pk., Africa	(1) herbivorous big game	85	28,000	12,712
Nairobi Nat. Pk., Africa	(2) herbivorous big game	134	47,700	21,656

FIG. 9-4 Interior of a temperate deciduous forest of sugar maple, basswood, and American elm in Wisconsin (courtesy U.S. Forest Service).

able grass forage, 47 per cent of forbs, and 30 per cent of browse. Browse and forbs are used more than grasses by pronghorn antelope and deer (Stoddart and Smith 1943). Because of difference in food preferences, competition between the latter big-game species and cattle, although significant, is not as great as is sometimes supposed. Furthermore, deer and wapiti are able to graze steep slopes and other areas which cattle ordinarily do not (Stoddart and Rasmussen 1945). Competition between deer and wapiti, sheep and goats is more direct, however, because sheep and goats also feed largely on forbs rather than on grass.

Overgrazing produces a change both in the kinds and numbers of animals present (Table 9-6). This is correlated with the change from mid-grasses to short grasses to weedy perennials. The short-horned grasshoppers increase in variety of species with this change, but in other orders of insects, the number of species present in overgrazed pastures either remains the same or declines. There is generally an increase in population level of all groups of arthropods, except beetles, with overgrazing until the pasture deteriorates to such an extent that erosion becomes severe, then there is a decline in abundance of all groups except the Hymenoptera and Lepidoptera.

Meadow voles, cotton rats, and cottontails are less numerous in overgrazed than in undisturbed grassland, but other rodents and lagomorphs increase in abundance. Tall grass in ungrazed pastures hinders the vision of jack rabbits, kangaroo rats, prairie dogs, and ground squirrels. Some rodents are benefited by the larger and more numerous seeds of the annual weedy species, and pocket gophers find more tap- and bulbous-rooted plants in deteriorated range (Bond 1945). Increased populations of insects and rodents are a result, not a cause, of overgrazing. If grazing by larger mammals is eliminated, succession back to thick grassland will occur in spite of the smaller animals, and prairie dogs and ground squirrels may actually be eliminated from the area (Osborn and Allan 1949).

In the luxuriant native prairie of early days, there was seldom overgrazing by such large mammals as bison, antelope, and wapiti, although this sometimes occurred in the more arid Great Plains. Insects and rodents occurred in populations that were in equilibrium with their food supply, and overpopulations of the species were held in check partly by the vegetation itself and partly by predatory birds, mammals, and reptiles. The most important of the larger predators were the hawks and owls, coyotes, foxes, badgers, black-footed ferrets, bullsnakes, and rattlesnakes (Shelford 1942). In California, it has been estimated that these predators eliminate about half of the annual increase of ground squirrels (Fitch 1948). Because coyotes and wolves occasionally took calves and lambs, they were systematically killed by ranchers; many other predators suffered with them. With the elimination of these predators, one of the checks on the rodent population was removed at a time when increased grazing by livestock rendered

FIG. 9-5 **Interior of a virgin coniferous forest of Engelmann spruce in Colorado (courtesy U.S. Forest Service).**

this control even more desirable. Damage done to the range by increased populations of rodents and rabbits has undoubtedly been much greater than the monetary value of an occasional killed lamb, calf, or chicken. In the great grasslands of the West, where human populations are low, there would be advantage not only in reducing the amount of grazing by livestock to the carrying capacity of the land but in restoring balanced populations of herbivorous and carnivorous species.

THE FOREST-EDGE COMMUNITY

Grassland animals are usually restrained from penetrating forests in the same way that true forest animals are restrained from penetrating grassland, although the home ranges of these species may overlap at the forest margin and in shrubby areas. Since shrubs are especially numerous at the forest-edge and animals have an opportunity to make use of these as well as both grassland and forest, the forest-edge biocies is well developed for some groups of animals. There are probably no soil or small ground animals characteristic of the forest-edge. There are some foliage insects that find their preferred niches here. Many insects of grassland and agricultural crops that overwinter as adults migrate into the forest-edge to hibernate. Since many game species of interest to man reach their greatest abundance on the forest-edge, he has become impressed by this so-called *edge effect.* When total populations of all species are measured, however, the density of birds (Table 9-11) or mammals is not always higher than in the forest. When two forest types come in contact, for instance different deciduous forest types or deciduous and coniferous forests, there is no consistent change in the density of animal species (Barick 1950). The forest-edge is the preferred nesting site of many birds (Johnston 1947).

Order	Normal prairie	Properly grazed	Slightly over-grazed	Heavily over-grazed	Severely overgrazed and eroded
Coleoptera	29	27	19	14	11
Hemiptera	17	11	22	36	14
Homoptera	21	24	22	26	8
Hymenoptera	9	11	6	30	45
Diptera	19	22	23	30	6
Orthoptera	15	16	34	20	15
Lepidoptera	11	13	22	17	38
Arachnida	25	21	25	21	9
Total	19	19	25	24	13

TABLE 9-6 **Relative abundance (per cent of total specimens collected) of various orders of arthropods in normal and overgrazed grasslands in Oklahoma (after Smith 1940).**

TABLE 9-7 Size of animal populations in forest and forest-edges, May to September, exclusive of mesofauna and microfauna of the soil.

Taxonomic group	Deciduous forest, central Ill.[1]	Coniferous forest, Utah[2]	Chaparral, Utah[3]
	Number per hectare		
Shrews, mice chipmunks	62	31	87
Squirrels, cottontails, raccoons, etc.	1	20	+
Birds	12	24	25
Snakes, lizards	+	+	+
Frogs, toads, salamanders	+	0	+
	Number per square meter		
Snails, slugs	79	+	1
Spiders	158	16	10
Harvestmen	12	0	0
Pseudoscorpions	10	0	4
Sawflies, wasps, bees, etc.	22	5	20
Ants	141	17	142
Flies	100	20	14
Moths, butterflies	8	0	+
Beetles	165	5	20
Leafhoppers, aphids	82	27	27
True bugs	40	3	10
Thrips	131	0	1
Psocids	1	0	0
Lacewings	1	0	+
Crickets, roaches, etc.	9	0	1
Insect larvae	307	4	20
Centipedes	67	5	3
Millipedes	31	1	2
Sowbug	24	0	0

[1] Including and extending data by Shelford 1951 (a, b)
[2] Hayward 1945
[3] Hayward 1948

THE FOREST COMMUNITY

Since the censusing of each group of animals furnishes special problems, there have been no studies of total animal populations in single forest communities. By Table 9-7, however, it appears that the ratio in numbers of individuals per hectare between different animal groups is of the order: 1 bird, 3 mammals; 13,000 snails and slugs, 20,000 centipedes, millipedes and sowbugs; 35,000 arachnids; and 225,000 large insects. The mesofauna would number in the tens of millions (Table9-8), and the microfauna in numbers so large as to be scarcely conceivable. In general, the number of individuals representing a species varies inversely with the body size characteristic of the species. There is, however, considerable variation in population levels both geographically and temporally. We must give special consideration to each of these various groups of animals.

Soil animals

Some animals, *geobionts* (Table 9-8), spend all their lives in the ground; certain protozoans, flatworms, nematodes, annelids, tardigrades, snails, millipedes, centipedes, some spiders, mites, pseudoscorpions, true scorpions, many small wingless insects, some beetles and other winged insects, and a few mammals are examples. Other animals, *geophils,* live in the ground only as eggs, larvae, or pupae, such as do many flies and beetles; in cocoons, as do some moths; or for hibernation, as do many beetles and bugs.

Soil animals are most abundant in undisturbed virgin areas. In a longleaf pine forest suffering frequent burning, the number of small animals in the humus layer was reduced to one-fifth and the number in the top 5 cm of the mineral soil was reduced to one-eleventh of the number in unburned areas (Heyward and Tissot 1936).

Some 250 species of flagellate, amoeboid, and ciliate protozoans have been recorded in the soil (Sandon 1927), but only a few species are limited in distribution exclusively to the soil since they also occur in freshwater habitats. Many species occur in practically worldwide distribution. Flagellates may range from 100,000 to 1,000,000 or more individuals per gram of soil; amoebae, from 50,000 to 500,000; and ciliates, from 50 to 1,000 (Waksman 1952). Over 150 species of rotifers are known as ground inhabitants, and about one-third of these species have been found only in the soil. They feed on organic material and, to a lesser extent, on nematodes and protozoans. Nematodes may occur to the extent of 1,000 to 10,000 individuals per cubic centimeter. Most of these forms belong to the Anguilluliformes and are more or less worldwide in distribution. They commonly possess mucous glands in the skin, the secretions of which aid locomotion. These nematodes are very resistant to desiccation and will quickly become active when moisture is added to soil that has been dried out for years. Tardigrades occur regularly, sometimes abundantly; they too are very tolerant of desiccation (Kühnelt 1950). Land planarians are not common except in moist tropical regions. Some of these soil animals are detritus-eaters, some bacterial and algal feeders, some partly carnivorous, and some partly parasitic on plant roots.

The majority of these small organisms are active only in soil water, present as a thin film lining the surfaces of the soil particles. Swimming forms are necessarily very small; often, they appear dwarfed compared to the size they have been brought to in cultures. Nematodes are somewhat less restricted in their movements. They can distort the surface of the water film by means of muscular movements, and thereby bridge intervening air spaces to the next soil particle. Amoeboid organisms and hypotrichous ciliates usually accommodate their shapes to irregularities of the solid surfaces over which they crawl and can become larger in size but still remain in the water film. The variety of micro-habitats in the soil accommodating the large number of species that occur includes spaces between surface litter, caverns walled off by soil aggregates, root channels, fissures, and pore spaces between individual soil particles. These micro-habitats vary in size, temperature, and moisture conditions (Birch and Clarke 1953).

Most of the insects, as well as the myriapod and arachnid groups that belong to geobiontic fauna, are wingless or nearly so (Lawrence 1953); many species are also eyeless. Special respiratory organs are either absent, the animals relying on their general body surface for gas exchange, or are more or less primitive. Most soil animals must, therefore, live in an environment saturated with moisture, and out of direct sunlight. The springtails jump around by means of a special springing apparatus. Millipedes and centipedes, of course, have numerous legs. Many of these animals feed on plant litter and fungus, but the pseudoscorpions, spiders, some of the mites, and centipedes are carnivorous. Most of these species are annuals or have even shorter life-cycles. Favorable soil moisture and food are most important in limiting their numbers; temperature and hydrogen-ion concentration are secondary factors. Differences in the character of soil, whether sand or clay, does not appear to affect the size of populations greatly; however, the amount of decaying humus present is important. In Denmark the biomass of soil organisms decreases from oak to beech to spruce forests (Table 9-9), but there is an increase in number of individuals in beech and spruce over the oaks, attributable to increased numbers of mites and springtails, which are so small that they do not greatly affect the biomass. Springtails also increase in abundance from oak to spruce to beech in the forests of Yugoslavia (Stevanovic 1956). Biomasses of mites and springtails in an English grassland area varied from less than 0.1 to 1.4 g/m^2; they were generally at peak dur-

TABLE 9-8 **Numbers of soil animals per m^2 (mostly mesofauna) in three different communities.**

Locality	North Carolina[1]	England[2]	Trinidad[3]
Community	Oak-Pine	Disturbed grassland	Tropical rain forest[4]
Season of censusing	Year round	November	July-Sept.
Depth of sampling	13 cm	30 cm	23 cm
Sowbugs	0	0	12
Pseudoscorpions	128	56	138
Spiders	92	142	
Mites	22,141	164,363	20,022
Millipedes	96	401	366
Pauropods	44	629	
Centipedes	34	648	
Symphylids	102	3,867	
Telson-tails	149	1,363	0
Japygids	135	6,605	42
Springtails	6,932	61,269	354
Termites	11	0	5,394
Thrips	355	1,129	42
Ants	164	141	2,736
Miscellaneous insects	101	23,047	992
Insect larvae	219	*	1,578

[1] Pearse 1946
[2] Salt *et al* 1948
[3] Strickland 1945
[4] From 5 samples from 3 forest reserves, total individuals × 6 = number per m^2
*Larvae classified with adults

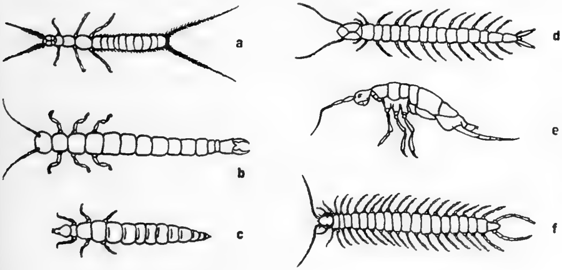


FIG. 9-6 **Soil fauna. (a) campodeid, (b) japygid, (c) proturan, (d) symphylid, (e) springtail, (f) centipede (from Kevan 1955).**

FIG. 9-7 **Some inhabitants of the ground stratum in a temperate deciduous forest. (a) camel cricket, (b) yellow-margined millipede, (c) round red millipede, (d)** ***Mesodon pennsylvanicus,*** **(e)** ***Allogona profunda,*** **(f)** ***Anguispira alternata,*** **(g)** ***Anguispira kochi,*** **(h)** ***Haplotrema*** **concava (Shelford 1913).**

ing the winter months (Macfadyen 1952). In a hemlock-yellow birch forest in Michigan, mites and springtails were over twice as numerous in winter as in summer (Wallwork 1959).

There are two main groups of annelids in the soil, the large red earthworms, Lumbricidae and Megascolecidae, and the small, whitish potworms, Enchytraeidae. In rich, moist, humus soil, the red annelids may reach populations of over one hundred individuals per square meter; potworms sometimes occur in hundreds of thousands per square meter. Earthworms ingest particles of mixed humus and mineral soil, absorb the organic matter out of them, and defecate around the entrances to and along the length of their burrows. Potworms feed more on plant and animal detritus, but may ingest some mineral particles. Potworms may also exert some control over parasitic nematodes of plant roots (Kühnelt 1950, Jacot 1940). Minimum numbers in Wales occur in late winter, maximum numbers in the early summer, and the biomass varies concomitantly from 2.7–13.2 g/m^2 (O'Connor 1957). The native North

FIG. 9-8 **Wood-eating beetle,** ***Passalus cornutus.*** **Top left, adult; top right, pupa; bottom, larva (Shelford 1913).**

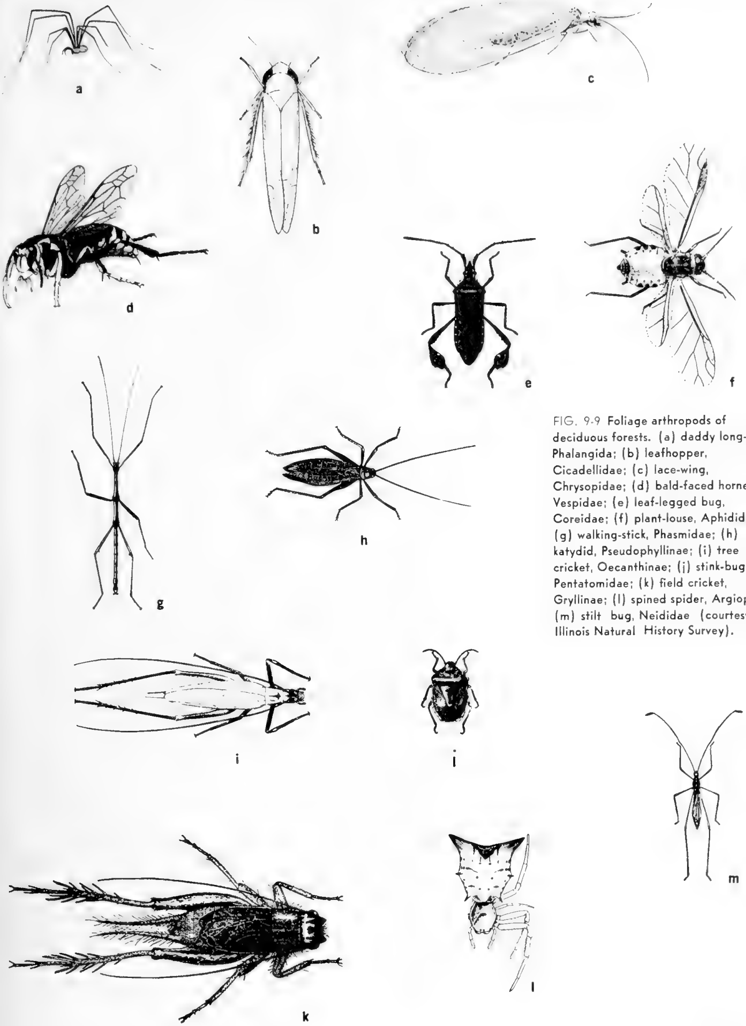


FIG. 9-9 Foliage arthropods of deciduous forests. (a) daddy long-legs, Phalangida; (b) leafhopper, Cicadellidae; (c) lace-wing, Chrysopidae; (d) bald-faced hornet, Vespidae; (e) leaf-legged bug, Coreidae; (f) plant-louse, Aphididae; (g) walking-stick, Phasmidae; (h) katydid, Pseudophyllinae; (i) tree cricket, Oecanthinae; (j) stink-bug, Pentatomidae; (k) field cricket, Gryllinae; (l) spined spider, Argiopidae; (m) stilt bug, Neididae (courtesy Illinois Natural History Survey).

American annelid fauna has been seriously disturbed by the widespread invasion of introduced *Lumbricus terrestris* and *Allolobophora caliginosa.* These species are found in forested areas, especially along rivers to which they have been carried by fishermen. In some localities, their activities have altered the basic character of the soil to the jeopardy of the entire original forest community.

The gastropod fauna is rich in moist, humus soil, but becomes scarce when the soil dries out. It is more abundant in deciduous than coniferous forests, because coniferous forest soils tend to be acid. In eastern North America there are three common genera of slugs, *Philomycus, Deroceras, Pallifera,* and a variety of snails belonging principally to the Polygyridae, Zonitidae, Entodontidae, Haplotrematidae, Pupillidae, and Succineidae. Fifty species of snails were collected in 74 hours of searching in the Great Smoky Mountains (Glenn Webb). The haplotremes are carnivorous, feeding on other snails, but otherwise the gastropods feed chiefly on detritus, algae, lichens, and fungus.

The assemblage of small animals that dwells under stones, rotting logs, and the bark of trees is sometimes called *cryptozoa.* Many species occurring in this microhabitat also commonly occur through the litter and soil generally, especially in moist climates with rich soil humus. In temperate forests, however, some snails, sowbugs, some spiders, lithobiid centipedes, julid and polydesmid millipedes, entomobryid springtails, roaches, earwigs, staphylinid, carabid and histerid beetles, and some ants reach maximum populations as cryptozoa (Cole 1946). The cryptozoan habitat is a favorite of salamanders. Many common soil animals are found as well in the special tree-hole forest microhabitat (Park *et al.* 1950); indeed, some species are specifically limited to tree-holes.

Decaying logs and stumps are preferred by many species. During the first three years following the cutting of the pine trees in a North Carolina stand, 130 species of insects, myriapods, annelids, mites, and mollusks were found (Savely 1939). Coleoptera was by far the most numerous order of insects. Of all species, approximately 7 per cent were phloem-feeders, 15 per cent sapwood-feeders, 44 per cent rotten wood- and fungus-feeders, 30 per cent predaceous, and 4 per cent parasitic. The phloem-eaters were most numerous during the first year. Their mode of feeding

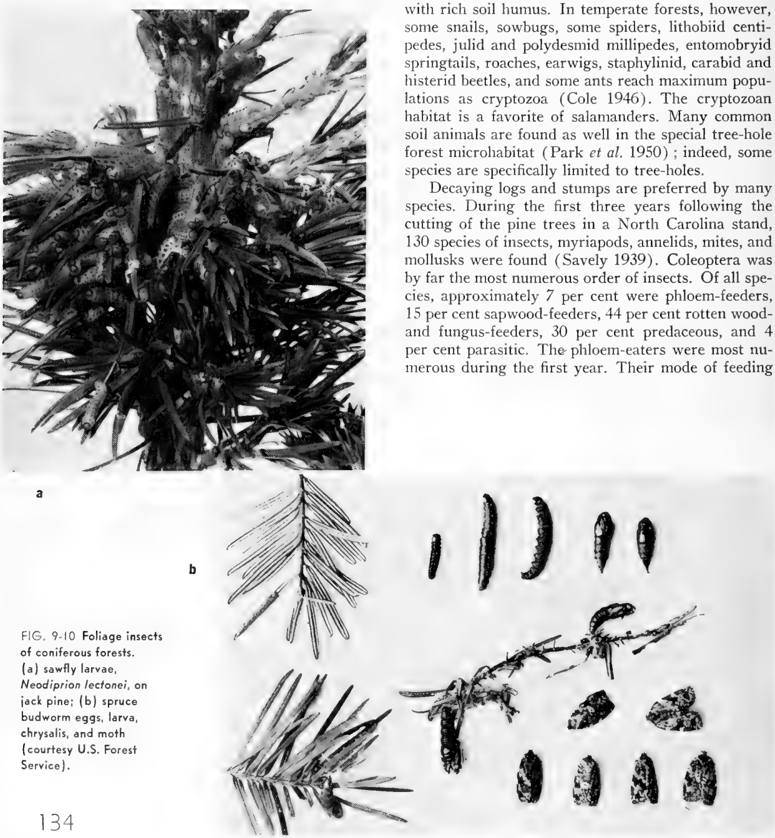


FIG. 9-10 **Foliage insects of coniferous forests. (a) sawfly larvae, *Neodiprion lectonei,* on jack pine; (b) spruce budworm eggs, larva, chrysalis, and moth (courtesy U.S. Forest Service).**

prepared the way for the later entrance of fungi, fungi-eating species, and predaceous forms.

In the decay of logs of such nothern trees as pine, spruce, and fir, the character of the food available is important to the succession that occurs (Graham 1925, Ingles 1931). Bark beetles require fresh green tissues of the inner bark and cambium, and hence occupy the tree only for the few weeks that these tissues remain. The long-horned beetles and wood borers require green tissue for their younger stages. As they mature, they are able to digest the solid wood. The horntail larva can digest solid wood as soon as it hatches. The outer bark is most difficult to digest but it does furnish food for some species of Lepidoptera and Diptera.

In addition to invertebrates, there are several vertebrates, particularly mice, shrews, moles, amphibians, and reptiles, that may be mentioned as part of the soil and ground fauna. These animals often have extensive underground runways and feed on the invertebrates in the soil, as well as on each other.

Foliage arthropods

Foliage insects and spiders are represented by large numbers both of species and individuals (Graham 1952). Spiders, ants, flies, beetles, leafhoppers, bugs, and larvae ordinarily predominate (Table 9-7); population depends directly on the amount of green foliage present. The species present depend on the type of vegetation, stratum, season, time of day, locality, and climate. Outbreaks of particular species may occur irregularly or periodically and several hundreds or even thousands of individuals may occur in each tree. Spruce budworms and walkingsticks are sometimes so abundant that their excrement or eggs dropping to the ground sounds like the patter of raindrops.

Birds

Breeding-bird populations in forest communities vary with the fertility of the forest, but are commonly between 100 and 400 pairs per 40 hectares (100 acres), which would be equivalent to 5 to 20 individual birds per hectare (2 to 4/acre) (Table 9-11). In addition, there is often a large non-breeding population present. On a 16 hectare (40 acre) spruce-fir forest in Maine there were 154 territorial males present prior to June 13. Between June 21 and July 5 a determined effort was made to reduce the population of songbirds, and a total of 352 males was taken from the area, more than were actually nesting at the start of the operations. Yet on July 11 there were still 40 males present and proclaiming territories. One hundred twenty-six females and 49 individuals of undetermined sex were also removed (Hensley and Cope 1951). This floating population is more numerous than the number of nest sites available in the community, but it functions as a pool from which individuals may replace any nesting birds that die, or take over any suitable niche that becomes available for one or another reason. This population pressure doubtless keeps the community saturated with breeding birds, tends to maintain the nesting population at a high peak of efficiency, and is a challenge to individuals to exploit new adaptations and to occupy new niches. It is therefore a potent factor in evolution.

FIG. 9-11 **Adult red-shafted flicker and young at nest in an aspen forest, Oregon (courtesy U.S. Forest Service).**

In a mixed deciduous-coniferous forest in Europe, a bird population of 662 individuals per 40 hectares (100 acres) was estimated to have a biomass of 47 kg (103 lb). In the same area, there were 528 individual mammals of biomass 264 kg (580 lb) (Turček 1952). The number and biomass of birds is generally less than that of mammals (Hamilton and Cook 1940).

Mammals

Rodents (mice, chipmunks, squirrels) and insectivores (shrews, moles) are the most abundant small mammals of forest communities. Resident sum-

TABLE 9-9 Number, biomass, and metabolism of ground invertebrates per m² in forests of Denmark (after Bornebusch 1930).

Type of Forest	Oak		Beech		Spruce	
Number of Stations	1		6		3	
Invertebrate group	Number	Biomass in grams	Number	Biomass in grams	Number	Biomass in grams
Lumbricid worms	122	61.0	79	15.8	50	2.5
Other humus-eating animals	2,675	15.0	9,338	10.6	10,807	7.0
Predacious animals	181	0.8	264	1.5	290	1.5
Totals	2,978	76.8	9,681	27.9	11,147	11.0

mer populations commonly vary from 25 to 100 per hectare (10 to 40 per acre). In rich, moist, undisturbed forests, populations may sometimes attain temporary levels of up to 500 per hectare (200 per acre). Considerable data on population sizes and biomasses of individual species have been compiled by Mohr (1940, 1947).

In forests of eastern North America (Hamilton and Cook 1940:469), small mammals fall into several categories. *The deer mice and the flying squirrels are adept climbers and often have their homes thirty feet or more* [10 meters] *from the ground in some hollow snag, deserted nest, or abandoned woodpecker hole. Flying squirrels feed among the trees and descend to the ground to forage about old logs and brush piles. They also dig down into the litter from the surface. Chipmunks forage in much the same manner, although they climb less frequently. Deer mice occupy several levels, from the trees to the burrows of moles and shrews. The red-backed mice, the lemming mice, and probably the jumping mice dig fairly permanent tunnels and runways through the soil and the litter. These they use as bases for food-gathering in both the litter and the upper layers of the mineral soil. These runways are often used by the shrews and the deer mice. The short-tailed shrews dig substantial tunnels. The diminutive long-tailed shrews thread their way through the easily parted litter and top-soil, and make intricate temporary labyrinths daily in search of food. The moles remain in their . . . tunnels during the daylight hours, but often come to the surface at night, no doubt attracted by the countless invertebrates that swarm over the ground with darkness. In winter they remain safe under the snow.*

In mixed deciduous and coniferous forests in the Sierra Nevadas the total number of rodents varied from 150 per hectare (60/acre) in July-August to 52 per hectare (21/acre) in December; their biomass varied from 27 to 4 kg per hectare (24 to 3.3 lb/acre) (Storer *et al.* 1944). The home ranges of individuals of these small rodents and insectivores are commonly only a fraction of a hectare (Blair 1953).

Of forest species, the larger the mammal, the fewer its numbers; and, usually, the wider an individual's range. The home ranges of the weasel, raccoon, and bear, are more extensive than those of rodents and insectivores. In the aggregate, their biomass does not exceed that of the more numerous smaller species. A population density of one deer per 20 hectares, for instance, translates into a deer biomass of about 2.8 kg per hectare (2.5 lb/acre).

Stratification

The community is a structure of the *subterranean, ground, herb, shrub,* and *tree* strata, and species are separated into different niches in relation to these strata (Elliot 1930). Food, shelter, and microclimatic differences are the chief limiting factors. Because microclimate in each stratum varies from hour to hour, day to day, and season to season, classification of a species by stratum must be in terms of the stratum it is observed to frequent for the major portion of a relatively long period of time. The inhabitants of the five strata divide into two major groupings, or societies. The soil invertebrates and some mammals move freely back and forth between subterranean and ground strata, and may be considered a society distinct from that which occupies the combined herb, shrub, and tree strata. Insects and birds depending on the foliage for food and reproduction sites move more freely among the latter three strata than between these strata and the ground. In terms of the strata which each occupies, however, the societies are not mutually exclusive, for ground animals such as millipedes and snails climb up onto herbs and tree trunks during humid weather, and foliage animals often rest on the ground, and search for food, hibernate, and lay eggs, there.

The majority of arthropod species carry on their main activities within a single stratum for their major activities (Table 9-10). The tree stratum spans a greater vertical distance than any other. Within this broad stratum, arthropods often show segregation to particular heights above the ground (Davidson 1930). Ants, spiders, and beetles appear to move more freely between different strata than do other species.

In point of macrofauna population densities of invertebrates, the ground stratum ranks highest, followed by subterranean and herb strata, while shrub and tree strata rank lowest. The largest mammal populations occur in the subterranean and ground strata.

In a European oak-hornbeam forest (Turček 1951) 15 per cent of the bird species nested on the ground, 25 per cent in the herb and shrub strata, 31 per cent in or on the trunks of the trees, and 29 per cent in the tree canopy. The largest number of individuals (32 per cent) occurred in the forest canopy, although the biomass of these birds constituted a smaller percentage of the total (16 per cent) than did the ground and herb population (67 per cent). In respect to feeding, however, the distribution was different: 52 per cent found their food on the ground, 9 per cent in the herbs and shrubs, 10 per cent on the tree trunks, 23 per cent in the tree foliage, and 6 per cent in the open spaces between the canopy, trees, and shrubs.

Seasonal changes

Outside of the tropics, the forest community changes drastically with the seasons such that four aspects may be recognized, each of which is divisible into two or three different sectors. The total population of the soil macrofauna in the temperate deciduous forest is highest during the hiemal aspect because of the migration of many foliage insects into this stratum to hibernate. Forest species hibernate in densities that vary randomly throughout the forest, except where there are differences in topography or substratum. Forest tracts adjacent to grass- or farmland, however, receive an influx of non-forest species that hibernate principally on the forest-edge generally, and along the south edge in particular, where exposure to solar radiation and protection from cold northerly winds produces warmer temperatures (Weese 1924).

During the vernal aspect, insects and other invertebrates come out of hibernation, and the adults of forms variously frequenting the herb, shrub, and tree foliage return to their characteristic stratum. The population of ground animals remains relatively high throughout the year, however, which can be attributed to the reproduction of the geobionts and to the fact that the immature stages of many foliage arthropods, particularly Diptera, Coleoptera, and Lepidoptera, occur in the ground. Various groups of these geobionts and geophils reach their peak numbers at different times during the year (Pearse 1946).

An insect species may show more than one population peak during the year (Shelford 1951), depending on the number of generations produced and the specific life-span. A species may appear, attain to very large numbers, and disappear, all in a matter of a few days, or a few weeks at most. Considerable variation also occurs from year to year in the population fluctuations of individual species and of whole groups, correlative with differences in weather, particularly temperature and moisture (Leopold and Jones 1947).

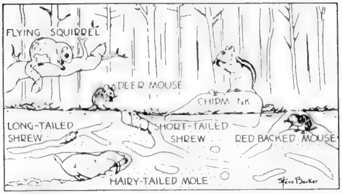


FIG. 9-12 **Relation of small mammals to the forest floor (Hamilton and Cook 1940).**

Bird populations in temperate zones reach peak populations with the passage of transients during the seasons of migration. These migration peaks are inconspicuous or absent in northern coniferous forests, since most birds that arrive stay to nest. In the tropics, birds are most abundant during the winter period of the north temperate zone, since the fauna then contains many migrant species from the north.

Mammal populations in temperate regions commonly reach their maximum numbers in the autumn, at the end of the breeding season. Populations decline progressively as winter wanes, the result of mortalities from severe weather, lack of food, and predation.

Comparison of animals in different forest types

There are more niches and microhabitats available in forest and forest-edge communities than in any other type of terrestrial community. The stratification and the diversification of plant forms are responsible for this. Many forest niches are much the

TABLE 9-10 **Stratal distribution of arthropod species in Missouri (Dowdy 1951).**

Distribution of species	Oak-hickory forest	Red cedar forest
Number of species	161	96
Confined to one stratum	69%	78%
Confined to two strata	19	15
Confined to three strata	11	5
Confined to four strata	1	2
Found in all five strata	0	0

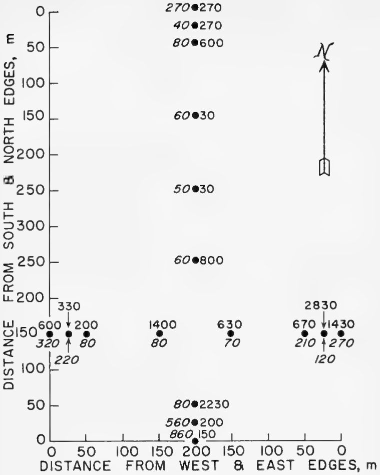


FIG. 9-13 **Population (number per m²) of hibernating insects in the soil during the winter at different locations in a 22-hectare (55 acre) rectangular deciduous forest tract (Trelease Woods) in central Illinois. The forest is in contact with grassland on the south side and with farmland on the other sides. The italicized numbers are field and crop insects that have invaded the forest to hibernate, the other numbers are true forest species (modified from Kennedy 1958).**

same, regardless of whether they occur in deciduous or evergreen forest, and regardless of geographic location (Blake 1926, Dirks-Edmunds 1947). Species occupying these niches differ, but are often taxonomically related; related or not, they have similar mores. Thus a predominant, shrub-inhabiting, plant-juice sucking leafhopper in an Illinois oak-maple forest is *Erythoneura obliqua,* but in a Maine pine-hemlock forest it is *Graphocephala coccinea.* The common herbivorous woods mouse in Illinois is *Peromyscus leucopus,* but in the Douglas fir-hemlock forests of Oregon it is *Clethrionomys occidentalis.* An insectivorous hole-nesting chickadee in Maine is *Parus hudsonicus;* in Illinois, *P. atricapillus;* and in Oregon, *P. rufescens.*

Coniferous forests have needle leaves; deciduous forests, broad-leaves. Some special, different niche adjustments are thus required which may not permit a species to successfully occupy both kinds of forest. The tube-building moth attaches its eggs to the pine leaf, and, when the larva hatches, it makes a nest of 6–15 needles, bound together with silk-like threads. The larva, and later the pupa, is protected within this tube but can come out and feed on the end of the leaves of which the tube is constructed. Deciduous leaves are clearly incompatible with these behavioral patterns, so nicely adapted to the peculiarities of pine needles. On the other hand, the red-eyed vireo experiences difficult feeding in coniferous trees because of the arrangement and close position of the needle leaves on all sides of the twig (Kendeigh 1945). While the vireo can feed in coniferous forests, it is considerably more profitable for the bird to confine itself to the deciduous forest, for which it is better adapted. Some animal kinds inhabit the soil and litter of both deciduous and coniferous forests, but a kind may be more abundant in one forest type than the other because coniferous and deciduous leaves form two distinct types of humus. Because of differences in foliage character, persistence through the year, climate, and the considerable difference in the taxonomic composition of the plants and animals involved, coniferous and deciduous forests are separated as distinct *biomes,* each with a number of *biociations* in different parts of the world.

Bird populations are not necessarily consistently higher in one type of forest than in the other (Table 9-11); rather, population varies with the luxuriancy of the vegetation. Animal populations in both coniferous and deciduous forests are generally highest in regions where ample rainfall brings rich development of vegetation as the basic food supply (Odum 1950). Population densities of both birds and mammals decrease progressively westward from the Appalachian Mountains to the eastern edge of the prairie as the climate becomes progressively drier (Wetzel 1949, Fauver 1950). The variety of snail species decreases in a similar manner from moist to dry forest types (Shimek 1930).

Forest and game management

The forest productive capacity of greatest economic interest is the timber yield. Forests are also of great importance to man for the protection of watersheds against erosion; for such recreational purposes as hunting, camping, and hiking; and for the inspirational values of unspoiled scenery and primitive nature. Complete logging, as practiced universally in colonial and even in modern times, destroys the forest, most of its animal life, and its usefulness for these purposes. Logging on a sustained yield basis converts the forest into a forest-edge community and allows the forest-edge animals to increase in abundance, while the animals dependent on dense forest decline.

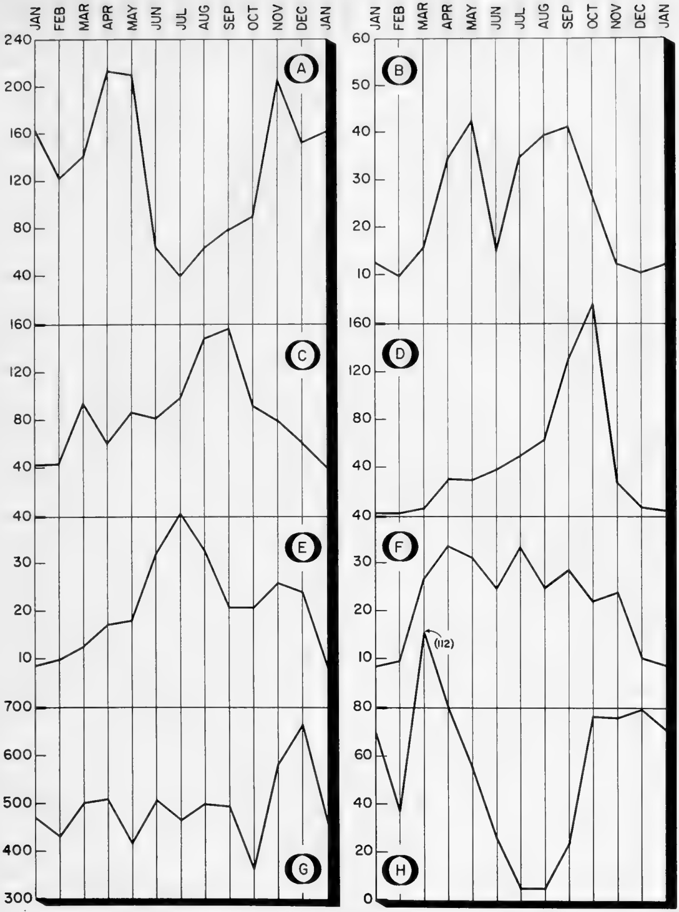


FIG. 9-14 Monthly variations in total population size of different animal groups in a temperate deciduous forest (Trelease Woods) of central Illinois. The data for each month are averages of 10-14 year records. (a) Diptera larvae; (b) Lepidoptera larvae; (c) spiders; (d) Homoptera; (e) snails; (f) centipedes; (g) invertebrates (macrofauna) in ground; (h) non-forest species.

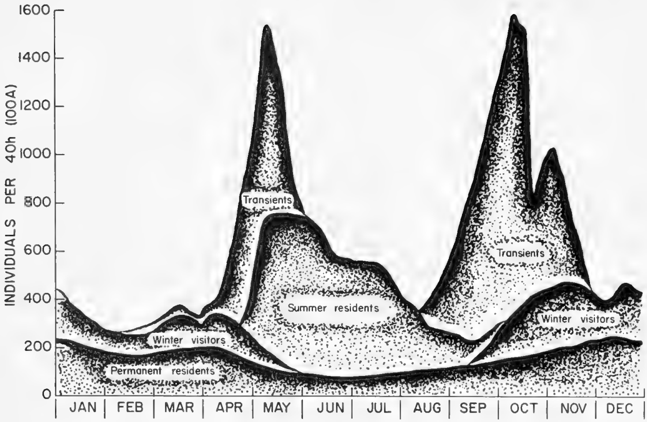


FIG. 9-15 Seasonal fluctuations in the bird populations of a deciduous forest area in Ohio. Transients include robins and the occasional visitors (modified from Williams 1936).

Such game animals as the gray squirrel, black and grizzly bears, moose, the fur-bearing marten, and the ruffed grouse and wild turkey belong primarily to the forest proper, although they often feed in the forest-edge, or brushland, and openings scattered through the forest. Populations of these species may be maintained simply by preserving large tracts of virgin or dense forests.

Most game animals of interest to the ordinary sportsman, however, belong to the forest-edge. These species are the cottontail, fox squirrel, deer, bobwhite, pheasant, and dove. Increase in populations of these species requires interspersing the forest with open areas, development of shrubby forest margins, or creation of artificial cover along fence rows, uncultivated field corners, around ponds, along drainage ditches or streams, on steep slopes subject to erosion, and on waste lands (Trippensee 1948). Intelligent management may involve control of plant succession to prevent its proceeding to a normal closed forest, and harvesting the forest for timber and game. Procedures for managing timber on a sustained yield basis are fundamentally the same as for managing populations of game animals on a permanent basis. Soil

TABLE 9-11 Average densities of total breeding-bird populations in forests and forest-edges of different types in eastern North America (compiled from Fawver 1950).

Type of vegetation	Number of areas censused	Number of species	Number of territorial males per 40 hectares (100 acres)
Spruce-fir (coniferous) forest	5	30	311
Mixed coniferous forest	6	33	207
Mixed hemlock - deciduous forest	5	28	224
Beech-maple-hemlock forest	5	31	190
Mixed deciduous forest	17	26	255
Deciduous floodplain forest	7	28	229
Oak-hickory forest	5	24	181
Mixed deciduous and southern pine forest	5	19	157
Southern pine forest	1	23	163
Broad-leaved evergreen forest	1	23	162
Coniferous forest-edge	7	30	241
Deciduous forest-edge	6	27	265

conservation and erosion control can also be readily combined with wildlife management, especially when trees and shrubs selected for planting to regulate soil erosion are species useful to game as cover and food.

The farmer can encourage establishment of small game species on his land by practices that do not interfere with the raising of crops. The maintenance of brushy fence rows does not increase the number of insect or other crop pests (Dambach 1948), as has sometimes been maintained. A knowledge of the fundamentals of life-history and ecology is essential to wildlife management, as wildlife management is applied ecology and involves the management of the total community, not merely game species in it (Leopold 1933).

PRESERVATION OF NATURAL AREAS

It is of utmost importance for the future of ecological studies that adequate samples of virgin primitive areas—forest communities, tundra, grassland, desert, tropical and rain forest, and all seral as well as all climax types of communities in all parts of the world—be preserved intact. Balanced primitive communities are the result of processes at work through eons of time. Primary communities once destroyed, there is never assurance that the secondary communities which develop can ever exactly duplicate them. This involves not only the replacement of all species in the original fauna, but also their replacement in the same relative numbers so that an integrated balanced community is fully re-established. The preservation of such natural areas is of historical value to future generations as a record of natural conditions over the country in pre-colonial days. Natural areas serve as controls for the agricultural development of the country, for the evaluation of various farming practices and uses of the land, and to show the potentialities of vegetative development of various parts of the continent. No one can know the potential value for food, medicine, or domestication of any organism that makes up primitive communities.

Large primitive areas are preserved in some of the National Parks, National Monuments, and in some of the larger of our state parks (Kendeigh 1951). Natural, wild, and wilderness areas have been set aside in several of the National Forests. Smaller areas of ecological value are being preserved in state, city, and private preserves. Not all community types are represented; more areas need to be set aside in other parts of the country, and constant vigilance must be exercised to keep them undisturbed. These projects are being sponsored by the Nature Conservancy, the National Parks Association, the Wilderness Society, and other organizations which deserve the support of all ecologists.

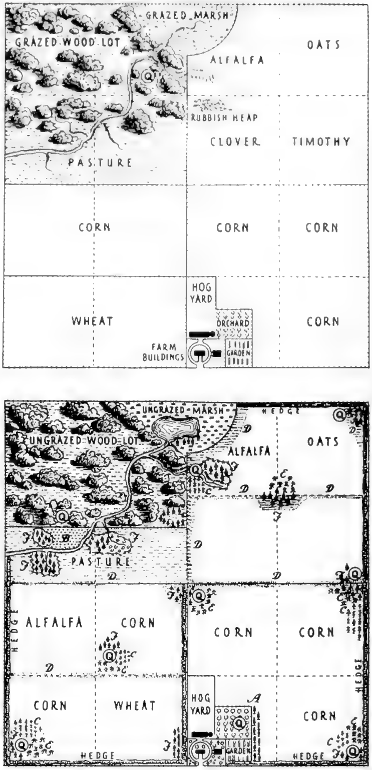


FIG. 9-16 **Sketch of a 100-acre farm before and after improvements to encourage small game. (A) windbreak, of some value to game as cover; (B) hardwood planting, perhaps black locust usable later for fenceposts; (C) a portion of the crop (corn) left, near cover, for wildlife; (D) a field or fence border; (E) emergency food, a few shocks of grain placed near cover; (F) cover planting of coniferous trees; (Q) a quail habitat with food and cover (Phelps 1954 in *Virginia Wildlife*).**

LIFE HISTORIES

We here choose four species to show life-history adjustments to the habitat and community: two mammals for the grassland, a bird for the forest-edge, and a millipede for the forest.

Voles (Microtus, Pedomys)

The meadow vole, *M. pennsylvanicus*, and prairie vole, *P. ochrogaster*, are small, dark gray or brownish, compactly built mice with short legs and tail, small eyes, and partly hidden ears. They spend most of their time in an elaborate system of tunnels, partly underground and partly as almost hidden galleries in dense grass. The food of these species consists mostly of grasses but also includes legumes, composites, fruits, and occasionally insects. Grass stems grow close together. The voles thrust them aside to form paths on the ground surface. These runways are heavily trafficked networks, and feeding is done in them. Runways formed through clover or alfalfa are less permanent. Underground passages lead to nests and chambers where food is stored. Nest cavities are round, lie 7 to 45 cm below the surface, and often have two tunnels leading up to the surface. The cavities are lined with dried grass and leaves (Jameson 1947, Martin 1956).

The voles may be active at any hour of day or night throughout the year, but the periods of greatest activity come in early morning and evening. The mean monthly home range of an individual is very small, commonly about 364 m^2 (.09 acre), although males wander somewhat farther than do females. There is no defense of territory. Because of their small home ranges and high rates of reproduction, vole populations in years of abundance may reach 366 or more per hectare (146 per acre). The level of population fluctuates through the years, however, in response to rainfall and competition, and there is some evidence of a four year cycle. Populations regularly decline each winter and increase to an annual peak in the autumn. Predators on the two voles are numerous and varied, and include hawks, owls, crows, weasels, foxes, coyotes, badgers, and snakes (Hamilton 1937, 1940, Martin 1956).

During the peak of a population cycle, breeding may continue throughout the year, but it is ordinarily curtailed during the winter and periods of summer drought. The number of young in a litter increases with the age of the female but commonly varies between three and five. The duration of the oestrus cycle in the female, if such a cycle actually occurs, is not known, but is likely only a few days long. Voles are promiscuous, and the female may accept a male within a few minutes or hours after the birth of her young and be capable of ovulating and conceiving a new litter within five or six days. The gestation period is short (about 21 days) and it is estimated that 8 to 10 *Microtus* litters may be produced in a favorable year (Hamilton 1941). *P. ochrogaster* is less prolific.

The young are born pink-skinned, hairless, blind, and with ear pinnae closed. They soon attach themselves to the teats of the mother, who may even drag them along as she forages. They weigh two or three grams at first but grow rapidly, gaining one-half to one gram per day. Meadow voles at sexual maturity weigh 25 to 30 grams; when fully adult, 40 to 50 grams. The backs of the young voles are covered with soft velvety hair on the fourth or fifth day after birth, the incisors erupt on the sixth or seventh day, and the eyes open and the pinnae unfold on the eighth or ninth day. With their eyes open they become more active and may take short trips away from the nest to nibble on succulent vegetation. The young voles are weaned at two to three weeks, but may remain with their mother for several days longer. Males may become sexually mature when five weeks old, and females may mate successfully when only four weeks old. The mortality rate in young mice is high, but the normal life span of adult meadow voles under natural conditions is 10 to 16 months. Prairie voles appear not to live as long (Hamilton 1941, Fitch 1957).

Bobwhite (Colinus virginianus)

The bobwhite is found over the eastern part of the United States and south through Central America (Stoddard 1931). It occupies open woodlands, shrubby fields, fence rows, and forest-edges bordering on grassy fields or farmlands. Nests are usually located within 16 meters of roads, paths, or cultivated fields. This vegetation serves as cover against both weather and enemies. The bird feeds primarily on seeds, occasionally on fruit and herbage, and, during the summer and autumn, on insects. It also ingests a considerable quantity of mineral matter in the form of grit. The young chicks feed largely on insects the first three weeks after hatching, but then become gramnivorous like the adults. With ample cover and food, the species may reach maximum population of 2.5 per hectare (1 per acre), but populations of one bird to 2–5 hectares are more common. In the South, populations are fairly stable year after year, but in the North they fluctuate widely (Kendeigh 1944).

The birds have a number of call notes for communication between individuals of a pair or covey. These notes serve to attract mates, express alarm or distress, indicate that the individual is lost, for feeding, to reassemble the covey, for battle cries, and so on. Pairing of male and female usually begins in April as the winter covey breaks up, and the males give their *bob-bob-white* calls. During this period, there may be song competition between males, fighting, chasing, plumage displays, and bluffing. Competition is intense because there are more males than females. Two to four weeks may elapse before the pair begins to nest, during which time the two birds stay close together.

Nesting may start in April in the South; May to August in the North. Nests are placed in good cover where the herb stratum is open enough so the birds can run around over the ground near the nest. A slight hollow is scratched in the ground, and the nest is commonly constructed of grasses, pine needles, mosses, or whatever is immediately available. A grassy arch is made overhead to serve as a roof and to conceal the nest from predators. It is ordinarily located on well drained high ground.

One egg daily is laid until the full clutch of 14 or so is attained. An occasional day may be skipped, and clutches laid early in the year are larger than those laid later. The incubation period lasts 23 days, and incubation may be performed either by the male or female; three out of four times it is the latter. During this period the incubating bird usually leaves the nest for a time to feed early in the morning and often again in late afternoon. The incubating bird joins its mate at a distance from the nest and they feed and rest together from one to occasionally nine hours, depending on the weather. The birds do not need surface water for drinking, but get what water they require from their food or from dew. About 86 per cent of eggs hatch, and all of these within about an hour. The young chicks quickly leave the nest and are cared for and brooded against cold, wetness, and too much sun by both parents for another two weeks. By that time, juvenal plumage is replacing the natal down, and the birds will flush and fly a short distance when disturbed. The young birds become similar in plumage to the adults at the end of 15 weeks. There is some feather molt about the head in the spring and a complete molt from August to October each year.

The winter covey forms in the autumn, and comprises one to three pairs of adults, their surviving young, and a few birds that were unmated. As birds die, small coveys unite and maintain an average size of about 14 birds. A covey may confine its activities within a range of 60 to 16 hectares (24 to 6 acres), and the ranges of adjacent coveys may overlap. The birds commonly freeze when approached by enemies, relying on their protective coloration for escape. If too closely approached they burst forth in rapid flight that carries them in all directions for 400–500 meters, whence they then drop down into other cover. When the enemy disappears the covey call reunites them again. Coveys feed together and roost together. They roost on the ground in compact circles with heads pointing outward.

FIG. 9-17 **Formation of egg-chambers by the millipede *Pseudopolydesmus serratus*. Top and bottom, base of two egg-chambers being formed; middle three, egg-chambers filled with eggs and partially capped over (Hanson 1948).**

Species predaceous on eggs, chicks, and adults include skunks, rats, foxes, weasels, opossums, raccoons, dogs, snakes, red ants (eggs), cats, shrikes (chicks), Cooper's and sharp-shinned hawks, and great horned owls. Numbers of parasites and disease organisms potentially dangerous to it are harbored by the species. Heavy rains may be destructive to nests and young birds in the summer, while extreme cold combined with long periods when snow covers the ground may kill adults during the winter. The population turnover during a year is therefore large.

Millipede (Pseudopolydesmus serratus)

This species feeds on decaying leaves and other organic material. Adults occur in populations up to 5 per m^2, and immature stages may be present up to several hundred per m^2. High populations, however, occur only in poorly-drained, moist forests. During periods of low precipitation, individuals migrate and become concentrated in wet depressions. The dependency of the species on moisture is further indicated by higher reproduction during wet than dry years.

Copulation occurs March to December, but there are two principal peaks of egg-laying; one in April, the other, during the first half of July. This results in two generations per year, but these are not genetically distinguishable.

There are 7 larval or instar stages. At hatching, the larva has only 7 post-cephalic somites and 3 pairs of legs. At each molt, more somites and legs are added until in the adult there are 20 post-cephalic somites and 30–31 pairs of legs. The first and second instars are whitish in color, but later instars develop a reddish-brown pigment. The April generation reaches the morphological adult stage in the autumn but sexual maturity not until the next spring. The July generation overwinters in the 5th to 7th instars, reaches the adult stage the following spring and sexual maturity in June or July. Molting takes place in small chambers similar to those in which the eggs are laid.

The egg chamber is unique. It is made of faecal pellets containing ingested soil and organic material. These pellets are placed in a ring of diameter about 6 mm. More and more pellets are piled on until the ring reaches a height of about 3 mm. Some 200 to 400 eggs are then deposited inside the ring after, which the ring is closed at the top to form a capsule. The whole process requires 6 to 12 hours. After breeding is completed, the adults die.

SUMMARY

Daily fluctuations of temperature, precipitation reaching the ground, light intensity, and wind velocity are greater in grassland than in forests, but relative humidity is usually less. A gradient in habitat conditions extends from above the vegetation to the ground in both grassland and forest. Segregation of animal species into subterranean, ground, herb, shrub, and tree strata is partly explained by differences in response to this gradient. North-facing slopes are generally cooler, moister, and with lower light intensities than South-facing slopes.

The species composition of animals differs between grassland, forest-edge, and forest. Within each community there is a vertical division into a subterranean-ground society and an herb or herb-shrub-tree society. Animal density and biomass are generally greater in the former. Food, shelter, and microclimate are the chief limiting factors. Outside of the tropics, there is considerable seasonal variation in the abundance of animals.

Many niches are similar in forests of different types; say, coniferous and deciduous. The species occupying these niches are often different, however, although they may have similar mores.

Grasses tolerate considerable grazing, and grassland productivity may provide a high carrying capacity for large grazing animals. Overgrazing by large populations of insects, rodents, or domestic stock, however, may bring deterioration of the range. Economic utilization of grassland requires proper balancing of grazing pressure against vegetative productivity throughout the year.

Forests are of great interest to man for timber, protection of soil against erosion, and recreation. Game species are usually more varied and abundant in the forest-edge than in the forest-interior. Game management is concerned with controlling the vegetation and habitat to produce the highest yield of the desired species and to regulate the number taken. It is necessary to know the intimate life-histories of the species concerned before this can be accomplished intelligently. Finally, it is of utmost importance to ecological study that adequate samples of primitive areas be preserved in an undisturbed condition.

10

Ecological Processes and Community Dynamics:

Dispersal, Migration, and Ecesis

In order to understand the geographic distribution local and otherwise of animals, the eventual succession or replacement of one community by another, and the stabilization of different species at different levels of abundance, we need to know several things. We must discover how organisms invade new habitats or geographic areas; how they react on the habitat; the manner in which they compete with or otherwise affect each other; and the factors that determine the success or failure of organisms in the struggle for existence. The processes of dispersal, migration, competition, speciation, reaction, coaction, and ecesis constitute the dynamics of the community, the understanding of which is a prime objective of ecological thought and research.

David Starr Jordan (1928) once stated that the general laws governing the distribution of animals can be reduced to three simple propositions. According to Jordan, a species of animal will be found in any part of the earth having conditions suitable for its maintenance unless (1) its individuals have been unable to reach this region because of barriers; or (2), having reached it, the species has been unable to maintain itself because of inability to adapt to the region or to compete with other forms; or (3), having arrived and survived, it has subsequently so evolved in the process of adaptation as to have become a species distinct from the original type.

DISPERSAL DYNAMICS

Dispersal is the spread of individuals away from their homesites. Dispersal movements are usually slow, and cover relatively short distances in the life time of an individual. The cumulative result of short dispersions by successive generations, however, may become conspicuous in the course of years, decades, or centuries, especially when it amounts to *range expansion* of a species into a new habitat or area. Some remarkable instances of range expansion have resulted from the purposeful introduction of the house sparrow into North America in 1852–53 and the European starling in 1890–91; and the accidental introductions of the black rat, Norway rat, and numerous insect pests, at various times. In similar fashion the gray squirrel and muskrat have been introduced into Europe (Elton 1958). Once man had helped them to overcome the ocean barrier that previously held them in check, these species spread unusually rapidly because of the optimum environment on the continent. There is reason to believe, however, that under entirely natural conditions the rates of dispersal of all species, once a barrier is passed, would be similar, varying only with respective reproductive potentials, characteristic speeds of locomotion, and relative abilities to find unoccupied niches, overcome competition,

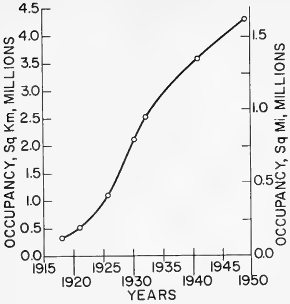


FIG. 10-1 **Dispersal of the European starling in North America between 1918 and 1949 (compiled from Kessel 1953).**

acclimatize to new climatic conditions, and acquire new behavior patterns.

Manner and means of dispersal

Animals find suitable habitats and niches in various ways. In a uniform environment, dispersal movements radiate in all directions from the home area. The greater the density of individuals in the home area, the more quickly distant areas are invaded, and the farther away do individuals move.

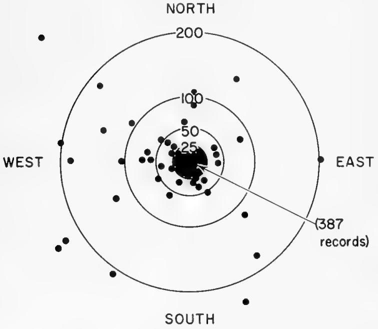


FIG. 10-2 **Relation of breeding localities to birthplaces among robins. Numerals on concentric circles are distances from the origin in miles (1 mile = 1.6 kilometers). Data points beyond the 200-mile radius are not placed to scale (Farner 1945).**

A common method of achieving dispersal is the broadcasting of enormous numbers of eggs, spores, encysted stages, or young so that they scatter into a wide variety of places in a more or less random manner. Those that come by chance into suitable environments persist and become established; those that enter into unfavorable locations are destroyed or never develop. Broadcasting is a wasteful procedure; it is especially characteristic of aquatic species. The freshwater clam annually produces hundreds, perhaps thousands, of eggs. Only two fertilized eggs need mature that the two parents be numerically replaced when they die, and thus the population of the species be maintained at a constant level. Contrastingly, in those forms, such as birds and mammals, that have developed a high degree of parental care, the number of eggs or young annually produced is commonly a half-dozen or less, and the offspring exercise considerable discrimination in their choice of suitable habitat.

Although the dispersal of broadcast offspring is not under the control of the parents or the young, it is not often truly random. Water and wind currents, and other agents of dispersal may channel eggs and spores in restricted directions. Such dispersal is described as *passive conveyance.* In streams, all agents of passive conveyance, except some other animals, direct dispersal downstream. Upstream dispersal must be the result of active locomotion.

Eggs of insects, snails, fish, or other aquatic organisms will sink unless they are buoyed up by currents, possess flotation mechanisms, or are attached to some floating object. Logs, masses of vegetation, and other debris are sometimes torn loose from the banks of rivers and float out to sea carrying the smaller animals attached to or trapped on them. It is estimated that over 300 debris rafts of significant size are formed each century and float out to sea from the mouths of the larger tropical rivers (Matthew 1915). The passengers on such rafts may come to be colonists of remote islands or even other continents.

The dispersal of fresh-water animals from one river to another is sometimes effected by erosion, when the process permits one river system to rob a branch of another river system (Crosby 1937). Following the recession of the continental glacier in North America, the proglacial Great Lakes had outlet down the Illinois and Mississippi Rivers. Later, a new outlet was established over Niagara Falls, and the Lakes became a part of the St. Lawrence River system.

Wind acts in a manner somewhat similar to water currents. Some terrestrial spiders have evolved a special mechanism allowing them to use mild air currents for dispersal. The young climb up on a clod of earth or other object and spin out long threads or flocculent masses from glands in their abdomen. This continues until enough buoyancy is created to lift the spider and carry it away, sometimes distances of hundreds of miles. Strong winds will often carry insects and even birds great distances away from their usual courses. Crop pests may be blown North during the summer and cause damage, but may never become permanently established because they are killed by the northern winter cold. Hurricanes are an important means of colonizing islands far at sea with terrestrial species (Elton 1925, Darlington 1938). There are authentic records of rains of fishes and other aquatic species that were sucked up and transported appreciable distances by tornadoes (Gislen 1948).

In studies done in England (Freeman 1946), it was estimated that the number of insects drifting through a rectangle 91 m (300 ft) high and 1610 m (1 mi) long amounted to 12,500,000 per hour. The number was highest during May, June, and September, at temperatures above 18°C. The aerial population over the forests and swamps of Louisiana has been measured (Glick 1939), by means of traps placed on the wings of airplanes, and found to average the following number of individuals per 1000 cubic meters of air:

Altitude	*Daytime*	*Night*
6 m (20 ft)	10.3	—
61 m (200 ft)	5.2	—
152 m (500 ft)	—	6.2
305 m (1000 ft)	2.2	2.6
610 m (2000 ft)	1.1	1.1
914 m (3000 ft)	0.6	0.5
1524 m (5000 ft)	0.3	0.4

Diptera were most numerous, followed during the daytime by Coleoptera, Homoptera, Hymenoptera, Araneida, Hemiptera, and others. Spiders and wingless insects were greatly reduced in numbers at night because of the lack of vertical convection currents. The density of insects in the air depends on the diurnal and seasonal activity rhythms of the animals to give them exposure to air currents in their terrestrial habitats. Those species tend to be most numerous that have the greatest wing area per unit weight, hence the greatest buoyancy. The insect population in the upper air is not distinct from that flying in the lower layers, but its density decreases with height in a well-defined logarithmic manner up to and over 1500 m (5000 ft) (Johnson 1957, Taylor 1960). Improved methods for obtaining aerial densities employ a suction pump to strain known volumes of air per unit of time (Johnson 1951).

Other animals serve as vehicles for passive transportation. Bits of vegetation, small animal life, and the eggs of worms, entomostracans, rotifers, insects, snails, and fish may cling to the feet of such waterbirds as ducks, rails, and herons and be carried many miles when the birds migrate. A species of *Succinea* snail, native only to St. Croix and Puerto Rico, was found alive in the feathers of a bobolink shot in Cuba. *Ferrissia* snails have been found attached to the wing covers of aquatic beetles and sphaeriid clams clamped on their legs. These insects occasionally fly from one body of water to another.

Some dispersal movements are determined by the manner in which the animals respond to environmental factors. Such *directed movements,* or taxes (p. 12) may induce the dispersal of animals upstream positive to current rather than downstream.

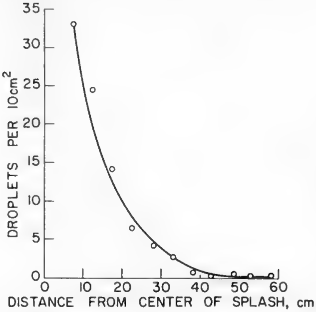


FIG. 10-3 **Decrease in concentration of water droplets beyond 5 cm from the center of splash (Wolfenbarger 1946, after Faulwetter).**

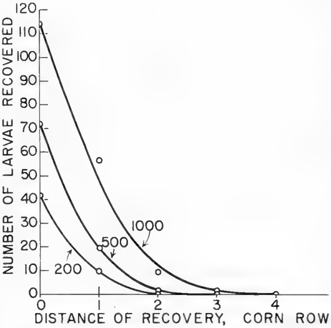


FIG. 10-4 **Effect of increase in population at source (200, 500, 1000 eggs deposited) on the dispersal of European corn borer larvae (Wolfenbarger 1946, after Neiswander and Savage).**

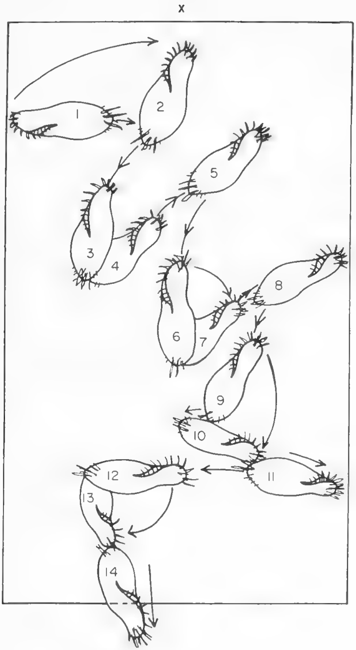


FIG. 10-5 **Response of the hypotrichian *Oxytricha fallax* to heat. The slide is heated at X. An *Oxytricha* at station 1 changes position as indicated by the arrows, repeatedly moving backwards, turning to the right, then moving forwards. Finally, at stations 13-14, it directs itself away from the heat, and moves in a straight path towards a cooler region (from Jennings 1906).**

Trial and error is involved to a considerable extent in the dispersal movements of animals. If, initially, an individual progresses into an unfavorable habitat, it may be able to withdraw and proceed in a new direction. This may continue many times until by chance it discovers an area that is favorable. Trial and error movements are manifested in all groups of animals. In higher types, and even in many lower types, the individual may learn by experience and reduce the number of false trials that it makes. Thus initially random movements may eventually evolve into directed behavior patterns.

Barriers

Dispersal continues until a barrier that makes further movement difficult or prevents successful colonization is encountered. Barriers are of different sorts and are classified as *physiographic, climatic,* and *biotic.* The difficulty of surmounting or bypassing any type of barrier varies greatly among species. River valleys, for instance, may be barriers to animals frequenting mountains; but to lowland species, river valleys are important dispersal highways.

To fresh-water organisms in river and lake habitats, intervening land masses are usually effective barriers. The headwaters of different river systems may lie only a few miles apart, yet contain quite different species because the continuous water route down to the mouth of one river and back up to the other may be a distance of several hundreds or thousands of miles. A waterfall may be a barrier for all non-flying aquatic species, and even riffles or swift water may prevent upstream dispersal of pond or lake species. The salt water intervening adjacent rivers flowing into the sea is a barrier to most fresh-water forms that might otherwise invade one river from the other.

Terrestrial organisms are hemmed in by a great variety of barriers. The oceans constitute the major physiographic barriers since they separate the faunas of the several continents and isolate islands from each other. Lakes are not effective barriers because they can be readily skirted, but wide rivers coursing long distances between banks of dense vegetation, as does the Amazon River through the tropical rain forests of South America, may limit the range of forest mammals, butterflies, flightless beetles, land snails, and even birds (Mayr 1942: 228–9). The Grand Canyon of the Colorado River separates the ranges of the Kaibab and Abert squirrels and several other species, even in country that is semi-arid and open (Goldman 1937). Mountains are sometimes considered barriers to lowland species, and valleys barriers to mountain forms. This is only true if the change in climate and vegetation that such barriers produce are unfavorable to the species.

Deserts are important climatic barriers since they are hot, and dry. Temperature affects animals directly, since species have definite limits of tolerance, comfort, and efficiency. Precipitation is important because it controls the type of vegetation that occurs in a region, and by so much the animals adapted to that type of vegetation. A low relative humidity may directly limit the dispersal of moist-skinned species. Excessive solar radiation limits some species to forest habitats, excluding them from open country; without recourse to shade, such animals would experience overheating and critical loss of water from the body. Short photoperiods may limit distribution northward during the winter, especially if low temperature obtains, and may influence southward distribution of northern animals in the summer. The length of the season between spring and autumn killing frosts, or between dates when its limits of temperature tolerance are reached in the spring and autumn, may determine whether or not a species can complete its life cycle at a given latitude. A corollary consideration is whether the accumulation of heat is sufficient to furnish cold-blooded animals and plants sufficient energy for growth and reproduction.

Biotic barriers consist of changes in vegetation, food, competitors, and predators. The adaptations and behavior patterns of many animals fit them to niches in specific types of vegetation; should the previously amenable vegetation change, the animals may have great difficulty in adapting to it. Tree squirrels, for instance, are replaced by ground squirrels in prairies and deserts. Most animals have a great adaptibility to food, so food is not so limiting a factor. Some insects, however, such as certain aphids, are narrowly limited to particular species of plants as a source of food. Where their food plant is not present, they cannot exist.

Competition between species is also a potent force in controlling distribution. The boundary between the ranges of the house wren and Bewick's wren in eastern North America is not sharply defined, varying as a function of competition between the two species. Either species can live in the range of the other, but in the North, the house wren usually wins in competition for territory and nest-sites. In the South, the Bewick's wren is more successful (Kendeigh 1934). Predators, such as the great horned owl and the swifter hawks, tend to urge the bobwhite to confine itself to a forest-edge habitat, where it is less vulnerable to attack. Trypanosome parasites carried by the tsetse fly are effective barriers against successful introduction of domestic ungulates in certain parts of Africa, and the rabbits introduced into Australia have limited the range and greatly reduced the abundance of several species of native marsupial.

Dispersal of young

The dispersal of a species is primarily accomplished in the immature stages. This is obviously true of eggs and spores, but banding and marking studies have shown that among the higher animals—birds and mammals—it is also the young which disperse the species. Once a bird has reached sexual maturity and nested, it has strong tendencies to return to the same area in following years. The distribution of young birds is not random, however, as they tend to return to the general vicinity of their birthplaces rather than uniformly over the range of the species. Thus only 0.5 per cent of 557 adult house wrens recovered a year after banding (Kendeigh 1941b) nested farther than 3.3 km (2 miles) from the site where they had nested the year of banding, but 15 per cent of the 182 birds banded as nestlings were recovered at greater distances, the longest of which were 32 km (20 miles), 56 km (35 miles), 80 km (50 miles) and 1120 km (700 miles). Dispersal distances for young of other species are proportionally comparable (Haartman 1949).

Of small mammals, it is characteristic that once an individual has selected a homesite, it rarely leaves it for another (Burt 1940, Blair 1953). It was observed that in the months following the time at which they had been captured, marked, and released, 95 per cent of 133 adult woodland white-footed mice resumed habitation within 183 m (200 yd) of the site of capture.

Rate of dispersal

If dispersal from birthplace were typically limited to one direction, then a simple mean of the distances to which the young disperse before they breed would give the dispersal rate per generation. It is the case, however, that dispersal proceeds peripherally in all available directions and may extend to surprising distances (Bateman 1950).

The area exposed to invasion and the average time required to saturate that area increase proportionally as the square of the linear distance (d^2) from the center, since the total area within which the individual could settle is πd^2. Therefore, the equation

$$\sqrt{\frac{\Sigma d^2}{n}}$$

for computing mean dispersal distance seems correct (Haldane 1948), although other equations have been suggested (Haartman 1949, Burla *et al.* 1950, Dice and Howard 1951). Consider the data on house wren nestling recovery distances, presented above. Excluding the truly extraordinary distance of 1120 km, and observing that only about 93 per cent of young female wrens nest when they are one year of age, we compute by this equation an annual dispersal rate of approximately 8 km (5 miles) for this species. The mean dispersal distance of one group of 154 young woodland white-footed mice (Burt 1940), according to the above equation, is about 176 m (192 yd). However, mice born in the spring mature sexually very quickly and breed in late summer or autumn, so the annual dispersal rate must be somewhat greater than this figure indicates.

Our dispersal rate data so far have described the outward diffusion of a local population through an area already occupied by the species. Once it has surmounted a barrier the dispersal rate of a species into an area previously unoccupied by it should be faster. The European starling was introduced into North America about 1890. From a central locus around New York City it spread at an accelerating pace until, in 1940, it had become established over 6,500,000 sq km (2,500,000 sq miles) (Wing 1943), a mean rate of about 130,000 sq km (50,000 sq miles) per year. With amelioration of the climate in Finland during recent years, the lapwing spread northward between 1899 and 1954 at a mean annual rate of 7 km (4.3 miles) (as computed from Fig. 9 in Kalela 1955); the roe deer, between 1850 and 1945, at a mean annual rate of about 9.5 km (5.8 miles) (computed from Fig. 1 in Kalela 1948). The Norway rat invaded southwestern Georgia and virtually displaced the previously established black rat at a rate of about 430 sq km (167 sq miles) per year (Ecke 1954). By way of contrast, it has taken the fresh-water amphipod *Gammarus pulex* the last 6000 years to disperse across 12 river systems from southern England into Scotland (Hynes 1954).

Causes of dispersal

It is the case that the reproductive rate of any species is so great that if all offspring survived the world would be overrun with that species within relatively few generations. Because species produce a surplus of young in most years, there is continuous pressure on individuals to move into all suitable niches, and to seek out new areas in which to settle. The impact of large numbers of individuals struggling for survival is described as *population pressure,* and is doubtless the most potent force inducing dispersal. It should be recognized, however, that population pressure is not uniformly constant year after year. When because of poor breeding conditions or catastrophe there is a reduction in the over-all population of a species, that decimated species may withdraw into its optimum habitat and be less put upon to exploit new or less desirable areas. In years favorable to the production of large surpluses of young, a species will often be found in less favorable habitats, even regions it would not otherwise occupy at all (Kluyver and Tinbergen 1953). The broadcasting of eggs or offspring, or the passive conveyance of them to other regions, varies directly with the size of the population producing them, and is hence as much an expression of population pressure as the active search for new areas engaged in by individuals under their own locomotion.

Animals cannot disperse successfully, if at all, into new areas to the characteristics of which they are not structurally, functionally, and behaviorally adapted. If an area the characteristics of which have excluded a species changes so that the species is adaptive to it with the equipment it has, that species can successfully invade. The American robin, song sparrow, chestnut-sided warbler, house wren, and prairie horned lark have invaded Georgia only in recent years as the logging of forests, initiation of early seral, grassy, and shrubby stages, and extensive general cultivation of the land have produced habitats meeting the requirements of these birds (Odum and Burleigh 1946). If an area the characteristics of which have excluded a species remains unchanged but the species acquires new structural, functional, or behavioral traits by which it can adapt to that area, the species can invade the area. If its newly acquired traits let the species remain adaptive to its former range, its range is expanded by inclusion of the newly-invaded area. If the food supply fails, homesites or vegetation be destroyed, or a pernicious change in climate occur there, animals may be forced to leave an area to which they were well-adapted and disperse, more or less temporarily, into an area to which they are less well-adapted. The snowy owl, for instance, depends heavily on lemmings and mice for food in its usual range, the Arctic tundra. In apparent correlation with the cyclic decline of the lemming population there, the owls invade our northern states.

DISPERSAL PATHWAYS

Theories of how animal and plant groups have dispersed over the face of the earth are based fundamentally on the hypothesis that the continental land masses were at one time intimately connected and only later drifted apart to their present locations, or the hypothesis that the continents have been permanently fixed in their present positions throughout geological time.

Continental drift theory

This theory postulates that throughout the Paleozoic and most of the Mesozoic the presently distributed continents were grouped into two great land masses: a northern Laurasia was separated from a southern Gondwana by the vast sea of Tethys, although narrow connections between the two might have occurred for short periods. In the Cretaceous the land masses fragmented, and the fragments subsequently drifted apart. Laurasia is supposed to have split into North America, Greenland, Europe, and most of Asia; Gondwana, into South America, Africa, Arabia, Madagascar, India, Australia, and Antarctica (Wegener 1924, DuToit 1937). This theory is suggested by the shapes of the continents that could conceivably be fitted together; by the characteristics of the Atlantic Ocean basin that makes it appear to have been formed by a rifting apart of land masses; by the similar geological stratigraphy shown by invertebrate fossils in South Africa and South America; by some similarities of present-day fauna and flora at the same latitudes on different continents; and by the difficulty tropical species have dispersing over arctic land bridges. Perhaps we should keep an open mind towards this theory (Wolfson 1955), but the weight of present-day evidence, both geological and biological does not strongly support it (Mayr 1952).

Stability of continents

Although the major land masses and ocean depths have probably remained substantially unchanged since life first originated, the continents have been repeatedly flooded to various extents by inland seas, elevated, and eroded. Continents now separated have been connected by land bridges in times past; one of the best known connected Asia and North America at the site of the Bering strait. A land bridge now connects North and South America at the isthmus of Panama, and Eurasia and Africa are connected by the isthmus of Suez. Land bridges may exist for only a short time in the geological sense, but they serve as important dispersal routes for those land animals and plants able to cross them. When a land bridge allows free passage of most animals and plants in either or both directions it is called a *corridor* (Simpson 1940). If the land bridge is narrow, has an unfavorable climate, a lack of suitable niches, or too many competitors, it is called a *filter*—only a few specially adapted species are able to pass over it. A *sweepstakes route* of dispersal is one over which only a few species pass, more or less by chance. Because of its general unfavorableness, it is generally only one-way. The island-hopping dispersal of organisms from southeastern Asia through the south Pacific has been accomplished by relatively few species; the more distant the island, the fewer the species that have reached it.

Mountain barriers are not permanent; in the course of time they erode away. New mountains may rise again in the same area or elsewhere. With such changes in physiography come changes in climate and vegetation as well. The explanation of present-day distribution of animal groups requires a knowledge of past changes in the geological history of the earth, as well as in present day characteristics of continents, oceans, and climates.

A glance at a globe quickly shows that the continental land masses are concentrated mostly in the northern hemisphere. There are three broad land extensions southward below the equator: the Malay Peninsula, East Indies, and Australia; Africa; and South America. The southern hemisphere otherwise consists largely of vast expanses of oceans. On a land route, North America intervenes South America and Eurasia. Eurasia is the largest continent, is central to all the others, and always has had a great diversity of climate and terrain. The size, arrangement, and positions of the continents are of importance to interpretation of the past evolution and dispersal of animals.

Considerable evidence (Matthew 1915) indicates that some large groups of animals, notably mammals, first evolved in Eurasia and then spread to other parts of the world. North America was a less important center of origin and dispersal. Periods of aridity and glaciation are known to have occurred in the northern continents during the Permian, at the end of the Triassic, at the beginning and end of the Cretaceous, and during the Pleistocene. Intervening warm, moist, uniform climates prevailed in the early Carboniferous, Jurassic, mid-Cretaceous, and Eocene.

During periods of continental emergence, climates on the northern continents changed from moist and warm to more arid and cold. Animals adaptively limited to moist, warm environments were restricted to tropical regions or dispersed outward into the southern land extensions. New, more advanced animal types adapted to the new conditions in the north appeared. Monotremes entered Australia at an early date. Marsupials probably originated in Eurasia and dispersed into Australia and South America during late Mesozoic or early Tertiary, although there is no fossil evidence for these suppositions (Darlington 1957). An opossum still occurs in North America, but no marsupial is now present in Eurasia. Marsupials did not get into Africa, but are present in South America and have adaptively radiated into a variety of forms in Australia. The predominance of marsupials in Australia is probably due to their chance success, at an early date, in surmounting the sweepstakes route of islands from the Asian mainland. They were the only placental forms in Australia until bats and members of the rat family arrived, much later. There have been successive waves of dispersal of higher mammalian forms into Africa and South America, but many recently-evolved mammalian types are largely confined to the northern hemisphere, where most of the primitive forms there have long since become extinct. The origin and dispersal of birds may have followed the same pattern as that of mammals, but their geological history is less easily traced because birds are not easily fossilized.

A modification of Matthew's theory appears necessary, at least for the cold-blooded vertebrates. Freshwater fishes, amphibians, and reptiles are most richly

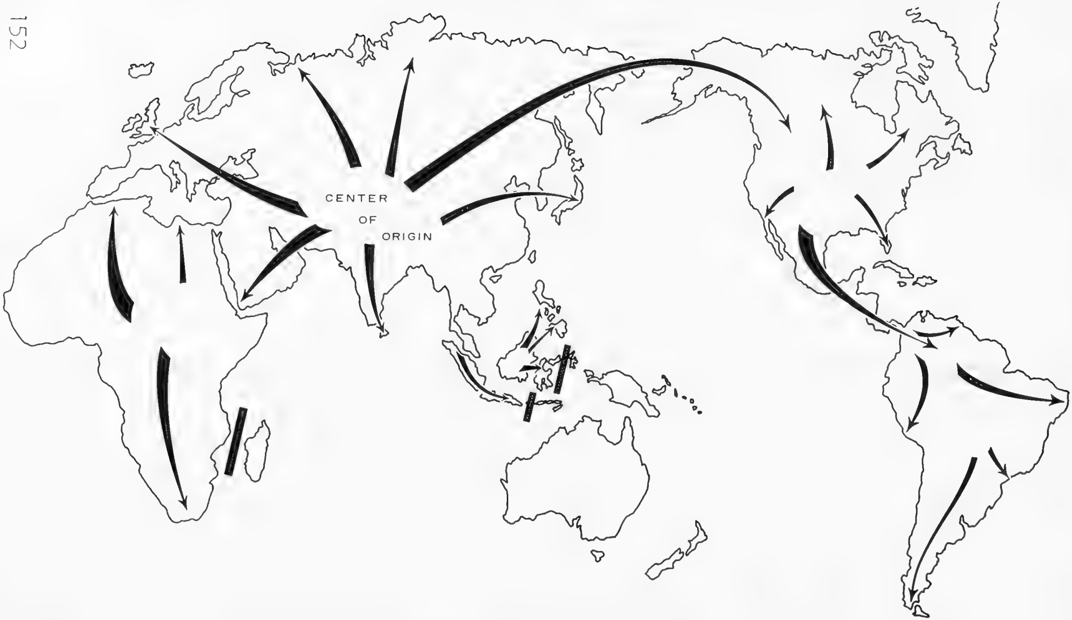


FIG. 10-6 Dispersal of toads *(Bufo)* over the world—except for Madagascar, some of the East Indies, and Australia—from a center of origin in the Old World Tropics (after Darlington 1957).

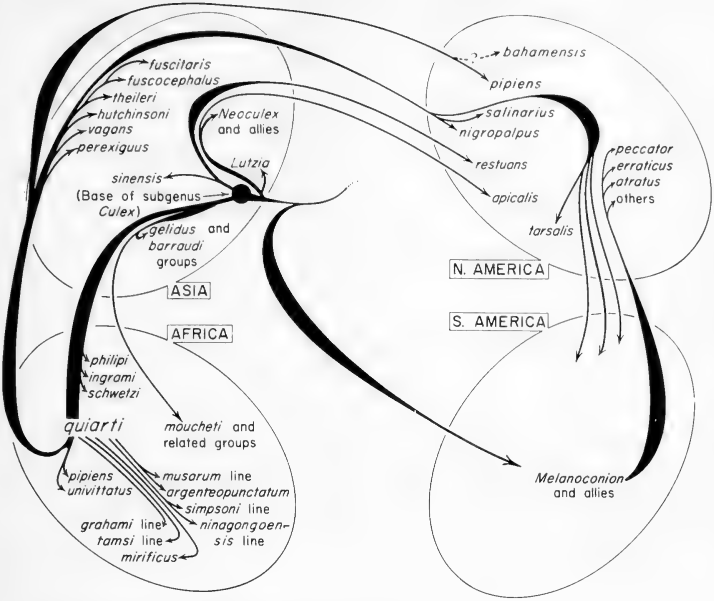


FIG. 10-7 **Phylogeny and dispersal of the mosquito genus *Culex* (Ross 1953).**

developed in tropical regions; all are definitely handicapped in dispersing into temperate or cold regions by the climatic barriers. Fresh-water fishes have evolved a richer north temperate and arctic fauna than amphibians and reptiles, since their aquatic habitat protects them better against extreme cold than does the terrestrial or semi-terrestrial habitat of the other two groups. Amphibians extend farther north than do reptiles. Evaluating all types of evidence, Darlington (1957) concludes that these three groups of cold-blooded vertebrates, and probably also the warm-blooded groups, reached their greatest taxonomic diversification during the Cretaceous and early Tertiary, and not in temperate Eurasia but in the Old World tropics, especially in the Orient. Uniform, warm, humid climates and a great variety of available niches, along with many possibilities for geographic isolation, appear to have induced evolution in these groups, stimuli quite different than those suggested by Matthew for the warm-blooded mammals. From the Old World tropics, dispersal proceeded into Africa, into Eurasia, across the Bering land bridge into North America, and finally across the Panama land bridge into South America. Subsequent evolutionary radiation of new forms occurred in each continent.

A northern route between Asia and North America by way of the Bering land bridge as a route of dispersal for tropical species presents problems in respect to climate. We know, however, that during the Cretaceous and early Tertiary the climate in these northern regions was much warmer than it is now. We may suppose that the bridge shut off the cold Arctic Sea from the Pacific Ocean, and that the southern shores of the land bridge were washed by the warm Japanese current. This would have made it possible for warm temperate species to use the bridge, but probably not tropical species, unless we suppose that the tolerance to cold of the ancestral stock of our

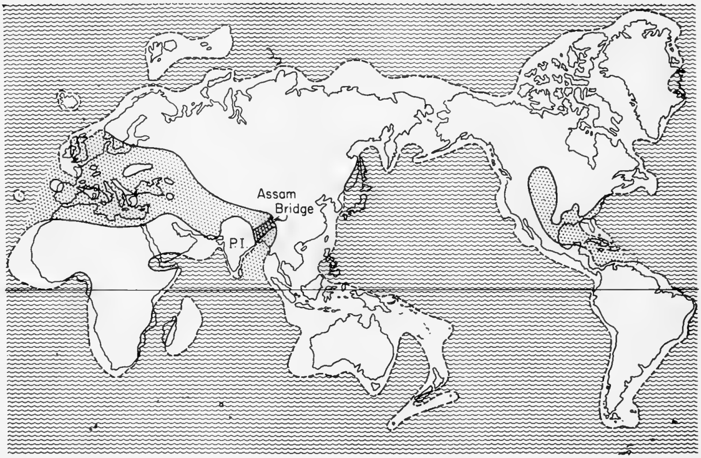


FIG. 10-8 **Paleogeography of the world during the Upper Cretaceous, showing land bridges and epeiric seas (Ross 1951).**

present tropical fauna and flora was greater than it is at the present time.

Another difficulty that southern species would encounter on the bridge would be the very long days of the summer and the very short ones of the winter. Tropical species are adjusted to fairly equal photoperiods at all seasons of the year. Seasonal differences in photoperiod are due to the inclination of the earth's axis and there is no positive evidence that this inclination has changed during geological time. Although it appears very likely that the Bering land bridge was an important route of dispersal between Asia and North America, considerably more study is required before we will satisfactorily understand how this was accomplished by various kinds of animals.

Centers of origin

The tracing of dispersal routes presupposes a starting point where the taxonomic group, whatever its size, first evolved. These starting points are called *centers of origin.* Various criteria for determining centers of origin have been suggested (Savage 1958), but caution must be exercised in applying them (Cain 1944). Of the many criteria proposed, the following two are especially important, although neither one is infallible:

1. LOCATION OF GREATEST DIFFERENTIATION OF THE TYPE OR THE GREATEST VARIETY OF ENDEMIC RACES, SPECIES, AND GENERA, INCLUDING PRIMITIVE FORMS OR FOSSILS. The older a group is and the longer it has occurred at a particular location, the more chance it has had to radiate into different habitats, become isolated, and evolve into new varieties. However, a shift of climate or a drastic change in physiography may render an original locality unhabitable and the group moves elsewhere. Also, a group losing its vitality may contract its range into some area other than the one in which it originated.

2. CONTINUITY AND CONVERGENCE OF LINES OF DISPERSAL. Dispersal from a center radiates in all directions in which conditions are favorable and until insurmountable barriers are encountered. Lines of dispersal may be readily distinguished where one or more taxonomic characters can be traced from primitive or generalized types through more and more specialized types the greater the distance involved. However, once a species filters through a break in a barrier and invades an extensive, new, and favorable habitat, there may be increased evolution of new types, and a secondary dispersal center formed. This has happened repeatedly in the geological past, so there is often difficulty in distinguishing which center is the original one for a group.

Island dispersal

Dispersal of animals from continents to islands and from one island to another presents special problems.

Many of the world's prominent islands occur on the continental shelf and are separated from the mainland only by shallow seas. At times of land emergence, as when glaciers lock up quantities of water as snow and ice enough to lower the level of the seas, these islands become connected by land bridges to the mainland, and dispersal of forms occurs. The British Isles have been thus connected to Europe; Japan, to Korea and Siberia; Sumatra, Java, and Borneo to Malaya; New Guinea and Tasmania, to Australia; and Newfoundland, to Labrador. On the other hand, the Bermudas, Azores, Hawaiian and other small Pacific islands, and possibly New Zealand, the West Indies, and Madagascar, could not have had mainland connections and thus have received their present faunas by some means other than overland dispersal (Chapter 20).

Islands adjacent to continents, unless very small or long separated, generally have faunas similar to that on the nearby mainland. Oceanic islands are more difficult to colonize, however, and often have unique unbalanced faunas or chance assemblages of species. Larger islands generally have a more varied fauna than do small islands; mammals, amphibians, and fresh-water forms are often absent or scarce. Flying birds, bats, lizards, insects, snails, and small invertebrate forms easily transported on rafts or blown in by strong winds are better represented.

Since island faunas are small in point of population compared with the mainland, there is less competition between species. A single genus or family may adaptively radiate into new niches to form a variety of species or races, as did the group of finches in the Galapagos Islands observed by Charles Darwin and later studied by Lack (1945), and insects, honeycreepers, and other forms in the Hawaiian Islands (Zimmerman 1948). Because of lack of competitors and predators, primitive animals isolated on islands may survive long after their relatives on the mainland have perished, as has, for instance, the reptilian *Sphenodon* on New Zealand. Confinement of a species to a limited range permits extensive inbreeding so that the population becomes more homozygous in its various genetic traits, hence much less adaptable to new situations than are larger heterozygous populations. Traits that would be eliminated by predation pressure on mainlands sometimes become established in populations on islands. All of these conditions render oceanic island species liable to extinction by invasion of mainland forms, and renders them impotent to reinvade the mainland.

Origin of North American fauna

A dry land bridge connected North America to Asia across the Bering Sea during most of the Tertiary and during glacial periods in the Pleistocene (Hopkins 1959). During early Tertiary, Alaska had a temperate climate, but as the climate became progressively colder in late Tertiary, there was increased filtering of animal groups having access to the bridge. At the present time all land connection has, of course, disappeared, although a few forms, particularly birds, are able to hop the narrow straits. Across this bridge came a heavy traffic of Asiatic mammals (Simpson 1947, Savage 1958), birds (Mayr 1946), reptiles, amphibians, and fish (Darlington 1957), modern insects (Ross 1951, 1953), and other groups. There was also some dispersal from North America into Asia, but this reverse movement was much less strong than the one from Asia into North America.

During the early part of the Tertiary, all major groups of mammals appear to have moved freely across the land corridor so that there was considerable similarity between the two continental faunas. However, from early Eocene to early Oligocene, new orders, families, and subfamilies arose that were distinctive to each continent. Later in the Tertiary, there were fewer groups dispersing across the bridge, and these were largely confined to genera within the higher taxa already established on each continent.

There is no evidence for a land bridge between North America and Europe via Greenland and Iceland since early Tertiary, although it is possible that one existed earlier. A few animal forms may have been able to hop from island to island across the North Atlantic, but the fauna of North America and Europe are not sufficiently similar to suggest any recent close connection of the continents. Some pantropical forms may have crossed the Pacific Ocean from island to island to reach the Western Hemisphere, but former land bridges across either the Pacific or South Atlantic oceans are highly unlikely.

A continuous land connection occurred between North and South American in late Cretaceous-Paleocene time. It was probably at that time that ancient types of mammals, birds, reptiles, amphibians, insects, and other groups got into South America from the north and differentiated into distinct families and other taxonomic categories (Dunn 1931). During most of the Tertiary, no land bridge existed between the two continents, although there were scattered islands separated by relatively narrow water gaps which some groups, particularly birds, may have been able to use. The land connection now in existence was apparently formed in the late Pliocene or Pleistocene.

Previous to late Pliocene there were about 29 families of land mammals confined to South America

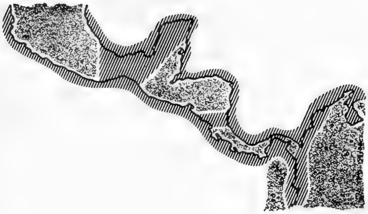


FIG. 10-9 **Tertiary water gaps (hatching) between North and South America (Mayr 1946).**

and 27 confined to North America; the two continents had not more than one or two families in common. During the Pleistocene, after the land bridge had been in existence for some time, 22 families were represented on both continents; 7 had dispersed from South to North America, 14 from North to South America, one is of uncertain origin. Some families have become extinct. The present faunas of the two continents contain 14 families in common, 15 families found only in South America, and 9 families only in North America. Thus there has been considerable dispersal over the land bridge in both directions, but not a complete exchange or unification of faunas (Simpson 1940).

The modern fauna of North America is thus derived principally from Eurasia and South America, and by autochthonous development. By autochthonous we refer to species evolved from very old indigent types that may or may not be represented by related forms on other continents. The proportion of any local fauna that is derived from one or the other of these sources varies with each geographic area and with each group of animals (Table 10-1). Northward on the continent and in the western mountains, the Eurasian bird element is strongly represented. The South American element becomes greater southward, especially in the lowlands of California, Mexico, and Central America. Many Eurasian forms have dispersed through North America into South America, but no modern forms, at least, of South American origin have been able to invade Asia through North America.

MIGRATION

Migration, like dispersal, involves movements and the invasion of new areas. Migration, as here defined, differs from dispersal in that it is a *periodic* movement back and forth between two areas (but see Urquhart 1958). In contrast, dispersal is a one-way outward movement. Migratory invasions of areas are temporary and repetitive, but invasions resulting from dispersal may be permanent.

Migration is best known in birds, as an invasion of breeding area alternating with an invasion of wintering area, annually. Representatives of other groups of animals also migrate, particularly mammals, fish, and insects (Heape 1931). Migration may be classified as annual, diurnal, or metamorphic (Clements and Shelford 1939). Annual and diurnal cycles are correlated with the two most pronounced time cycles in the physical environment. Metamorphic migrations are movements from one habitat to another in different stages of an animal's life cycle.

Annual migrations

Annual migrations may involve a change of latitude, or altitude, or be more local in extent.

Latitudinal migrations may traverse only a few miles or may traverse almost from pole to pole. In terms of their occurrence in an area bird species are described as *permanent residents,* species represented in an area throughout the year even though some individuals migrate; *summer residents,* species present only during the warmer part of the year, which includes a breeding season that may extend from early spring to late autumn; *winter visitors,* species present only during the winter or non-breeding period; *transients,* species ephemerally present only during mi-

TABLE 10-1 **Analysis of geographical origin of the breeding bird populations of various communities in North America (Mayr 1946, Snyder 1950, Hensley 1954).**

		Eurasian		North American		South American		Unanalyzed	
Community	**Locality**	**Species**	**Pairs**	**Species**	**Pairs**	**Species**	**Pairs**	**Species**	**Pairs**
Western coniferous forest	Rocky Mountains	65%	98%	17%	2%	6%	+	12%	+
Boreal forest	Maine, Ontario	52	20	30	79	3	+	15	1
Deciduous forest	Ohio	28	23	32	52	28	23	12	2
Desert scrub	Arizona	27	39	35	53	22	6	17	+
Desert scrub	California	11	14	78	49	11	37	0	0

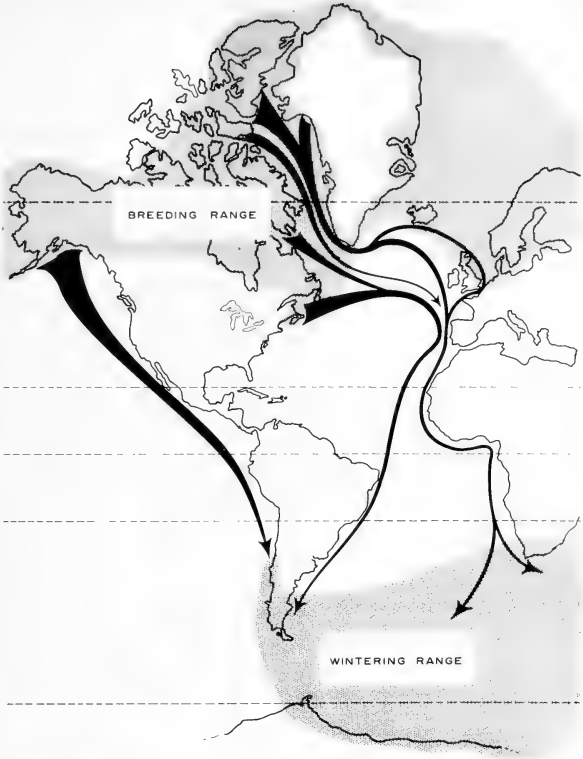


FIG. 10-10 **Migration routes, the longest known, of the arctic tern (Lincoln 1950).**

gration periods, neither breeding nor wintering in the area; and *accidentals,* species that are rare or irregular in occurrence. The bird population in most communities reaches peaks during the vernal and autumnal aspects, as transients arrive and temporarily swell populations. The autumnal peak is usually the greater because adult populations are incremented by the large number of young birds hatched during the breeding season. Latitudinal bird migrations also occur in the southern hemisphere but are less conspicuous because of the small continental land masses there and small populations of birds involved.

There are many causes of bird migration, varying in relative importance with different species. Aquatic species must leave northern areas before their food supply is cut off by the freezing of the lakes, ponds, and rivers. Insectivorous species unable to change to other types of food must migrate before insects go into hibernation or disappear. The metabolism and food requirements of many song birds are so high that even when food is abundant they cannot eat enough during the short winter day to give them sufficient energy to survive the long, cold winter night. Migration northward in the spring escapes the high summer temperatures of the south and gets the migration into latitudes where the days are long (Kendeigh 1934). Whatever its immediate causes, migration presumably evolved because survival was more successful among those individuals that departed than among those that remained (Lack 1954a).

The timing of migration is not usually regulated, however, by the factors just listed as causes, for most birds migrate days, weeks, even months before the beginning of intolerable conditions in the autumn and after they disappear in the spring. The annual stimulus to migration is complex and involves changes in physiological state, energy balance, and hormones (Kendeigh *et al.* 1960). The chief environmental-factor stimuli are changes in length of day and night and changes in temperature with the progress of the seasons. The regularity of migration by which species arrive at a given point about the same date year after year is probably a response to the regularity of change in day length. The fact that species may arrive a few days early or late of the usual arrival date is doubtless a result of the superimposed effect of variations in temperature, to which the birds are also responding.

The mechanics of migration, fly-ways, flocking behavior, migration routes, and so forth, are too intricate for detailed analysis here (Lincoln 1950). Much research is now in progress analyzing the factors involved; let it be sufficient merely to add that migratory behavior is organized as an instinctive behavior pattern in the bird's nervous system. If a stimulus is not presented, the behavior will not be expressed. The stimulus arises when the interaction between internal physiological rhythms and environmental cycles reaches a critical stage.

Annual latitudinal migrations are not limited to birds. Bison regularly migrated from northern parts of the Great Plains to pass the winter in southerly reaches, traversing a distance of 300 to 600 km (200–400 miles). Some bats, particularly the hoary and red bats regularly migrate between Canada and the northern states. The fur seal breeds in the Pribilof Islands in the Bering Sea during the summer, and migrates southward as much as 4800 km (3000 miles) for the winter.

Some insects migrate. The monarch butterfly breeds in the northern states and migrates several thousands of miles to winter as far south as the Central American tropics. A small proportion of individuals successfully make the return migration in the spring. Evidence is accumulating to indicate two-way migratory behavior in other species of butterflies and insects (Uvarov 1928, Fraenkel 1932, Williams 1958).

Migratory locusts or grasshopers occur both in the eastern and western hemispheres. *Schistocera gregaria* inhabits the arid grassland and semideserts of Africa and southern and western Asia (Uvarov 1928); *Melanoplus mexicanus* occurs in the northern Great Plains of North America. In both species, solitary and migratory phases occur which differ in points of size, wing length, and coloration. The migratory phase apparently develops under conditions of higher temperatures and good breeding conditions so that over-populations occur. When migration begins, immense swarms of adult flying individuals move great distances. Migration in the nymphal hopper stage is more limited. Vegetation is ravenously devoured wherever the swarm stops. Such migrations were extensive in North America between 1876 and 1879 when populations moved from the northern Rocky Mountain area into the states immediately west of the Mississippi River. Eggs were deposited at the terminus of the migration flights and at least some of the succeeding generation exhibited return flights in following years.

Altitudinal migrations are movements of no more than a few miles up and down the slopes of mountains. By descending to lower altitudes in the autumn, an organism obtains some of the same benefits secured by those species that undertake latitudinal migrations; i.e., less snow, higher temperatures, and more food. Birds restricted to alpine habitats in the summer are common winter residents of lowland areas. Some of the larger mammals, such as the mule deer (Russell 1932) and the American wapiti (Altmann 1952) have very regular migration habits in respect to herding, timing of movements, and migration routes. They move to the high alpine meadows soon after the vegetation renews its growth in the spring, and come back down to the valleys in time to avoid the deep winter snows of the higher slopes.

Local migrations do not necessarily involve a change of latitude or altitude and are often quite limited in distance covered. However, in tropical grasslands and savannas where wet and dry seasons bring great changes in available water, vegetation, and food, there is a great exodus of both mammals and birds during the dry season and an influx during the rainy season.

The Atlantic salmon, after reaching sexual maturity, may ascend fresh-water streams in subsequent years to spawn and return each time to the sea. Many deep-water fishes spawn annually in shallow waters and then return to deep water again. Turtles come onto the land to lay their eggs; snakes disperse from their winter dens with the advent of warm weather in the spring; tree frogs go to small pools to mate and spawn; and resident birds move onto their breeding territories.

Insects perform regular migrations both into hibernation and out of hibernation. In the autumn, forest species migrate downward and may be found in peak numbers first in the shrubs, then in the herbs, then in their hibernacula in the ground. Many insects of the forest-edge, meadows, and agricultural crops also hibernate in the forest, usually a few meters in from the South-exposed edge where they derive some heat from the winter sun. These insects usually migrate into the forest in the same stratum, herb or shrub, in which they occur during the summer, then downwards into the soil. These flights into the forest occur with declining temperatures and are sometimes spectacularly large numbers of individuals. As they come out of hibernation in the spring the direction of movement the insects take is just the reverse that taken in the autumn; i.e., upward into their proper stratum, then horizontally outward into open country (Weese 1924).

Daily migrations

Ascent of plankton towards the surface at night and descent to greater depths during the day occur both in the sea and in lakes. The lake-dwelling culicid larva *Chaoborus* lies on the bottom during the day but becomes pelagic at night. Snails, slugs, and millipedes in the deciduous forest lie quiescent under logs or litter during the day, but come out at night to crawl around on the forest floor or even climb up on the vegetation to a height of perhaps a few meters. Although these excursions are restricted in range, they are more or less regular and periodic, and may be thought of as migrations.

Metamorphic migrations

Aquatic larvae and naiads of several orders of insects eventually change into adults that leave the aquatic habitat and become aerial. The adult stage is often short-lived. The eggs are deposited in water, or the immature stages return again to water to begin the cycle over again. The length of the cycle may be part or the whole of a year, or a longer period. The seventeen-year cicada is a well-known insect whose nymphs spend 17 years underground feeding on juices from the roots of trees. The adults appear above ground in large numbers in late May, mate, lay their eggs on twigs of various trees, and then disappear, all in a few weeks. The eggs hatch in about six weeks, and the nymphs drop to the ground and bury themselves for another long period of years.

The anadromous Pacific salmon ascends freshwater streams but once to spawn. The breeders die; it is their offspring that return to the ocean to develop for a period of years before they make the migration. The two species of catadromous eels, of the western hemisphere and of Europe, migrate to the open sea in the region northeast of the West Indies in order to reproduce. The immature stage of the eel, not the adults, returns to the two continents.

ECESIS

Dispersal or migration of individuals into new areas is without great ecological significance unless those individuals become established and can build up significant populations. The process by which organisms become established in new areas is called *ecesis*. Ecesis will occur there if a species disperse into a habitat favorable to it, and if the species can then secure its proper niche or become adjusted to a new niche, new competitors, predators, parasites, and disease organisms. Ecesis, to go to completion, requires first the establishment of individuals in an area, then the growth of the population that they form, and finally or simultaneously, the maturing of community structure with the invasion of many other species.

Ecesis is often of a temporary nature. Temporary ecesis is the rule with migrant species, as the periodic change of location is normal in their life behavior. Ecesis as range expansion is not surely permanent until the species demonstrates that it can survive critical years in weather cycles. For instance, northward dispersal of tropical forests is, after a point, thwarted by frosts that occur only at rare intervals. Insects may continuously expand their ranges for a period of years, only to be forced back hundreds of miles by a severe drought or cold spell.

Growth of populations

The growth of a species population from a single individual or pair of individuals is governed by the same laws that govern the growth of the individual itself from zygote to adult organism. When either the size of the individual or the cumulative growth of the population is plotted against time, a characteristic sigmoid curve or logistic curve results. This phenomenon was first demonstrated by Verhulst in 1839. This curve has been used to describe the population growth of such diverse organisms as yeast, *Paramecium, Drosophila, Tribolium,* and man (Pearl 1927, Park 1939), and even the growth of communities in particular habitats when many species are simultaneously present. Under natural conditions, however, growth of animal populations is subject to so many variable factors, including the change from one morphological stage to another in the life cycle of many species, and the change in the physical environment both daily and seasonally, that the curve is often

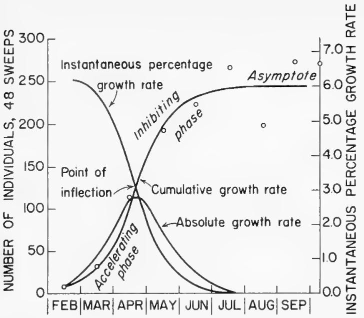


FIG. 10-11 **Annual ecesis of the invertebrate community in the herb and shrub strata of a deciduous forest.**

$$K = \frac{223 + 266 + 218 + 273 + 272}{5} = 250;\ a = \log e\ \frac{250 - 3.5}{3.5} = 4.25;\ r = \frac{\log e\,(20/3.5)}{28} = 0.062;\ N = \frac{250}{1 + e^{(4.25 - 0.062\,t)}}$$

not fully expressed, even though its trend is present inherently.

The sigmoid curve shows that a population grows slowly at first, then at an *accelerating rate* which is at maximum at the *point of inflection,* after which the population continues to increase but at a *decelerating* rate, finally becoming stabilized at the upper asymptote. Most growth curves are symmetrical, and the point of inflection is one-half the value of the asymptote. The lower concave part of the curve is called the *accelerating phase of growth* and the upper convex part of the curve, the *inhibiting phase of growth.*

If the number of new individuals added during each unit of time, *absolute growth rate,* is plotted against time midway in each period, a bell-shaped curve is obtained, the peak of this curve coinciding with the point of inflection on the sigmoid curve. However, the number of individuals involved in the absolute growth rate varies with the length of the time unit used, and the time unit of greatest significance varies from one species to another. Comparisons of growth rate of different populations are difficult unless instantaneous growth rates are obtained.

The *instantaneous growth rate* is the rate of growth at a point on a time scale and is usually expressed in terms of increase per individual or unit biomass per unit of time. It cannot be measured, but it can be calculated from the logistic curve by the differential equation (Park 1939, Andrewartha and Birch 1954)

$$\frac{dN}{dt} = rN \cdot \frac{K - N}{K}$$

where N is the size of the populations at any time t; dN/dt stands for the instantaneous rate of change (dN) in the size of the populations during an interval in time (dt) and hence may represent the growth rate at any desired time on the growth curve; r is the biotic potential, innate capacity, or the intrinsic rate of increase per individual per unit of time in an environment where there are no limiting factors; and K is the maximum size of the population reached at the asymptote. This equation means that the rate of growth equals the potential rate of increase in the size of the population (rN), multiplied by the fraction of the maximum population size (carrying capacity) still remaining to be filled $(K - N)/K$. In its integrated form,

$$N = \frac{K}{1 + e^{(a - rt)}}$$

where the constant a is the natural logarithm of $(K - N)/N$ when t is zero.

In order to solve the equation for the logistic growth curve, it is necessary to determine the intrinsic growth rate, r. In an environment without limiting factors, population growth is logarithmic. The factor r, the value of which varies with species, is the exponent that indicates this growth rate. The elephant, for instance, has a very slow growth rate. It has been estimated, however, that if all offspring survived and in turn reproduced, a single pair could give rise to 19,000,000 elephants in 750 years. On the other hand, a single stem mother of the common cabbage aphid gives rise to an average of 41 young, and there may be 12 generations per year between March 31 and August 15. If they all lived, the progeny resulting would number 564,087,257,509,154,652 individuals in only 4.5 months (Herrick 1926). It is of considerable ecological value to determine both the maximum potential rate at which a species could increase under ideal conditions and the factors that prevent this increase from being realized.

The intrinsic rate of increase, r, has been defined as *the maximal rate of increase attained at any particular combination of temperature, moisture, quality of food, and so on, when the quantity of food, space, and other animals of the same kind are kept at an optimum and other organisms of different kinds are excluded from the experiment* (Andrewartha and Birch 1954 p. 33). Such an ideal environment may be set up under controlled experimental conditions. Actually, it is sometimes approximated under natural conditions during the very early stages of the accelerating phase of growth. Under such conditions the value of r may be approximated from the equation

$$r = \frac{\log_e (N_{t2}/N_{t1})}{t_2 - t_1}$$

Thus if a population is doubled in a period of three weeks, or if the mean length of life of a generation is three weeks, then $r = \log_e 2/3 = 0.2310$ per individual per week.

A number of factors affect the intrinsic growth of a species: number of young at each reproduction, the number of reproductions in a given period of time, the sex ratio of the species, the age distribution of the population, their age at reaching sexual maturity, and so forth. The value of r has been obtained for comparatively few species (Table 15-7; Edmondson 1946, Odum 1959, Solomon 1953, DeWitt 1954, Oliff 1953, Root 1960).

In Fig. 10-11 the logistic curve has been fitted to the annual ecesis of the invertebrate community of the herb and shrub strata of a deciduous forest (raw data from Fig. 9-14). The upper asymptote, K, was obtained by averaging the five randomly fluctuating density values for June through October. The value of r was derived from the increase in community size for 28 days in February-March, but different values of r can be substituted in the integrated equation above until a curve is obtained that best fits empirical data.

The value of r being known, the equation for instantaneous growth rate was solved for different parts of the curve to give the following values: March, 1.08 individuals per day; April, 3.55; May, 2.65; June, 0.59. By plotting intermediate times it appears that the highest growth rate, 3.87, comes about April 24, at the point of inflection of the growth curve, and also at the time of greatest absolute growth.

r is an important constant, the potential rate of population growth with ecesis taking place on an area, where *ideal* conditions prevail. Neither such conditions nor, by so much, an actual rate equivalent to r are realized in Nature except that r may be infrequently approximated in the initial phases of growth. The actual rate is best expressed by the instantaneous growth rate. It is necessary to take equivalent stages in the growth curves for making growth rate comparisons between different populations. The point of inflection is of considerable significance in this regard; it represents the same equivalent age of populations whether they respectively attain to the asymptote in a matter of hours, days, months, or year. The *instantaneous percentage growth rate*

$$100 \cdot \frac{dN/dt}{N}$$

declines progressively with time.

In study of the process of population growth there are many advantages to working in the laboratory with populations of a single species held under experimental conditions where environmental factors can be closely controlled and varied at will (Park 1941). In such studies, the rate of growth of the flour beetle in experimental cultures has been found to vary with temperature, humidity, and light; according as whether fresh flour is added each day; whether competing forms or predators are introduced; and so on. The final population density turns out to be the same regardless of the number of beetles originally introduced into the flour, but it varies with the volume of the medium and other factors. The accelerating phase of growth is probably induced by frequent and successful mating contacts between individuals as populations increase in size. The inhibiting phase of growth is a result of decreasing food supply, accumulation of excreta which correlates with reduced fecundity of the adults; lowered rate of metamorphosis of the immature and increased mortality of the larvae, and cannibalism of the adults on the eggs.

Under natural conditions logistic growth curves for populations of single species are clearly evident when a species invades a new area that is favorable; when a species is recovering from a catastrophe or cyclic depression; and as a species builds up its population in the spring after the termination of a winter dormancy or migration. The many factors in natural environments that modify rates of population growth and determine the levels at which populations become stabilized at the asymptote will be considered in Chapter 16.

The total community is an aggregation of many species. When a bare area becomes receptive to propagation of life, only a few hardy plant species become established at first. These pioneer species react on the habitat by providing humus, food, shelter, and shade, making conditions in which other, more sensitive plant and animal, species can invade and become established. With many species present, interactions or coactions between them bring about the establishment of dominance, influence, and complete community organization. The result is a closed community. A community thus fully organized discourages invasion by new species. It persists for the longer or shorter time until there is further change or development of the habitat permitting succession to a new community. Each invasion and ecesis of species to form new communities follows the sigmoid or logistic curve. Thus the process of growth and ecesis is much the same whether it is at the level of the individual cell, organism, species population, or the complex community.

Ecesis of plant communities, as recognized by the species of plant dominants, is often more rapid than ecesis of complete animal communities. For example, some six to eight plant stages may be recognized in the floodplain sere, each stage giving way to the next in an orderly succession (Chapter 8). However, except for a poor representation of forest-edge species along the banks of the river itself, there is only one

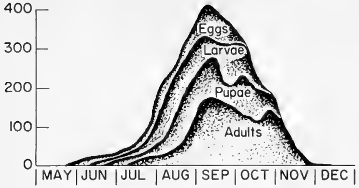


FIG. 10-12 **Seasonal growth and decline of a nest colony of common hornets, *Vespa crabo*, in France (Bodenheimer in *Biol. Rev.* 1937, after Janet).**

animal community. This animal community, the deciduous forest biociation, begins its ecesis with the establishment of the first trees, and with each advanced stage in the plant sere more and more animal species invade. The establishment of the complete animal community is not attained until the late or final stages of the plant sere are reached. In the sand and pond seres there are three or four distinct animal communities recognizable that definitely succeed one another, but the ecesis of each animal community is not accomplished until there has been a succession of several plant communities. One must not expect, therefore, the complete ecesis of a distinct animal community to correspond with each distinct plant community but only when there is a change and full development of a distinct type of vegetation.

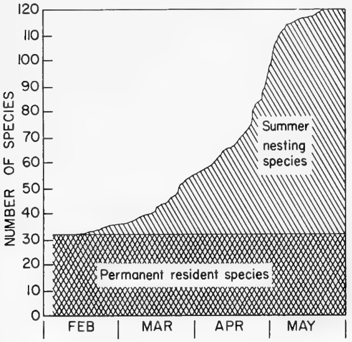


FIG. 10-13 **Ecesis of nesting bird species in central Illinois during the prevernal and vernal aspects (compiled from Smith 1930).**

SUMMARY

Dispersal of animals into new areas may be a range expansion of a species if individuals find unoccupied niches, are able to overcome competition, or are able to acclimatize and adapt to the conditions. Dispersal is chiefly by the immature stages that are broadcast randomly in all directions, conveyed passively by wind, current, or other animals, respond to environmental factors by directed movements or taxes, or find their way by trial and error. Dispersal continues at measurable rates until a physiographic, climatic, or biotic barrier is reached. Factors that induce dispersal include population pressure, failure of food supplies or loss of favorable homesites, opening up of new areas elsewhere, and pre-adaptation for new and different niches.

The origin of taxonomic groups of organisms may be traced to various centers, usually distinguished by the occurrence of the greatest amount of differentiation within the group and the convergence of lines of dispersal. According to Matthew, the major vertebrate groups first evolved in temperate Asia; according to Darlington, that event took place in the Oriental tropics. The present distribution of related forms over the face of the world has been accounted for by the continental drift theory and the likelier idea of dispersal over land bridges that have periodically come and gone during geological time.

The fauna of continental islands is derived mainly from the adjacent mainland over such bridges in the past, but the fauna of the more distant oceanic islands are often unique and unbalanced, and dependent on the accidental dispersal of miscellaneous species. The fauna of North America is derived principally from Eurasia, South America, and by autochthonous development.

Migration, like dispersal, involves movements and invasion of new areas, but differs from dispersal in that the movements are periodic back-and-forth movements between two areas. Migrations may be annual or daily, or may be in the form of changes of habitat at different stages in a life cycle. Annual migrations may be latitudinal, altitudinal, or local. Annual migration is best developed in birds but also occurs in mammals, fish, and insects.

Ecesis is the establishment of organisms in an area into which animals have come by dispersal or migration. This involves the establishment of individuals, the growth of populations, the invasion of more and more species, and finally the development of mature communities. The growth of species populations and of complex communities commonly follows a sigmoid or logistic curve that may be defined in mathematical terms.

11

Ecological Processes and Community Dynamics:

Reactions, Soil Formation, and Chemical Cycles

The building up of species populations in a new habitat brings various *reactions* of the organisms with the habitat which, together with coactions between different members of the community, bring about succession of communities. We need now to examine these processes.

PLANT REACTIONS

We have already considered, many of the reactions of plants such as reduction of light and wind intensities, mitigation of temperature extremes, interception of rainfall, and increase in relative humidity. Plants also exert important effects on the formation, structure, and characteristics of the soil or substratum produced by accumulation of dead plant remains: they further the weathering of rock through acid excretion and the mechanical action of roots; they offer obstruction to wind- and water-borne materials; they help stabilize moving sand and talus slopes and help prevent erosion generally; they variously increase or decrease the water content of soil; they foster decomposition of raw humus into usable nutrients, and so forth. Water plants form marl. It is by these reactions that plants exert dominance in terrestrial communities, and establish the physical conditions of the habitat which must be acceptable to all minor plants and animals that dwell there. Succession of plant stages eventually brings the interactions between habitat and community into equilibrium upon the establishment of the climax (Weaver and Clements 1938).

SOIL FORMATION

Texture, porosity, consistency, arrangement of particles, chemical nature, and organic content of soils are determined by three sets of factors: the parental rock material, the biota, and the climate. Differences in topography modify the relative effects of these three factors, and plenty of time is required before their full effects are realized.

Parental rock

The basic rock from which the mineral portion of a soil is derived determines, to a large extent, not only its chemical composition but also its structure. For instance, soils derived from limestone are highly calcareous and more alkaline than soils derived from sandstone. Clay soils are derived from feldspar; sandy soils, from quartzite. Clay forms a finely-textured, compact, water-retaining soil. Sand is coarse-textured and porous. Loam is a mixture of sand and clay and makes the best soil. The presence of iron oxides and silicates produces the red and yellow colors of some soils. Humus produces black soils. Soil from swamps or bogs and very rich in organic material is called muck.

Residual soils are formed *in situ* from underlying bedrock. Soils may, however, be formed in one locality and moved considerable distances. Soils transported and deposited by wind are called *loess;* by water, *alluvium;* by glaciers, *till.*

Biota

Plants and animals have a highly important role in the formation of soil, both as they affect its structure (Jacot 1936, 1940) and as they aid in the production of humus. Plants contribute to the mechanical and chemical weathering of rock. Plant roots, especially those of trees, can split large rocks. Lichens, mosses, and even bacteria and fungi excrete acids, in the course of metabolism, which dissolve the substances that cement rock granules together. When plant roots die, fungi convert them to dry, soft, spongy material (punk), used as food by saprophytic micro-arthropods. Usually the bark of the root remains intact the longest. Hollow tubes are thus formed that permit water and air to penetrate considerable depths into the soil. These channels gradually become filled with silt and animal excreta.

The addition of plant and animal organic matter to heavy compact soils or clay tends to open the soil, making it more porous. Addition of organic matter to sandy soils binds the particles closer together, making the soil less porous.

Earthworms may be divided into deep- and shallow-working species (Kevan 1955). Deep-working species dig narrow tube-like channels which may reach 2–3 m down through overlying soil to parent rock. Earthworms ingest soil while burrowing, digest and absorb organic matter from it, and egest the residue in a semi-liquid form which is used to cement the walls of the burrow or else is deposited at the surface as castings. Earthworms prefer easily digested succulent vegetation and dung for the purpose, but in the autumn may pull the freshly fallen leaves down into their burrows to use as food or nest linings. Ejected petioles may form midden piles around burrow entrances. In an undisturbed virgin prairie in Texas, earthworm casts made a layer 2–3 mm thick over the entire ground surface and when air-dried weighed about 2400 g/m^2 (10.7 tons/acre) (Dyksterhuis and Schmutz 1947). Earthworms are not, however, important soil builders in disturbed grassland; they may be absent altogether in arid regions. In other studies (Evans and Guild 1947), the dry weight of casts brought to the surface annually by earthworms varied from 475 g/m^2 (2.1 tons/acre) in a moderately hot dry climate, to 24,000 g/m^2 (107 tons/acre) in the White River valley of the Sudan, during the rainy season. Earthworm casts compared with the surrounding soil show higher total nitrogen, organic carbon, exchangeable calcium, exchangeable magnesium, available phosphorus, exchangeable potassium, organic matter, base capacity, pH, and moisture equivalent (Lunt and Jacobson 1944). Only certain species make these surface castings; other species void the ingested soil into subterranean spaces.

The ant *Lasius niger neoniger* spends most of its time in its underground burrows and deposits excavated soil upon the ground surface around burrow entrances. In an old field community in Michigan such deposits amounted, at one sampling, to 85.5 g/m^2 (750 lb/acre). However, entrances are abandoned and new ones made, so that in the course of a few weeks a much larger quantity of soil is brought up (Talbot 1953).

In the semi-arid Great Plains of western North America there is at least one species of ant that excavates extensively underground and builds a conical mound of this excavated material above the surface. A single such mound weighs approximately 77 kg (170 lb); there are as many as 50 such mounds per hectare (20 per acre) in some localities. Plainly, these little excavators move prodigious amounts of soil. The relatively sterile subsoil is gradually mixed with organic material and spread over the surface of the ground, thus increasing the depth of the fertile top-soil. Scarabeid beetles, bees, wasps, and in tropical regions mound-building termites also move considerable subsoil to the surface (Thorp 1949).

The crayfish *Cambarus diogenes* often occurs in poorly drained fields; it burrows down to the water table, sometimes a depth of three meters. Excavated material is brought to the surface and built into chimney-like affairs which may be 20 cm high and almost that much in diameter. Where crayfish are abundant, as much as 600 to 2000 g/m^2 (2.7 to 8.9 tons/acre) of soil per year may thus be moved (Thorp 1949).

The burrows of prairie dogs and badgers may extend 2 to 3 meters below the surface, and a single mound of excavated dirt weigh from 100 to 10,000 kg. Mounds made by pocket gophers and ground squirrels weigh from 7 to 180 kg each; it is not unusual to find 42 such mounds per hectare (17 per acre). These animals thus move from 7 to 9 kg of subsoil for each square meter of surface (30–40 tons/acre) in a period of several months (Taylor 1935, Thorp 1949).

Large terrestrial animals trample the soil into greater compaction and destroy vegetation at sites where numerous individuals foregather; around water holes in grassland where bison and antelope come to drink, for instance, or winter yards of deer and moose, trails on hillsides, wallowing places, and so on. These reactions are usually very local, however.

As animals burrow and bring large quantities of loose soil to ground surface exposure, the likelihood of water and wind erosion destruction is greatly increased, especially true if the burrowing is done on hillsides where the flow of water is faster and where the animals always tend to deposit the soil on the downslope side of burrow entrances. On the other hand, the very same activities may decrease erosion where a soil is, in consequence, made more porous so that there is less water runoff.

Humus

In soil, organic matter that is partly or entirely decomposed is called *humus*. The amount of humus varies from less than one per cent to as much as 20 per cent of the soil; peat soil may be largely organic material, but much of it resists decomposition, and hence is not true humus. Decomposition breaks down complex organic compounds into simpler ones that are washed back into the soil, thus becoming available again as nutrients. On virgin prairie in Texas the ground litter of dead grasses and herbs amounted to over 300 g/m² when measured in April (Dyksterhuis and Schmutz 1947). The annual dry weight of leaves that fall to the ground in deciduous and coniferous forests varies from year to year, from site to site, and with the density of the trees, but is in the range of 100 to 900 g/m². In mature climax forests the rate of decomposition of the litter and re-absorption by plants of the nutrients thus yielded keeps pace with the annual accumulation so that an equilibrium is established. In seral stages, decomposition and utilization do not keep up with the annual accumulation so that the organic content of the forest floor increases with time. Under spruce, sugar maple, and birch in New Hampshire, the organic ground matter equals 3 kg/m², but in Florida where high temperatures and rainfall favor rapid decomposition and leaching, there may be only 0.4 kg/m² under old growth longleaf pine (Kittredge 1948, Ovington 1954).

The thick organic layer on the ground moderates extremes in the daily and seasonal rhythms of soil temperature, retards freezing of the ground in the autumn and thawing in the spring, and retains soil moisture. Because of humus formation (involving oxidation) and the respiration of plant parts and animals underground, soil air contains little oxygen but much carbon dioxide, and it possesses a higher moisture content than does the general atmosphere above ground. This is especially marked in warm summer months when these processes go on more rapidly. The decay of organic matter usually makes the top soil somewhat acid (most commonly pH 5 to 7), but in the mineral subsoil, the acids are often neutralized by the basic salts commonly present.

The mineral content of leaf fall varies according to the species of tree, but in the northern United States it averages about as follows (Chandler 1941, 1944):

Element	*Hardwood forests*	*Coniferous forests*
calcium	7.3 g/m²	3.0 g/m²
nitrogen	1.8	2.6
potassium	1.5	0.7
magnesium	1.0	0.5
phosphorus	0.4	0.2

Silicon, copper, manganese, carbon, and zinc are also present in the leaves of hardwood trees. Carbon is relatively more abundant and nitrogen less abundant in coniferous than in deciduous leaves; commonly the carbon/nitrogen ratio is 55:20 (Ovington 1954).

Both plants and animals are important agents effecting the decomposition of organic matter and the formation of humus. An animal digests and metabolizes plant foods, the total quantity of which is returned to the soil, in part as the excreta of the living animal, the rest as the body of the dead animal. Fully formed humus is, in fact, derived mostly of fecal material. The larger herbivorous and carnivorous animals pass urine and feces containing simple nitrogenous compounds and compounds of phosphorus, potassium, and traces of calcium, magnesium, sulfur, and other elements. Humus is but one point in a continuous cycle of decomposition of plant and animal organic matter, absorption of decomposition products by plants, ingestion and metabolization of plant matter by animals, decomposition of plant and animal organic matter, —ad infinitum. The consumption by saprovores and herbivores of living and dead plant matter and the consumption of herbivores by carnivores, neither add nor subtract from the total nutrient supply of an ecosystem. The chemical elements available in the air, water, and soil of an ecosystem pass, in one compound and another, from one organism to another, and through one stage in the cycle after another, and they continue thus to circulate within the ecosystem unless and until they are physically withdrawn from it. To remove plant and animal crops from an ecosystem is to withdraw nutrients from it, and thus to reduce the fertility of the system. Fertility can then be maintained only if the nutrient supply is kept replenished by artificial fertilization.

Kangaroo rats defecate promiscuously throughout their underground burrow systems. The soluble nitrate content of the soil in the region of one burrow system averaged 221 ppm and in another one 570 ppm, compared with a maximum of 15 ppm in the

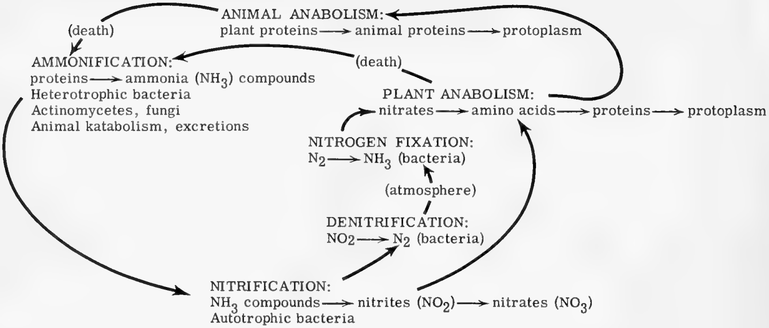


FIG. 11-1 **Steps and processes in the nitrogen cycle.**

surrounding desert soil generally (Greene and Reynard 1932). It is a reasonable estimate that the total bird population in a deciduous forest would deposit 0.1 g dry weight of organic excrement per square meter in a year's time; the mammal population, perhaps 0.5 g; and the total invertebrate fauna, possibly 2–3 g. The accumulation of excrement under the roosts of birds is sometimes enough to kill the ground vegetation and even the trees (Young 1936). The guano deposits on the coast of and islands off Peru and elsewhere in the world were originally several meters thick, as the result of centuries of occupancy by nesting colonies of marine birds, but have now been largely depleted by man for use as crop fertilizer (Hutchinson 1950). Bat excrement, deposited in caves, was exploited in years past as a source of saltpeter for gunpowder.

The conversion of raw organic matter into materials suitable for re-absorption and utilization by plants is a complicated process and depends almost entirely on the reactions of plants and animals (Lutz and Chandler 1946, Waksman 1952). The digestion of animals produces both mechanical and chemical changes in raw humus that can be measured quantitatively (Franz and Leitenberger 1948). The nonnitrogenous substances in fresh litter are sugars, starches, pectins, pentosans, celluloses, cutins, tannins, lignins, oils, fats, waxes, and resins. Most of these substances are readily broken down in the soil by fungi, actinomycetes, bacteria, and protozoans, but tannins, lignins, waxes, and resins decompose very slowly. The end products of complete decomposition are H_2O and CO_2, but sometimes decomposition is incomplete and organic acids are formed instead.

The most important soil organisms concerned in the decomposition of the litter are the bacteria, both aerobic and anaerobic forms. They are commonly divided into two types. *Heterotrophic* bacteria obtain their energy from the oxidation of the carbohydrates and fatty substances as above described. They use this energy for the synthesis of cell substances and the production of enzymes that break down complex compounds in the litter into simpler compounds, including proteins into ammonia compounds. They then use part of the ammonia compounds in synthesizing the amino acids they need in building their own proteins. *Autotrophic* bacteria, in turn, are of two types: *Chemosynthetic* species that obtain their energy from the oxidation of inorganic compounds (hydrogen, sulfur, hydrogen sulfide, iron, ammonia) and *photosynthetic* species, which include purple and green sulfur bacteria, possess a form of chlorophyll, and utilize the energy of sunlight. Chemosynthetic bacteria convert ammonia compounds into nitrites and nitrates, part of which they use in their own anabolism, the rest becoming available for plants to absorb. Photosynthetic bacteria use the ammonia compounds in their own anabolism but do not render them directly available to plants. Chemosynthetic bacteria are more abundant than photosynthetic bacteria in soil; photosynthetic bacteria are the more abundant in water.

Nitrogen cycle

In the nitrogen cycle proteins are broken down yielding ammonia (NH_3) compounds in the course of the metabolic processes of all animals and by the activities of heterotrophic bacteria, filamentous fungi, and actinomycetes. The process is called *ammonification*. Some of the ammonia is oxidized to form

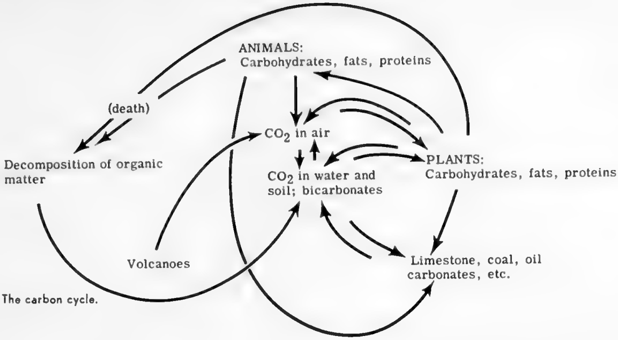


FIG. 11-2 **The carbon cycle.**

nitrites (NO_2) and nitrates (NO_3) through the action of autotrophic bacteria; the process is called *nitrification*. Other types of bacteria act on ammonia in the process of *denitrification*, by which nitrogen (N_2) is liberated into the atmosphere. Nitrogen is removed from the air by the *nitrogen-fixing* bacteria which live either freely in the soil or as symbionts in the root nodules of legumes and some non-legumes; *Ceanothus, Elaeagnus, Alnus,* and *Myrica,* among others. Some blue-green algae, fungi, and yeasts also fix nitrogen.

Nitrates and perhaps also the simpler nitrogen compounds are absorbed and used by plants for the synthesis of amino acids and proteins. Ammonia compounds, nitrates, and other substances are added to the soil in small amounts with rainfall; sources of these nitrogen compounds are volcanic eruptions, terrestrial decomposition, and atmosphere nitrogen fixed by lightning. An attempt to estimate the quantities of nitrogen involved in the different parts of the cycle has been made by Hutchinson (1944).

Carbon cycle

Animals obtain much of their carbon, as well as nitrogen, from plants, although some forms are also able to fix carbon directly from salts dissolved in water (Hammen and Osborne 1959). In photosynthesis, carbon dioxide obtained from the air and from dissolved bicarbonates in the substratum is combined with water to form carbohydrates, a portion of which may be converted to fats. Plants combine carbon with oxygen, nitrogen, hydrogen, and sulphur to form proteins. Carbon dioxide in the air comes chiefly from the respiration of animals, but small amounts arise from the respiration of plants, the decay and fermentation of organic matter, springs, volcanic action, and solution of sedimentary rock. Volcanoes were probably the original providers of carbon dioxide to the biosphere. Organisms tie up carbon dioxide as carbonates in skeletons and shells. Carbon is also tied up in the formation of peat, oil, shale, and coal. When limestone and other carbonaceous sediments are exposed to water erosion, the carbonates may be hydrolized to bicarbonates and thus become a source of CO_2. The concentration of carbon dioxide in the air is stabilized at 0.03 per cent by the buffering action of bicarbonates and carbonates in the oceans and fresh-water bodies (Hutchinson 1948):

$$CO_2 + H_2O \rightleftarrows H_2CO_3 \rightleftarrows HCO_3^- \rightleftarrows CO_3^{-2}$$

On the other hand, oxygen in the air (20 per cent) is derived almost entirely from the photosynthesis of plants.

Other elements

In addition to oxygen, carbon, hydrogen, and nitrogen, animals require at least 13 other elements that are all derived from the soil: calcium, phosphorus (Hutchinson 1948), potassium, sodium, chlorine, sulfur, magnesium, iron, copper, manganese, iodine, cobalt, and zinc. Only traces of some of these elements are required, but calcium is required in large amounts for skeletons, shells, antlers, and other organs, and in the metabolism generally. Phosphorus is a constituent of nucleoproteins, phospholipids, and skeleton. Goiter occurs in mankind and some animals in regions deficient in iodine. These elements are obtained from food, drinking water, salt licks, and grit taken into the stomach. A salt lick is a local, usually clayey, area characterized by a high concentration of salts where deer and other animals foregather to lick the soil for the salt. Soils deficient in or lacking these various elements support sparse animal populations; individuals are in more or less poor health; reproduction rates are low (Albrecht 1944, Crawford 1950).

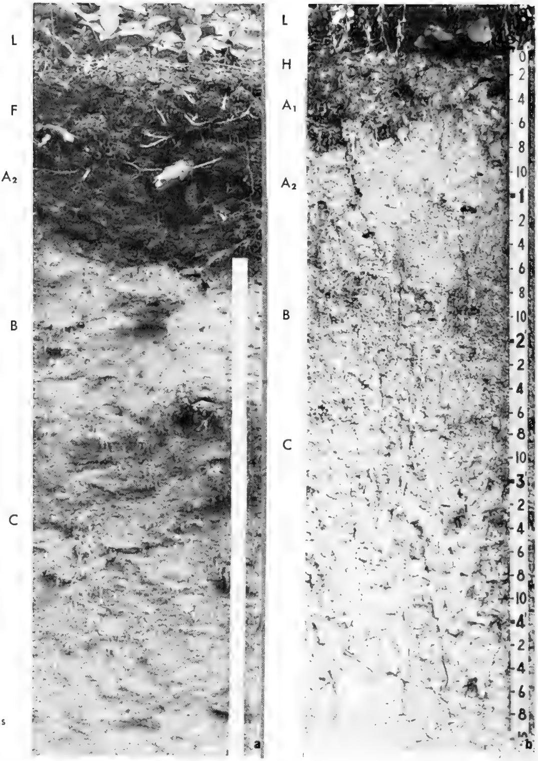


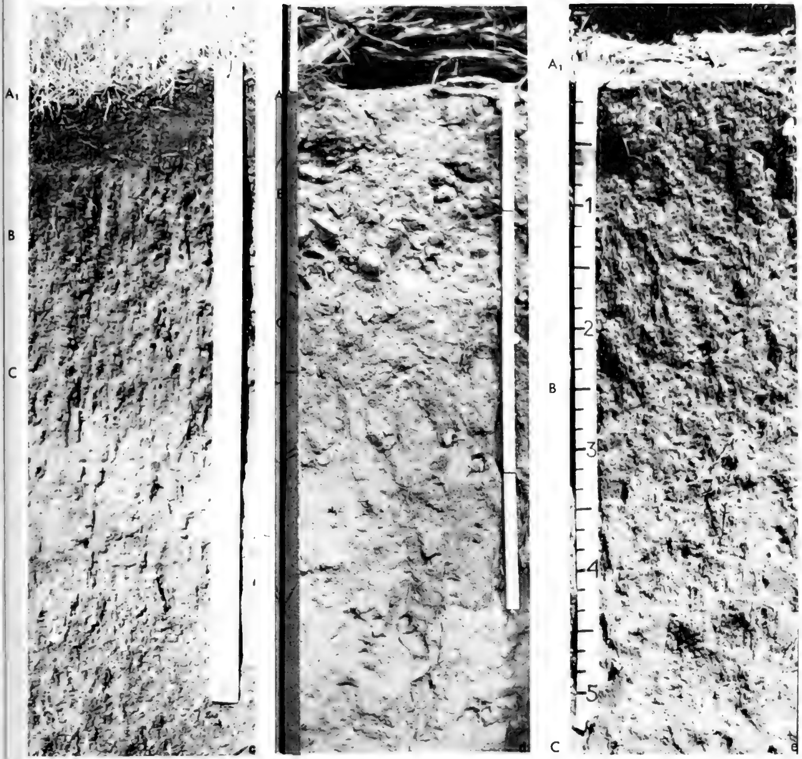
FIG. 11-3 (a) profile of a podzol (mor) from sandy glacial till under coniferous forest in Maine (courtesy Charles E. Kellogg) (b) profile of a gray-brown podzolic soil (mull) formed from loess under oak-hickory in Iowa. (c) profile of a chernozern formed from glacial drift under prairie in South Dakota—white spots are calcium carbonate. (d) profile of a sierozem, a desertic soil, derived from alluvium under sagebrush in Nevada. (e) profile of a latosol derived from gneiss under broad-leaved evergreen forest in Brazil. Pinholes and larger channels, formed by roots and insects, extend to 6 feet. Scale in feet and inches (courtesy Roy W. Simonson). The lettering along the margins of the profiles indicate the soil horizons (see page 170).

An excess of some elements is harmful. Too much fluorine in drinking water causes mottling of teeth and possibly pathological changes. Selenium in soils of arid plains becomes dangerous when it reaches 0.5 ppm, since some grasses, asters, and certain legumes absorb and retain it in concentrations that can be highly injurious to herbivorous animals. Wild animals have apparently learned to avoid eating these particular plants, but domestic stock blunder into them, eat them, and die (Knight 1937). Certain plants concentrate specific elements, a factor which may affect the food habits of animals. Black tupelo concentrates cobalt, and inkberry concentrates zinc to a much greater extent than do other species growing in the same areas (Beeson *et al.* 1955).

Climate

Water, temperature, and wind are important weather factors affecting soil formation. Water is an agent of rock erosion and transportation, sorting, and deposition of soil-building erosion products. Water freezes and expands in cracks and crevices of massive rock structures, breaking them into fragments and particles. Daily and seasonal heating and cooling cycles produce cracking because of different coefficients of expansion of the minerals in the rock. Wind erosion is particularly devastating in arid regions; fine soil particles may be lifted and transported many miles.

Weathering of rock is a chemical as well as physi-



cal process. Hydrolysis of some rock materials brings absorption of carbon dioxide and the formation of soluble bicarbonates. Hydration softens and increases the mass of some minerals, so that physical weathering of the rock bearing them is facilitated. Oxidation discoloring many rocks, especially those containing iron, is symptomatic of chemical changes in progress; binding materials are weakened and crumbling occurs easily. Finally, many substances simply go into solution and are carried away. Where precipitation is frequent, water percolating through the soil carries soil nutrients to greater depths than where precipitation is light. In hot dry climates, organic matter may oxidize completely and so quickly its nutrients are lost to plants and microfauna.

The climate prevailing there is a determinant of the kinds and prosperity of plant and animal life in an area. The biota has much less effect on soil formation in arid climates than in humid climates. By so much, desert vegetation is usually quite as locally distinctive as local soils are distinctive, but in humid regions, where many plant stages succeed one another, climax vegetations may be essentially the same regardless of whether the sere originally started on limestone, sandstone, or in a pond. Because of the interactions of parental rock, biota, and climate, different soil profiles are formed, each characteristic of a specific climatic region and type of climax vegetation. An understanding of soil profiles is prerequisite to understanding vagaries of animal distribution.

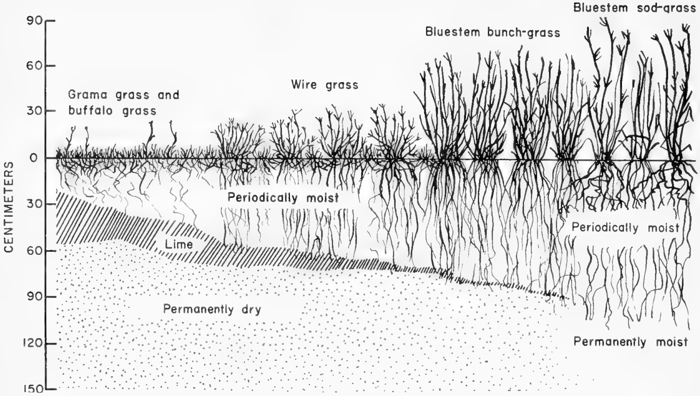


FIG. 11-4 **Relation of lime hardpan to types of prairie vegetation extending from west to east in central North America (Shantz 1923).**

SOIL PROFILES

As a result of the specific circumstances of weathering, biotic reactions, and climatic influences it has experienced, a mature soil has a definite structure characteristic of its different environment (Lutz and Chandler 1946). The living plant draws nutrient materials from the deeper layers of the soil, but those materials are deposited on the surface soil, where the dead plant decays. Rain falling on the ground surface carries the nutrients and salts back down into the soil, at least as far as the water percolates. This sequence of events produces a definite layering of the soil. Each layer is called a *soil horizon,* and the series of horizons characteristic of a soil is called the *soil profile.*

Horizons

The A horizon is one of organic decomposition and leaching; the B horizon, one of precipitation of materials carried down from above; the C horizon is the layer of parent soil material; the D horizon is the underlying stratum of rock or sediment.

Horizon A can be subdivided to reflect phases in the decomposition continuum. A_{00}, the L horizon, is fresh litter or litter only slightly altered. A_0 comprises an F horizon of fermentation where plant materials are partly decomposed but still identifiable, and an H horizon where decomposition has brought the organic material into an amorphous mass. The A_1 horizon, directly below, is dark-colored and of flocculent texture, a mixture of organic material and the mineral soil. A_2 is light-colored and of coarser texture, since leaching is maximum. Occasionally an A_3 is recognized as a transition to B. The B horizon is sometimes also subdivided; suffice it to say that the salts and humus leached out of A are deposited here. The horizon is often brownish or yellowish in color and columnar in structure. The A horizon is commonly called topsoil; the B horizon, subsoil.

A *mature* or fully developed soil profile is characteristic of climax or late seral stages of a succession. Horizons are not fully expressed in early seral stages, so these profiles are called *immature* or undeveloped. Mature profiles are found only under virgin vegetation, for erosion and cultivation disturb horizons. Profiles are best developed in humid climates where abundant precipitation carries humus and salts well into the soil.

Hardpan

In arid regions, evaporation may be in excess of rainfall. Moisture in the soil has no opportunity to percolate downwards; rather, it rises to the surface of the ground and is lost. Where rainfall is inadequate for efficient leaching, *hardpan* may form in the B horizon as the result of deposition here of ferric oxide, alumina, colloidal clay, or calcium salts. This layer becomes so compact and hard that it is impervious to root penetration and the burrowing of animals, although during periods of wet weather it disappears temporarily. In arid regions, the hardpan may be at or close to the surface; but in more humid climates it occurs at progressively greater depths until it disappears altogether.

Mull and mor humus

Distinction between mull and mor humus is made primarily for forest soils. Both humus types of soil may be subdivided but these subdivisions need not concern us here (Romell and Heiberg 1931, Lutz and Chandler 1946).

Mull is a porous, friable humus layer of crumbly or granular structure and only slightly matted, if at all. The A_1 horizon is well developed; bacteria are abundant, annelids numerous, and nitrification occurs.

Mor is a strongly matted or compacted humus layer. There is no A_1 horizon; the transition from humus layer to mineral soil is abrupt. The underlying soil is more acid, bacteria are much less numerous, and nitrification is usually reduced if not absent. Abundant fungi reduce the raw humus to punky material; thereafter it is worked on by the small arthropods. Decomposition of mor is much less rapid than of mull. Annelids are few or absent, and moles are less common than in mull soils. Snails are scarce in acid soils. In general, the biomass of organisms inhabiting a mor soil is smaller, species are less diverse, and individuals are smaller than in mull soils.

Mor humus is common in cold regions and at high elevations, but is not limited to such climatic zones. It occurs especially under coniferous forests, even in warm climates, and under ericaceous vegetation. It is also found in very wet or very dry habitats where there is accumulation of poorly decomposed or sharply delimited humus layers on top of the mineral soil, sand, or rock underlying. Mull humus commonly develops in warm, humid climates and is found especially under hardwood or deciduous forests. Patterns of animal and plant distribution correlate closely with these two humus types; indeed, the formation of each is a result, in the main, of unique combinations of biota reactions, climate, and mineral soil characteristics (Romell 1935, Fenton 1947).

Depth distribution of organisms

The small animals in the soil, including protozoans and nematodes, are most abundant in the L, F, and H horizons, becoming rapidly less abundant in the mineral soil (Table 11-1). Bacteria, actinomycetes, and fungi are also most abundant in these top layers, especially in F and H, although they occur well down into the B and C horizons.

The depth distribution of soil animals depends on temperature and varies with season. When the top layers freeze during the winter months, much of the fauna keeps well below the frost line, although many species are tolerant of freezing. During the cold months the depth at which most soil insects, mollusks, and annelids occur varies from about 9 cm in silty clay-loam to 38 cm in gravelly clay-soil (Dowdy 1944). With the return of warm weather, the fauna ascends to the top horizons.

SOIL TYPES

The interrelations between the basic mineral content of the parent substrate, biotic reactions,

TABLE 11-1 **Depth of distribution of soil arthropods in the Adirondack Mountains. The figures indicate approximate number of individuals per m^2 in the total thickness of each layer (computed from data given by Eaton and Chandler 1942).**

Soil horizon	Depth, cm	Mites	Springtails	All others
	Mor humus under red spruce and balsam fir			
L & F	0-5	150,000	19,800	1,400
H	5-25	62,000	19,200	400
A_2	25-33	1,500	0	0
B	33-58	1,900	100	0
	Mull humus under beech, sugar maple, and yellow birch			
L & F	0-5	62,000	17,800	2,800
A_1	5-15	15,000	6,200	600
B	15-55	6,200	5,800	200

and climate can be seen through an analysis of the development of the great soil types of the world. For the purpose, we will here adopt the simple, recent classification of Simonson (1957).

Podzolic soils are formed in humid temperate climates, under forest vegetation. The A_2 horizon is moderately well developed, for there is sustained leaching. Soils are more or less acid and only moderately fertile. *Podzols* develop under coniferous forest and have a mor type of humus. *Gray-brown* and *brown* podzolic soils are found under hardwood forests and have a mull humus.

Latosolic soils develop in humid tropical or semitropical forested regions. Humus is quickly oxidized by action of microorganisms and hence does not accumulate. Chemical weathering of the parental material is intense. Water drainage through the porous soil is rapid, so leaching is extensive. In early stages of its formation, the soil is neutral or slightly alkaline, but as leaching continues, it becomes acidic. The soil has a thin organic layer (A_0 and A_1 horizons) on a reddish, leached soil (A_2 horizon) that extends to great depths below the surface.

Chernozemic soils occur in humid to semiarid temperate climates under grass vegetation. The grasses on dying return considerable organic matter to the soil. The A_1 horizon is consequently dark in color and of great thickness. The soil contains more bases and hence is less acid than in the two types above. The B horizon in humid regions is indistinct, but where there is less rainfall, calcium salts may accumulate to form a hardpan. Prairie soils in temperate climates are among the most fertile soils of the world, but fertility decreases in the tropical and desert climates.

Desertic soils are characteristic of arid climates and contain very little organic matter. A profile is poorly developed. The surface soil is brownish gray, and grades quickly into the calcium carbonate horizon which usually forms a hardpan just below the surface. Wind erosion removes the finer soil particles, leaving the coarser material to form a hard pavement. The soils are but slightly weathered and leached; lacking nitrogen, they are infertile.

Mountain and *mountain valley* soils vary from shallow layers on eroding rocks to deep organic soils of valleys and swampy areas.

Tundra soils occur in cold northern areas where the substratum remains continuously frozen and the vegetation of lichens, mosses, herbs, and shrubs makes a peaty surface layer. The region is poorly drained and characterized by many scattered shallow ponds.

Alluvial soils, may be important locally. These soils are mostly without a developed profile and are the result of deposition by streams. They are usually very fertile and support luxuriant vegetation.

Saline soils are found in dry climates where rapid evaporation of water results in surface deposition and accumulation of salts leached from surrounding upland areas.

These are only the main types of soils, but they are sufficient, however, to show considerable correlation with the geographic distribution of the major ecological communities, biomes. In a detailed classification, many subdivisions and intermediate categories would be recognized (Kellogg 1936, Lutz and Chandler 1946).

REACTIONS IN WATER

Considerable attention has already been paid to the reactions of animals and plants in streams (Chapter 5), lakes (Chapter 6), and ponds (Chapter 7). These involve changes both in the chemical and physical characteristics of the habitat and are fundamentally the same as occur on land.

Water plants, especially those such as water lilies and water-hyacinths which float, and surface concentrations of both zoo- and phytoplankton reduce light intensities like forest canopies. There is accumulation of plant and animal remains and fecal material on the bottom of the water bodies just as on land, and this material is worked over by bacteria and a large variety of micro-organisms which differ only in taxonomic composition, not in activities, from those on land (Henrici 1939). Water plants obstruct the flow of water and cause deposition of suspended materials simulating the reduction of wind velocities inside forests. An important physical reaction is the damming of streams by beavers so that ponds are formed. Such beaver activity can sometimes be usefully co-ordinated with waterflow management (Beard 1953). These ponds eventually fill with silt and organic matter, succession occurs, and so-called beaver meadows are produced (Van Dersal 1937).

The nitrogen cycle (Cooper 1937), and carbon cycle in aquatic ecosystems are essentially the same as on land. The absorption of oxygen by organisms and by the decomposition of organic matter in some lakes and ponds causes in the habitat a seasonal change of profound importance.

Water conditioning

All modifications in the habitat produced through the reactions of organisms represent a conditioning effect, whether the habitats are terrestrial or aquatic. The term has been used most commonly, however, in respect to changes produced in small bodies of water, especially under experimental control. Water is conditioned when physical or chemical changes occur as the result of organisms living in it. Compared with unconditioned water, these changes may have either a harmful or a beneficial effect on organisms introduced into the water after the original organisms have been removed. Water is said to be *homotypically* conditioned when the changes were previously produced by individuals of the same species as being studied and *heterotypically* conditioned when the changes were produced by a different species.

Harmful effects of conditioning on longevity, growth, or reproduction are more easily explained than are beneficial effects. Harmful effects are often consequences of oxygen depletion, reduction in food resources, accumulation of excreta, or secretion of toxins or growth-inhibiting substances. Overcrowding of frog tadpoles in culture dishes is associated with the occurrence of peculiar round vacuolated cells in the intestinal tract and feces that appear responsible for curtailment of further growth (Rose 1960).

Under laboratory conditions, so-called killer stocks of *Paramecium aurelia* produce a toxin, paramecin, at the rate of one unit-particle per animal per five hours. One unit-particle is enough to kill one individual of so-called sensitive stock of the same species as well as being lethal to other species of *Paramecium* (Austin 1948). Conditioning that becomes unfavorable homotypically may sometimes be favorable, or at least tolerable, heterotypically. Thus in protozoan infusions there is a microsere of one species succeeding another.

Experimental studies, on the other hand, have demonstrated that goldfish grow faster in water that has been homotypically conditioned for 24 hours than in unconditioned water. Both fish and amphibian larvae also do better in water conditioned by the presence of mollusks than in unconditioned water (Shaw 1932). The marine flatworm *Procerodes wheatlandi* will survive much longer when transferred to fresh water conditioned by the presence of either live or dead individuals of the same species or by fresh-water species of flatworms than they do in unconditioned fresh water. The longer survival in toxic solutions, faster growth, and greater reproduction of protozoans, snails, flatworms, cladocerans, amphibian larvae, and fish occurring in aggregations rather than as isolated individuals is attributable to water conditioning.

Various factors are involved in producing favorable conditioning: minute organic particles in suspension resulting from excreta, regurgitated food, or disintegration of dead animals previously present may become concentrated in the alimentary tract of the animals and serve as an unsuspected food resource (Allee and Frank 1949); mucus or slime secreted by organisms may coagulate, precipitate, or reduce the potency of toxic substances; salts liberated from the body may change the osmotic properties of the culture medium; or there may be liberation of growth-promoting substances from one animal that affects other animals (Allee *et al.* 1949). Many of these effects, both favorable and unfavorable, are doubtlessly at work in natural habitats and should be carefully studied as part of the internal dynamics of the biotic community. It may well be, for instance, that during the course of evolution organisms have become adapted to tolerate or take advantage of these external metabolites given off by their neighbors with the result that the metabolites have become an important part of their environment (Lucas 1947).

SUMMARY

The characteristics of soil are determined by the parent rock material, the reactions of plants and animals, and climate. The burrowing of earthworms, ants and other ground insects, crayfish, and rodents brings subsoil to the surface where it becomes mixed with humus. Animal metabolic processes aid in the formation of humus by breaking down complex organic matter into simpler compounds which the animals then excrete. Bacteria, actinomycetes, and fungi are doubtless even more important in this respect. Animals require nitrogen, carbon, oxygen, hydrogen as well as some 13 other elements, and hence are involved in nutrient cycles of these elements in the ecosystem.

Climate is directly involved in the weathering of soil particles, insofar as rainwater percolating into the ground carries nutrients into the soil, and indirectly in determining the kind and luxuriance of the vegetation and animal life that occurs in the area. As a result, mature soils of climax stabilized ecosystems have profiles characteristic both of types of vegetation and of climatic regions. The species composition and density of ground animals vary with the profile horizon and with the various soil-types found in various parts of the world.

Nutrient cycles occur in aquatic as well as terrestrial ecosystems. Organisms may modify or condition the chemical and nutrient characteristics of aquatic habitats in various ways to affect the occurrence of other individuals of the same or different species.

12

Cooperation and Disoperation

As organisms aggregate in a habitat, they necessarily establish interrelations of various kinds with one another. Between organisms, coactions that are beneficial to one or more of the participants constitute *cooperation* (Allee *et al.* 1949, Allee 1951). Cooperation may occur between members of the same species or between different species. Interspecific cooperation includes mutualism, commensalism, and many other sorts of interrelations within the community. As opposed to cooperation, coactions between individuals or species that are harmful to one or more of the participants constitute *disoperations.* We will consider parasitism, predation, and competition as disoperations.

INTRASPECIFIC COOPERATION

An early manifestation of cooperation in the evolution of animals is the grouping of free-living protozoans to form colonies, and the further development of such colonies into multi-cellular metazoans that thereafter behave and respond as unit organisms. Whether the first gathering of protozoan cells to form colonies developed for better protection from some enemy or environmental condition, improved utilization of food supplies, or more efficient reproduction, it is impossible to say. The colonial form, however, must have had survival value to persist.

Colonization quickly led to division of labor between somatic and reproductive cells, as occurs in *Volvox,* and later to division of labor between somatic cells themselves, so that different cells or organs became specialized to serve the particular functions of digestion, respiration, circulation, and so on. Cooperation between cells, tissues, and organs gave greater metabolic efficiency to the whole individual and resulted in evolution to the highest types of animals. Similarly, the aggregation of individuals must have survival value, because it persists. Hundreds, sometimes thousands, of spotted lady-beetles hibernate under leaves at the forest-edge. Mayflies, midges, and mosquitoes swarm for mating purposes. Millions of bats roost together in large caves, notably in the Carlsbad Caverns in New Mexico. The migratory locust moves from one locality to another in immense hordes, and birds usually migrate in flocks. Highly organized societies are found in such insect groups as termites, ants, bees and wasps, as well as in some breeding colonies of birds and mammals.

Benefits derived from aggregating are both physiological and psychological. Individual honey-bees are poikilothermal, but when hive temperatures drop below 14°C (57°F) during the winter, they form clusters and maintain a mass temperature several degrees above outside temperatures. This is brought about by increased metabolic oxidation of honey in their bodies and by increased muscular activity. Furthermore the compact cluster presents surface area of heat loss that is less than the total surface area of the individuals separately (Milum 1928). When there is danger of overheating, the bees in the hive spread out on the combs and fan with their wings to create a circulation of air. They will also carry water into the hive and place small quantities both outside and inside the comb cells. The forced air circulation evaporates the water and cools the hive. Bees also cool themselves by constantly moving their tongues in and out of their mouths, exposing to evaporation the moisture that is present on them as a thin film (Lindauer 1955). Temperature regulation is less well developed in other social Hymenoptera (Himmer 1932).

Coveys of bobwhite quail roost in close circles, at night. Perhaps this enables detection of predators approaching from any direction, but it is certain that the birds can by that behavior tolerate lower air temperatures and for a longer time than isolated birds can (Gerstell 1939). Similarly, mice huddle in low air temperatures, a behavior that reduces heat radiation and consequent need for frequent feeding (Prychodko 1958).

Colloidal silver is toxic to fish. Ten goldfish were simultaneously exposed to a liter of water dosed with colloidal silver. They lived an average of 507 minutes each. Fish individually exposed to a similar concentration of silver in the same volume of water lived an average of 182 minutes. The slime from the grouped fish was sufficient to precipitate much of the colloidal silver and render the solution less toxic (Allee and Bowen 1932). Photosensitive animals survive longer when exposed to excessive illumination in groups than singly because of partial shading of one by another, but fresh-water planaria exposed to ultraviolet live longer in groups even when no shading is involved (Allee and Wilder 1939). Marine flatworms *Procerodes* survive longer in fresh water in groups than singly because the first worms that die from the group release calcium into the water, conditioning it and giving protection to the animals that remain (Oesting and Allee 1935).

A single muskox or bison may succumb to a pack of wolves. When in a group, the males form a circle facing outward with the females and young inside, whereby they are usually able to ward off the attack. By the same token, a single wolf has difficulty killing a deer; a single coyote, killing a pronghorn antelope. But in packs the wolves can overpower a deer, and by individually taking turns in relay fashion, a pack of coyotes can chase a pronghorn to exhaustion.

Whether an animal occurs singly or in groups may affect its learning rate and behavior. The common cockroach and the shell parakeet learn simple mazes less rapidly when other individuals are around than when alone, but goldfishes, minnows, and green sunfishes learn mazes faster in groups; phenomena spoken of respectively as negative and positive *social facilitation.* Many animals are more active and alert in groups than alone; in groups, individual imitations of others' behavior are common. Cormorants and pelicans fish more proficiently in groups than alone because group behavior is organized and each individual plays a certain role (Allee 1951).

The beneficial effects of aggregation are lost if the aggregation is either too small or too large. For instance, the longevity of *Drosophila* is greatest with a population density of 35 to 55 flies per one ounce culture bottle (Pearl, Miner, and Parker 1927). Smaller densities are unable to control the growth of the yeasts on which they feed; greater densities exhaust the food supply and excessive amounts of excreta accumulate. Likewise an initial population of 4 *Tribolium* beetles per 32 g of flour reproduces more rapidly during the 25 days following than smaller or larger initial populations (Park 1932). For all kinds of animals, competition for food and other resources of the habitat becomes more and more intense as populations increase in size above an optimum. The benefits resulting from an increase in the size of aggregations up to the optimum represents cooperation; the harmful effects resulting from aggregations that are too large is disoperation.

The simplest animal aggregations exhibit little social organization, for the individual organisms are brought together more or less ephemerally by chance, by sexual attraction, for reproduction, or because of a similar response to environmental factors. An evolution of organization may, however, be traced through intermediate stages to the complex division of labor found in some insect societies. Specialization occurs both in morphology and behavior. The three primary castes of termites and ants are the winged reproductive males and females, the wingless sterile soldiers that possess large mandibles and irritating glandular secretions, and the smaller, wingless, often sterile workers. The soldiers defend the colony against predaceous enemies; this function is assumed by workers in bees and wasps, among which a distinct soldier caste is lacking. In termites, the soldiers may be either males or females; in ants, they are females. The worker caste in ants usually females, but in higher termites it may consist of either males or females. In primitive termites the nymphs of other castes substitute for the workers. The workers collect food, cultivate gardens of fungi, take care of domesticated aphids or coccids, feed the other castes, and build shelters. The earliest organized social life of primitive man was perhaps neither so highly organized nor so far advanced in an evolutionary sense as these complex societies of insects, even

FIG. 12-1 **Model of a royal cell of the termite, showing different castes. The queen has an enlarged abdomen; her head is turned to the right. The king is in the left center. Two soldiers with pointed heads are in the upper right. Most of the rest are workers (courtesy Buffalo Society of Natural Sciences).**

though it was from the greater psychological potentialities of primitive man that modern civilization arose (Allee *et al.* 1949, Allee 1951).

In these social relations, indeed in all sorts of symbiotic relations between individuals, one or both partners must have specialized behavior to effect and maintain the relationship. Chemical stimuli are important in this respect and have received much study to date but physical stimuli, such as color, shape, texture, temperature, and so on may also have primary integrative importance as releasers for specific behavior responses, the products of long evolution (Davenport 1955).

MUTUALISM

Mutualism is an association between two or more species in which all derive benefit in feeding or in some other way. The term symbiosis has often been applied to this relationship, but *symbiosis* properly refers to the intimate association of two or more dissimilar organisms, regardless of benefits or the lack of them, and hence includes mutualism, commensalism, and parasitism.

Mutualism, as is true also with commensalism and parasitism, may be *facultative,* when the species involved are capable of existence independent of one another, or *obligative,* when the relationship is imperative to the existence of one or both species. Considerable study and experimentation is sometimes required to decide whether a particular relationship is facultative or obligative, or even whether it is truly mutualistic. Mutualism is sometimes considered as, fundamentally, reciprocal parasitism. Many examples of ecological interest of mutualism, commensalism, and parasitism are cited by Pearse (1939) and Allee *et al.* (1949) ; only a few will be given here.

Mutualism in plants is demonstrated in the associations of fungi and algae to form lichens, of nitrogen-fixing bacteria with the roots of legumes, and of fungal mycorrhizae with the roots of many flowering plants.

There are many intimate relations between plants and animals (Buchner 1953). Mutualism is suspected in the presence of photosynthetic algal cells in the protective ectoderm of green hydra, and those associated with turbellarians, mollusks, annelids, bryozoans, rotifers, protozoans, and the egg capsules of salamanders. The algae give off oxygen, benefiting the animals, which in turn supply carbon dioxide and nitrogen to the plants. The thick growth of algae often found on the carapace of the aquatic turtles is important mostly as camouflage for the turtles (Neill and Allen 1954). Certain beetles, ants (Bailey 1920, Weber 1957), and termites cultivate fungi for food. Bacteria in the caeca and intestine of herbivorous birds and mammals aid in the digestion of cellulose. The cross-pollination of flowers by the agency of insects and birds seeking nectar and pollen is of such great importance that many structural adaptations in both plant and animal fit the one to the other to insure the success of the function (Robertson 1927, Dorst 1946).

Animals, especially birds and mammals, are of great importance as agents of plant distribution (McAtee 1947). Seeds, fruits, even entire plants become attached to feathers or fur, or ingested seeds are eaten and eliminated unharmed with the feces. When bare seeds are eaten they are usually macerated, digested, and entirely destroyed unless they have very hard coats. But fruits are fed upon primarily for pulp, and most of the seeds pass through the alimentary tract unharmed. Animal transportation of ingested seeds is perhaps the most important means by which fruit species are dispersed (Taylor 1936). Furthermore, germination of the seeds is frequently improved by mechanical abrasion in the stomach and thinning of the seed coat by digestice juices, making it more permeable to water and oxygen (Krefting and Roe 1949). Germination of acorns and nuts is improved if they are buried in the ground rather than left lying on the ground surface. Squirrels, chipmunks, wood rats, and some birds, particularly jays (Chettleburgh 1952) and woodpeckers, cache acorns and nuts as a winter food supply, hiding them in cavities and nooks or burying them in the soil. Perhaps most are recovered and eaten; Cahalane (1942) found that 99 per cent of the acorns buried by the fox squirrel in a locality where the animals were numerous were recovered by the animals, largely through the sense of smell. One per cent of the thousands of nuts produced by it during the lifetime of a tree that are buried but not recovered would be adequate to insure the continuance of the forest. Invasion of oak and hickory trees into sandy areas is greatly accelerated by, and is sometimes dependent on, this coaction of squirrels (Olmsted 1937), and the dispersal of forests up the slopes of mountains against gravity may also depend in large part on transportation of the heavy seed by animals (Grinnell 1936). The interesting concept involved here is that plants have evolved fruits and nuts that are highly attractive to animals as food substances. However, the production of prodigious numbers of fruits and nuts during their lifetimes insures that at least some will escape consumption and will be more widely and effectively dispersed.

Large populations of such herbivores as rabbits and deer sometimes do considerable damage to new propagation of herbs and trees, but the effects of overbrowsing cannot be dismissed as all bad (Webb 1957). Removal of the lower branches of established trees by deer may not seriously affect the vigor of the trees; indeed, such pruning may actually increase their value as lumber. Deer pawing the leaf-litter may thereby plant, so to speak, some seeds that would not otherwise become established. Thinning dense stands of young trees may allow residuals to grow more rapidly; much of new growth is doomed anyway because of root competition, and shading cast by established trees. Some species of shrubs and trees actually produce more annual growth under heavy than light browsing. Other species, however, may be killed when small by heavy browsing, although they tolerate considerable browsing when mature. Detrimental effects of both browsing and grazing become evident in an area in the form of excessive invasion of new species which are little used as food, and disappearance or stunting of the food species that are desirable (Graham 1954).

Some tropical acacias have evolved foliar nectaries or other food bodies as well as enlarged hollow stipules, spines, or other structures to attract stinging ants. In return, the plants obtain protection from herbivorous mammalian and insect enemies (Brown 1960).

Interspecific mutualism is nicely demonstrated by the flagellate *Trichonympha,* an obligate in the gut of several species of wood-eating termites (but not in the family Termitidae) where it digests cellulose (Cleveland 1924). *Trichonympha* and related species also occur in the alimentary trace of the wood-eating roach *Cryptocercus* (Cleveland 1934). The termite and roach reduce the wood to small fragments, passing them through the alimentary canal to the hindgut where the protozoans digest the cellulose, changing it into sugar. The host benefits the protozoa by removing harmful metabolic waste products and maintaining anaerobic conditions in the intestine (Hungate 1939).

The ruminant stomach and the horse coecum contain enormous numbers of ciliates and bacteria, some of which digest cellulose. The micro-organisms reproduce the equivalent of their biomass each day. This provides the host with about 20 per cent of its nitrogen requirement (Hungate 1960).

COMMENSALISM

Commensalism defines the coaction in which two or more species are mutually associated in activities centering on food and one species, at least, derives benefit from the association while the other associates are neither benefited nor harmed. It is often difficult to establish definitely the nature of the relations between species; and phenomena considered at one time to be commensalism have been later found to be parasitism or mutualism. The concept of commensalism has been broadened, in recent years, to apply to coactions other than those centering on food; cover, support, protection, and locomotion are now frequently included (Baer 1951).

The remora fish are remarkable for having the spinous dorsal fin modified to form a sucking disk on top of the head by means of which they become attached to the body of the shark, swordfish, tunny, barracuda, or sea turtle. They are of small size and are not burdensome to the host. The host benefits the remora, however, for when the host feeds, the scraps of food floating back are swept up by the remora. Many small animals become attached to the outside of larger ones, such as the protozoans *Trichodina* and *Kerona* on *Hydra,* vorticellids on various other aquatic organisms, branchiobdellid annelids on crayfish, and so on. Commensals may also be internal; consider, for instance, the harmless protozoans that occur in the intestinal tract of mammals, including man.

The pitcher of the pitcher plant found in bogs furnishes a breeding site or home for certain species of midge flies, mosquitoes, and tree toads. Many kinds of micro-organisms, both plant and animal, live in the canal system of sponges.

The nest of one species often furnishes shelter and protection for other species as well. Ant nests may contain guest species of various other insects. Large hawk nests sometimes have nests of smaller species tucked in their sides (Durango 1949); some birds place their nests close to wasps, bees, or ants for the protection offered by these insects (Hindwood 1955). Woodchuck burrows are used also by rabbits, skunks, and raccoons, especially in the winter. During dry periods the water in crayfish burrows, a meter below the ground surface, often teem with entomostraca (Creaser 1931).

COMMUNITY ORGANIZATION

The final stage in the evolution of cooperation is the biotic community. Analogous to a multicellular individual, the community is composed of organic units, in this case organisms and species rather than cells and tissues. It has a definite anatomy in its stratification, niches, and food chains. The community, too, is a thing born, and it exhibits the same characteristics of growth and old age as do individuals. There is succession of stages to the climax community like the series of instars in the life cycle of an insect. If the community is injured, it heals the wounds in its structure through secondary succession. The community is self-sustaining in that it absorbs energy from the sun and metabolizes it at various trophic levels in order to do work. There is division of labor, analogous to the functions of the various organs in the body of a single individual; plant species manufacture the food that animals need, and dominant species create environment conditions within the community suitable for the existence of other species. There is transmission of stimuli, intercommunication, between individuals and species by voice, odor, sight, and contact. There is control over the numbers of individuals of each species in the balance of nature. The result is that the biotic community is a highly integrated recognizable unit in which species exhibit various degrees of interdependency. The existence of each component depends to a certain extent on coooperation between them all, so that the community responds and behaves as an organic entity. That such complicated interrelationships have come about through evolution indicates that they have survival value for the component species involved.

PARASITISM

Parasitism is the relation between two individuals wherein the *parasite* receives benefit at the expense of the *host;* parasitism is therefore a form of disoperation. Parasitism is mainly a food coaction, but the parasite derives shelter and protection from the host, as well. A parasite does not ordinarily kill its host, at least not until the parasite has completed its reproductive cycle. Were the parasite to kill its host immediately on infecting it, the parasite would be unable to reproduce and would quickly become extinct. The balance between parasite and host is upset if the host produces antibodies or other substances which hamper normal development of the parasite. In general the parasite derives benefit from the relation while the host suffers harm, but tolerable harm.

Classification

Parasites are commonly classified as *ectoparasites,* those which live on the outside of the host, and *endoparasites,* those which live in the alimentary tract, body cavities, various organs, or blood or other tissues of the host (Baer 1951). Ectoparasites may be parasitic only in the immature stages—the hairworm larvae, parasitic in aquatic insects; only the adults parasitic—fleas, on birds and mammals; or both larvae and adults may be parasitic—the bloodsucking lice and flies, biting lice, mites, and ticks that occur on birds, mammals, and sometimes reptiles, and the monogenetic trematodes on fish. Similar relations obtain among endoparasites, although it is more common to have all stages parasitic: entozoic amoebae, trichomonad flagellates, opalinid ciliates, sporozoans, pentastomids, nematodes, digenetic trematodes, acanthocephalons, cestodes, and some copepods.

Animals may also be parasitic on plants. Nematodes infest the roots of plants. Galls are formed by wasps or gnats especially on oaks, hickories, willows, roses, goldenrods, and asters. Mites stimulate formation of witches' brooms in hackberry. A variety of insects the larvae of which are leaf miners, wood borers, cambium feeders, and fruit eaters, should be included here. Plants themselves may be parasites either on other plants or on animals. Bacteria and fungi are among the most important disease-producing organisms in animals.

Social parasitism describes the exploitation of one species by another, for various advantages. Old World cuckoos and the brown-headed cowbird of North America do not build nests of their own; rather, they deposit their eggs in the nests of other species, abandoning eggs and young to the care of foster parents (Weller 1959). The bald eagle sometimes robs the osprey of fish that it has just caught. One species of ant waylays foraging workers of another species and snatches away the food they are transporting; the robber species may deliberately rob another nest of food. Some species of ants make slaves of the workers of other species. Various other types of dependency of one species on another have evolved, not only between ants, but also in other social insects, such as termites, wasps, and bees. Social insects are apparently the only animals other than man to have succeeded in domesticating other species, and of cultivating plants, particularly fungi, for food (Wheeler 1923).

Evolution and adaptations

The ancestors of ectoparasites were clearly free-living forms. It is not difficult to imagine how a small organism living freely in water or vegetation could accidentally have settled on the outside of a larger species and found conditions favorable for survival. There would even be selective advantage in such a niche if the organism found a rich source of food. The biting lice probably evolved from psocid insects that live beneath the bark of trees. They may have transferred from this niche to bird nests and then to the birds themselves. Most ectoparasitic insects probably are derivatives of carnivores, saprovores, or suckers of plant juices.

Endoparasites may in some cases have evolved from ectoparasites; more likely, they came directly from free-living ancestors or from commensals. For example, free-living nematodes and scavenger beetles both feed upon decaying organic material, and it is easy to visualize how the beetles could have accidentally consumed one or more nematodes. Many kinds which have since become parasites, such as protozoans and flatworms, could have had their first entrance into the alimentary tracts of prospective hosts via drinking water, and subsequently invaded other organs in the body. The invaders would have found their hosts abundant food sources, but would have needed some preadaptation to live at the low oxygen concentrations characteristic of digestive tract, to resist being consumed by the digestive juices of the host, and to keep from being carried out with the feces. As succeeding generations of parasites became increasingly adapted to live either on or in their hosts, many kinds lost the capacity for a free-living existence. Specialization to internal parasitism has cost the loss of locomotor, sense, and digestive organs, none of which are needed, and led to the development of organs of attachment, increased reproductive capacity, and, in several forms, to polyembryony, intermediate hosts, and a complicated life cycle (Lapage 1951).

Some parasitic species are more highly evolved than others. Many parasites, for instance, pass their entire existence in a single host; others require one, two, even three intermediate hosts. It is of ecological significance that both primary and intermediate hosts of a parasite occur in the same habitat or community. Even then the hazards to successful passage from one host to another are so great and mortality so high that prodigious quantities of offspring are produced to insure that at least a few individuals will complete the cycle.

Parasites are transferred from one host to another by active locomotion of the parasite itself; by ingestion, as one animal sucks the blood of or eats another; by ingestion, as an animal takes in eggs, spores, or encysted stages of the parasite along with its food or drinking water; as a result of bodily contact between hosts; or by transportation from host to host by way of vectors. As an illustration of vectors, the bacteria that cause tularemia in man are carried from rabbit to rabbit by ticks. Man contracts the disease when he handles infected rabbits, but the incidence of infection is greatly reduced in the autumn when cold weather forces the ticks to leave the rabbits and go into hibernation (Yeatter and Thompson 1952).

FIG. 12-2 **Life cycle of a snake tapeworm. The eggs are voided into the water with the feces of the snake, where they are ingested by the copepod *Cyclops* (lower right). A procercoid (middle right) develops in the copepod, from the egg. If the copepod is eaten by a fish, the procercoid changes into a plerocercoid (upper right) and becomes encysted in the liver or mesenteries. When the fish is eaten by a water snake, the mature tapeworm develops (upper left). Other intermediary hosts are tadpoles and frogs (Thomas 1944).**

Host specificity

Copepods are of all parasites the most ubiquitous in their host relationships, being reported from various invertebrate groups and from fish. Most parasitic genera, however, are adapted to hosts of one phylum only. The acanthocephalans *Gracilisentis* and *Tanarhamphus* are yet more specific, normally found only in the gizzards of shad fish; *Octospinifer* is found only in catostomids; *Eocollis,* only in centrarchids. Each order of birds possesses its own particular species of tapeworms; this is true even when several orders of birds live in the same habitats, as do, for instance, grebes, loons, herons, ducks, waders, flamingoes, and cormorants (Baer 1951). Species of flagellate protozoans that occur in termite alimentary tracts are largely host-specific (Kirby 1937). However, considerable caution needs to be exercised in assigning host specificity to protozoans. Many species have invaded more than one taxonomic host group; and often several species of a single genus of Protozoa frequent the same host species.

Some species of gall wasps attack only one species of oak. Where a single species parasitizes two or more host species, the shape and structure of the gall formed around the egg and larva on both hosts is essentially similar. When several insects are found on the same oak, each kind of parasite produces its own characteristic gall form. Apparently the characteristics of the gall that develops depend more on the kind of enzyme secreted by the parasite than on differences of host tissues (Kinsey 1930).

Restriction of parasites to special niches is demonstrated by species of biting lice restricted to the head and body regions of birds. Some nematode species are found throughout the body in connective tissue, but not in the gut; some occur only in the digestive tract and associated organs; certain species occur in the glandular crop of birds, but others only in the caecum; many species occur exclusively in the lungs or in the frontal sinuses. Such fine restriction of parasites to particular hosts or organs is a consequence of precise physiological and morphological adaptations that permit the parasite to survive and complete the life-cycle only under very special conditions.

Host-specificity can make the taxonomies of many parasites useful for corroborating phylogenetic relationships of their hosts (Kellogg 1913). The South American bird *Cariama cristata* has been shifted from one order to another, and was at one time even put into a special order. A study of its helminth parasites disclosed two species of nematodes and two genera of cestodes present which occur together elsewhere only in Eurasian bustards. The occurrence of these forms in groups so far removed geographically from one another could be coincidental or the result of parallel evolution, but for a number of reasons it seems more likely that *Cariama* and the bustards are derived of a common ancestor which became infected with these parasites, the parasites persisting in spite of evolutionary divergence and geographic separation of hosts. It is interesting to note that this relationship of the hosts is sustained by recent taxonomic study of them by ornithologists (Baer 1951).

Effect on host: disease

By *disease* we mean a condition which so affects the body or a part of it as to impair normal functioning. Parasites may not cause immediate mortality, but they cause damage to body structures which, should it become excessive, may cause death. We may perhaps better visualize the role parasites play in producing disease by listing some of the more common agents of mortality in organisms, in addition to predators and parasitoids, which will be described beyond.

1. **Worm parasites,** such as tapeworms, nematodes, and acanthocephalans may wander through the host's body doing mechanical injury as well as destroying and consuming tissues. The host may respond by forming a fibrous capsule or cyst around an imbedded parasite.

2. **Protozoan parasites** are especially important in the alimentary tract and in the blood. A sporozoan species of *Eimeria* damages the walls of the intestine

in upland game birds, producing coccidiosis; *Toxoplasma* becomes encysted in the brain of rodents; *Leucocytozoon* is a blood parasite common among waterfowl and game birds.

3. **Bacteria** cause a variety of diseases, notably tularemia, paratyphoid, and tuberculosis among birds and mammals, as well as other diseases in lower types of organisms.

4. **Viruses** are so submicroscopic in size that many kinds pass through the finest filters. They are the potent agents of hoof and mouth disease in deer, spotted fever in rodents, encephalitis and distemper in foxes and dogs.

5. **Fungus** spores of *Aspergillus* that occur in moldy pine litter may be drawn into the lungs of ground-feeding birds where they germinate and grow, causing aspergillosis. Fungus may also develop on the external surface of animals.

6. **External parasites** such as ticks, fleas, lice, mites, and flies do not commonly produce serious mortality by themselves, but they are often vectors transmitting protozoa, bacteria, and viruses from one animal to another. Heavy infestations of external parasites may, however, lower the vitality or vigor of an animal and cause diseases of fur (mange) or feathers.

7. **Nutritional deficiencies** in vitamins or minerals, or improper balance between carbohydrates, proteins, and fats, may produce malformations, lack of vigor, even death. Variations in amount, composition, and intensity of solar radiation may affect the vitamin content of the food an animal consumes. Long restriction to emergency foods of low energy content and outright starvation often cause considerable loss of life during periods of climatic stress.

8. **Food poisoning,** *botulism,* occurs when certain foods become contaminated with the toxins released by the bacterium *Clostridium botulinum.* Many waterfowl are stricken in some localities. Waterfowl also often pick up and swallow gun-shot from marshes in which there has been much hunting, and get lead poisoning.

9. **Physiological stress** (Selye 1955) is a term that has come to be applied to changes produced in the body non-specifically by many different agencies which may accompany any disease. Effects of stress include loss of appetite and vigor, aches and pains, and loss of weight. Internally, the stress syndrome is characterized by acute involution of the lymphatic organs, diminution of the blood eosinophiles, enlargement and increased secretory activity of the adrenal cortex, and a variety of changes in the chemical constitution of the blood and tissues.

Stress gives rise to abnormal conditions, but it simultaneously elicits from the body defense mechanisms against those abnormal conditions. It is presently believed that the anterior pituitary gland and the adrenal cortex are chiefly responsible for integrating the defense mechanisms. Three stages are involved: *the alarm reaction,* in which adaptation has not yet been acquired; *the stage of resistance,* in which the body's adaptation is optimum; and *the stage of exhaustion,* in which the acquired adaptation is lost. Characteristic of the exhaustion phase are, among others, hypoglycemia, adrenal cortical hypertrophy, decreased liver glycogen, and negative nitrogen balance.

10. **Accidents** must be included as an important cause of mortality.

Organisms that produce disease generally fall into one or two categories. They are either present in the body at all times but not normally virulent, or they are normally absent but are virulent from the moment the host is infected by them. Even the healthiest animals chronically entrain many parasites and noxious organisms in the body, but these organisms wreak overt harm only when they become unusually abundant, when virulent mutant strains develop, or if, for one or another reason, the host's vitality and resistance decline to the point where the host is no longer able to withstand the effects of their presence. Any animal suffering an unusually heavy infestation of parasites will show the tax thus put upon its vitality as a loss of vigor and weight, decreased growth rate, and low resistance to vicissitudes of its natural environment. Normally, a more or less mutual tolerance exists between host and parasite such that the demands of the parasite are in equilibrium with the host's capacity to meet them. Host-tolerant parasites have been naturally selected for; mutant strains that are exceptionally virulent quickly die out because they kill the host, without which they cannot survive.

A single attack, even a mild one, of some diseases often confers a partial or complete *immunity* from further attacks of the same disease, even though the agent of the disease may still be carried in the body of the recovered victim. Immunity is an acquired physiological adaptation by which the immune is able to withstand the presence of an otherwise noxious organism, suffering little or no deleterious consequence of that presence. The fact of immunity is demonstrated when parasites not conspicuously harmful to their normal hosts are introduced into a species to which they are normally exotic. The novel host has had no prior occasion or opportunity to adapt im-

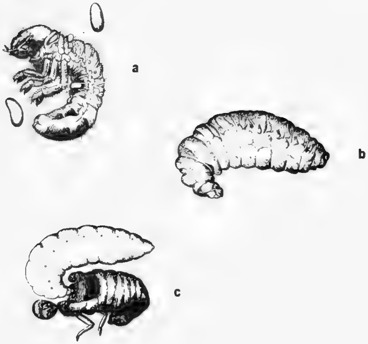


FIG. 12-3 **Development of a parasitoid black digger wasp. (a) eggs in position on the host larva, (b) the developing larva, (c) the fully grown larva devouring the remainder of the host (courtesy Illinois Natural History Survey).**

munitively to the alien parasite, and may sicken, even die, of the effects of the parasite's presence, the same effects in kind and intensity which the normal host easily takes in stride. For instance, a trypanosome that is a natural parasite in many of the larger wild mammals of Africa evokes no spectacular effects in its usual hosts. But when the parasite is vectored by the tsetse fly to man, it causes sleeping sickness; to cattle, nagana. A good bibliography of references to diseases in wild mammals and birds is given by Halloran (1955); Davis (1946) discusses diseases of fish, especially trout.

PARASITOIDISM

Some Diptera and Hymenoptera deposit their eggs in the immature stages of other insects; the larvae on hatching feed on the host until they are full grown. The relation of the larva to its host is frequently described as one of parasitism. But it is fundamentally different from parasitism in that the host invariably dies of the larval depredations before the larva emerges, but the larva invariably lives in spite of the host's death. The relationship resembles that of predator to prey, except that, unlike the true predator, the larva lives within the body of its prey and kills it slowly as it feeds, not suddenly before it feeds. Such larvae are, for these reasons, best thought of as *parasitoids*.

Parasitoids may in turn be infested with *hyperparasitoids*. In the Chicago, Illinois, region *Samia cecropia*, a saturniid moth, suffers the destruction of nearly 23 per cent of its cocoons by an ichneumonid parasitoid, *Spilocryptus extrematis*, which deposits an average of 33 eggs on the inside of each cocoon or on the surface of the larva. The host larva dies in a few hours after the parasitoid hatches, and the ichneumonid larva moves about freely, feeding on the cuticle or burrowing into the tissues to drink the body fluids. Another ichneumonid, *Aenoplex smithii*, was found as a secondary parasitoid, feeding on the larvae of *S. extrematis* in about 13 per cent of the cecropia cocoons infested by the latter species. A chalcidid, *Dibrachys boucheanus*, fed both upon *S. extrematis* and, as a tertiary parasitoid, upon *A. smithii*. Another chalcidid, *Pleurotropis tarsalis*, infected cocoons containing *D. boucheanus* and eventually killed the larva as a quarternary parasitoid (Marsh 1937). To have five links in an inverted parasitoid food chain is perhaps unusual, but hyperparasitoidism is common and of importance in controlling the size and interrelations of animal populations.

Predation is a form of disoperation, at least in point of immediate effects, since one animal kills another for food. Predation is important in community dynamics in so many ways that we will postpone discussion of it until we consider food coactions (Chapter 13), productivity (Chapter 14), and regulation of population size (Chapters 16, 17).

COMPETITION

Competition is the more or less active demand in excess of the immediate supply of material or condition exerted by two or more organisms (Clements and Shelford 1939: 159). The materials and conditions sought by animals include food, space, cover, and mates. When these materials are in more than adequate supply for the demands of those organisms seeking them, competition does not occur; when they are inadequate to satisfy the needs of all the organisms seeking them, the weakest, least adapted, or least aggressive individuals are forced to do without, or go elsewhere. Competition may result in death for some competitors, but this is from fighting or being deprived of food or space rather than being killed for food as in predation, or by disease as in extreme parasitism.

Competition may be either direct or indirect. It is *direct* where there is active antagonism, struggle, or combat between individuals; *indirect*, when one individual or species monopolizes a resource or renders a habitat unfavorable to the establishment of other organisms having similar requirements. Direct competition, or *interference*, is evident in the fighting of bull seals for larger harems and of grouse for a better position in the social hierarchy; in chasing and color displays (a sort of saber-rattling) by fish and birds for defense of territories; and in the singing and calling of birds, some mammals, and frogs as bids for mates.

Indirect competition, sometimes called *exploitation* (Brian 1956), is common among plants when certain species monopolize the water and nutrient resources of the soil or available light so that competing species cannot maintain themselves (Clements, Weaver, and Hanson 1929). Animals may also render a habitat unsuitable by their excreta for a species which otherwise would occur. Once an area is well saturated with established individuals, it is often more economical of energy for new individuals to seek homes elsewhere, even in less favorable situations, than to intrude. To be successful by indirect competition, a species needs to get established in an area first, or if the invasion of various species is nearly simultaneous, then to have a more rapid rate of reproduction and growth, or a greater longevity, so as to utilize the resources of the habitat to the fullest possible extent (Crombie 1947).

Competition is usually keenest between individuals of the same species, *intraspecific competition,* because they have identical requirements for food, mates, and so on, and because they are more nearly equal in their structural, functional, and behavioral adaptations. *Interspecific competition* occurs where different species require in common at least some materials or conditions. The severity of competition depends on the extent of similarity or overlap in the requirements of different individuals and the shortage of the supply in the habitat. It is generally the case that the more unlike the kinds of competing organisms, the less intense the competition. Yet birds compete with squirrels for acorns, nuts, and seeds; insects and ungulates compete for food in grassland; the bladderwort plant competes with small fish for entomostraca and other plankton.

Competition has five important effects on the animal community:

1. Establishment of social hierarchies
2. Establishment of territories
3. Regulation of population size
4. Segregation of species into different niches
5. Speciation

The first two effects are chiefly intraspecific; will be considered in this chapter. Regulation of population size involves both intra- and interspecific competition, and many other types of coaction as well, and will be considered in Chapters 15, 16, and 17. The last two effects are interspecific; they will be discussed in Chapters 18 and 19. It is important to realize that, when these effects are fully manifested, there is a decrease in tension and intensity of competition as each individual or species takes its place in the orderly structure and organization of the community. Let us see how this works out in the instances of social hierarchies and the establishment of territories.

Social hierarchies

When groups of individuals of certain animal species are confined to limited areas, frequent fights or pecking of one another occur. By way of these encounters, the more aggressive and successful individuals establish a hegemony to which the more submissive individuals acquiese. A *social hierarchy* is thus established; the phenomenon was first clearly described for the domestic fowl (Schjelderup-Ebbe 1922).

The so-called peck-order in the domestic fowl is a linear one. Close observation of marked individuals showed that, in a flock of 13 birds, one bird became the supreme despot of the whole flock; another bird was submissive to the first but despotic over the remaining 11; and so it went on down to the last bird, which had the right to peck none but was pecked by all. This type of social aggressiveness or *despotism* is called *peck-right.* In practice, certain individuals establish the right to peck others and not get pecked back. In the middle of a series, the order is sometimes less fixed, and reversals or triangles occasionally occur. Although most easily demonstrated in the crowded conditions of captivity, peck-right has also been observed to obtain under free natural conditions. The peck-right type of social hierarchy has been found to occur in several other species of birds, in several species of mammals and fish, and in a few lizards, crayfish, and insects.

Possession of the following characteristics usually gives an individual at least some advantage in gaining a high position in the despotic order: strength; good health; maturity; relatively large size; hegemony over own territory; responsibility of acting to protect young; accompaniment by members of his own group when meeting a stranger; male over female, at least during the nonbreeding season; female mated with a strong male; the hormone testosterone; and innate aggressiveness (Allee *et al.* 1949: 413–414). A high position in the social order is advantageous to the individual as it gives him priority over food, mates, territory, and other resources of the habitat (Collias 1944) and is sometimes, but not always, correlated with leadership in the group.

In some species the social hierarchy is not as overt as that we've described. In *peck dominance* the individual that is usually subordinate is successful in a certain number of conflicts. Position in the despotic order is a function of ratios of success in continuing conflicts rather than on the results of the initial con-

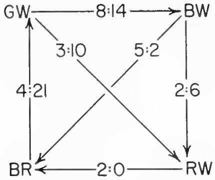


FIG. 12-4 **Peck-dominance between the lowest four birds in a flock of seven common pigeons. All four birds were dominated by the three other birds of the flock. The ratios show the proportion of times each bird was successful in its encounters with other individuals (Masure and Allee 1934).**

tact an individual has with each member of the group, Figure 12-4 shows bird BR successfully subdued GW in 21 encounters but was subdued by GW in 4 encounters. Thus, an individual can occupy any position in the hierarchy as long as he is able to maintain that position against all challengers. The individual who loses a challenge from below is without position, and can gain a position only by successful challenge. The individual who has successfully challenged a higher position from a lower moves up to the higher, leaving the lower position open—who shall fill the vacated position is determined by combat among those eligible to try for it, among whom is the former holder of the higher position. Plainly the positions in the hierarchy are fixed in order, but occupancy of those positions is fluid. A more fluid form of social aggressiveness is *supersedence,* in which a successfully challenging individual usurps the position of another individual momentarily possessing special advantages in the presence of food or some other thing. This type of relation has been described for the golden-crowned sparrow (Tompkins 1933) and may likely be found in many other species.

There have been few studies of social despotism as an interspecific phenomenon (Neuman 1956). The range of aggressiveness between individuals within any species is so wide that strong individuals of one species may be despotic over weak individuals of another even though the majority of individuals in the first species are submissive. However, the sharp-tailed grouse is usually dominant over the ring-necked pheasant, and the latter is usually dominant over the prairie chicken (Sharp 1957). The manner in which different species fit into a social hierarchy may be the key to structure and organization of communities.

Territory and home range

The establishment of territories, especially during the breeding season, is another expression of despotism, but a special one. A *territory* is any area defended against intruders. It may be the entire home range over which the animal is active, or only a small portion around the nest. Although many animals tend to be gregarious during the non-breeding seasons, they frequently take up isolated positions and become intolerant of the close presence of others when undertaking reproduction. A *home range* is that area regularly traversed by an individual in search of food and mates, and caring for young.

The establishment of territories is best developed in birds (Hinde 1956), but also occurs in some other vertebrates (Carpenter 1958), possibly including some amphibians (Sexton 1960), and certain invertebrates (wood ant, Elton 1932; dragonflies, Jacobs 1955). There is increasing evidence that most adult animals, except for small aquatic species, establish

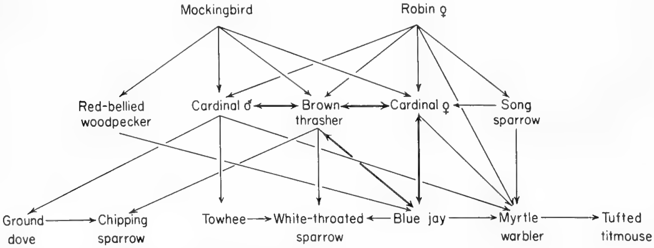


FIG. 12-5 **A social hierarchy between species of birds visiting a feeding station during the winter (Dennis 1950).**

home ranges, if not territories, at least during the breeding season (snails, Edelstam and Palmer 1950; toads, Bogert 1947; fish, Hasler and Wisby 1958; turtles, Cagle 1944; mammals, Seton 1909, 1925–28). Immature animals, species in migration, or shifting populations during non-breeding seasons commonly do not have definite areas to which they confine their activities. An area should not be called a territory unless one can ascertain that it is defended against intruders of the same species.

In order to determine that a home range exists, and to measure the size of it if it does, it is necessary to verify continuous occupancy of the suspected area by the same individual animal. Animals are trapped, marked and released as many times as are necessary clearly to establish the shape and extent of the area over which they wander in carrying out their normal activities. Best procedures for arranging the location of traps so as to reveal true home range and for statistical analysis of the records of recapture are reviewed by Dice and Clark (1953) and Stickel (1954). This can only be done if the individual can be identified by some peculiarity in its coloration or body characteristics, or by some system of applied marking (Taber and Cowan in Mosby 1960). Birds are commonly live-trapped and banded with numbered aluminum bands placed around the legs. Mammals may be live-trapped and marked by distinctive toe clipping, ear notching, or tattooing. Snakes may be marked by removing scales from conspicuous locations on the body; frogs and toads may be identified by punctures in the web between the toes, toe clipping, or by tags; turtles can be made to unwind a spool of string by which their trail is marked; fish fins can be clipped, or numbered tags attached to the jaw or gill covert or fin; and so on. The trouble with these techniques is that the animal must be trapped and handled to be identified. The ideal marking would be one obviating all this disturbing clumsiness while permitting easy and positive identification.

Various methods of marking animals have been developed so that they may be individually recognized without recapture: colored bands; dyeing parts of the body; attaching colored feathers to the tails of birds. Luminous paint applied to small aquatic animals allows their movements to be traced in the dark (Lockhead 1939). Attempts have been made recently to dose animals with radioactive cobalt or phosphorous and trace their movements with a Geiger counter (Miller 1957).

Territoriality has become so ingrained in the behavior of some types of animal that simple advertisement of possession often constitutes adequate defense. Such advertisement takes the form of song or other vocal expression in birds, some mammals, and some frogs, or the deposition of scent, a characteristic of many mammals (Holzapfel 1939, Graf 1956). If an intruder persists in invading a territory, however, the owner will variously display bright threatening coloration, scold or growl, give chase, or actually engage in physical combat.

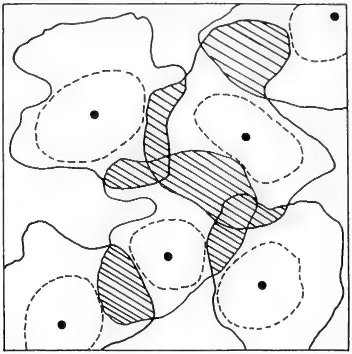


FIG. 12-6 **Theoretical relation between home ranges (area enclosed within solid lines) and territories (area enclosed within broken lines). The black dots represent nesting sites (Burt 1943).**

FIG. 12-7 **Travels of a box turtle over its home range during a week, July 7-14 (Stickel 1950).**

Maintenance of a definite territory has several benefits: a definite breeding location in which the nest can be confidently established and protected is afforded; it aids the acquisition of mates; it insures an area of sufficient size to provide food both for the adults and, later, for the young; and it frees the possessor of the onus of despotic interference by other individuals. The extent to which these advantages are attained varies with the species (Nice 1941). Although competition for territory is most keen between individuals of the same species, it also occurs between different species the space requirements of which overlap (Simmons 1951, Sharp 1957). A home range, on the other hand, only provides a breeding location. Possession of territory lessens the pressure of competition during the reproductive period, particularly for the female, when the entire energy and attention of animals needs to be devoted to the production of offspring.

SUMMARY

Beneficial cooperation is evident in division of labor between cells, tissues, and organs within the individual, between individuals in societies, and between species living together in communities. Benefits derived from cooperation are physiological and behavioral and may affect survival, reproductive success, and more efficient use of natural resources. Cooperation between species that is intimate and beneficial to both participants is called mutualism; where only one participant benefits, commensalism. These relations may be either facultative or obligative. Where one or more of the participants is harmed there is disoperation, of which parasitism, parasitoidism, competition, and predation are the examples. Distinction is made between true parasites, social parasites, and parasitoids. True parasites and their hosts have evolved adaptive interrelations so that coexistence occurs for varying lengths of time. The host is generally weakened, however, and virulent strains of the parasite may cause high mortalities. Causes of mortality or disease among organisms are predators, parasitoids, worm parasites, protozoan parasites, bacteria, viruses, fungi, external parasites, nutritional deficiencies, toxication, physiological stress, and accidents.

Competition may be exerted directly through interference in the activities of one organism by another, or indirectly in the form of excessive exploitation of natural resources. It may be either intraspecific or interspecific. Competition may result in establishment of social hierarchies, establishment of territories, regulation of population size, segregation of species into different niches, or speciation. The over-all effect of competition is to relegate the individual and species to an orderly place in the structure and organization of the community with the result that there is decrease in tension and disturbance.

13

Ecological Processes and Community Dynamics:

Food and Feeding Relationships

Food-getting necessarily involves interrelations between organisms and between species; these interrelations are among the most important coactions in any community. Animals are adapted variously to capture and utilize certain types of food, and to avoid being captured by other animals. One must understand these adaptations and interrelations to appreciate properly the role that food-getting plays in the dynamics of the community.

FEEDING BEHAVIOR

Free-living animals are commonly classified on the basis of normal feeding behavior, thus:

Herbivores:	feed on living plants
Carnivores:	feed on animals that they kill
Omnivores:	feed on both plants and animals
Saprovores:	feed on dead plants and animals, and excreta

These categories are not sharply defined, as few species are highly restricted in their diet. Plant-feeding forms occasionally eat animal matter, and carnivores sometimes eat fruit or other plant parts, or carrion. The classification is useful, however, and applies to both terrestrial and aquatic forms, and to any taxonomic group.

The various categories are capable of further subdivision. Thus, herbivores include large cursorial grazers, such as bison, antelope, the muskox, caribou, sheep; small surface-living grazers, such as rabbits, mice, grasshoppers; subterranean-living grazers, such as woodchucks, prairie dogs, kangaroo rats, ground squirrels; browsers, which feed on buds and twigs of trees and shrubs rather than strictly on grass or ground herbs, such as wapiti, deer, moose, grouse, and defoliating types of insects such as the hemlock looper, spruce budworm, and larch sawfly; seed-, nut-, and fruit-eaters, such as squirrels, chipmunks, gallinaceous birds, sparrows; plant-juice suckers, such as aphids, leafhoppers, mosquitoes, chinch bugs; and cambium feeders, such as bark beetles, gall flies, cynipids (Clements and Shelford 1939).

Carnivores are also called predators. Carnivores restricting their food chiefly to insects are called insectivores; those limiting themselves largely to fish are called piscivores; and so on. Parasitoids eventually consume their hosts, and hence are a special type of carnivore. Some plants are carnivorous. The pitcher-plant, Venus' fly-trap, and sundew, that grow in bogs or wet places, and bladderwort, that occurs in ponds, depend for their nitrogen supply largely on animals that they capture and consume. Perhaps the bacteria, fungi, and viruses that cause disease in animals also belong to this classification.

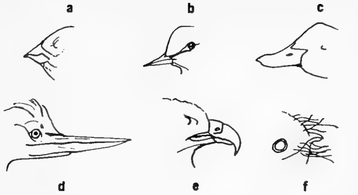


FIG. 13-1 **Adaptations in the bills of birds. (a) a seed-eating sparrow; (b) an insect-eating warbler; (c) a plant-eating duck; (d) a fish-eating heron; (e) a predaceous hawk; (f) an aerial insect-eating whippoorwill.**

Many species eat both plant and animal matter, on occasion, or at particular seasons, but animals are considered to be truly omnivorous only if they feed on plants and animals in nearly equal amounts or indiscriminately. Omnivores occasionally also consume dead organic matter. Some aquatic organisms are filter-feeders and may consume everything within a particular size range that passes through their feeding apparatus (Jorgensen 1955). However, filter-feeders may demonstrate selectivity by feeding in neighborhoods where certain species predominate. Some copepods select particles of a particular size, rejecting larger ones, by regulating the distance between the maxillae in the filter mechanism (Hutchinson 1951).

Probably most, if not all, animals have chemoreceptors of some sort, either to discriminate chemical substances dissolved in drinking water or food (taste), or chemical substances that are water- or air-borne (smell). Essential oils and alkaloids in plants are important as conditions of acceptability to insects. Hairiness, other surface features, or the visual stimuli that plants present are also conditions of attractiveness or acceptability of a food item.

The food preference of any species depends on chromosomal inheritance, parental training, and personal experience of that species, but the relative significance of each of these factors has not been evaluated for most animals. Young birds and mammals, in their first experiences at independent feeding, may pick up a variety of material but reject those items that are distasteful or indigestible; they soon learn to distinguish acceptable substances. This process is established as the parents feed offspring only those things traditional to the species, or so direct the feeding movements that untraditional food is excluded. Some adult insects lay their eggs on material that will serve the larvae as food. The larvae acquire the habit of feeding on that material, and do not readily change to something else as adults (Brues 1924, Thorpe 1939).

FEEDING ADAPTATIONS

Among kinds of mammals, teeth show considerable adaptive radiation, correlation with type of food consumed. The molar and premolar teeth of insectivorous species, such as shrews and bats, are low and have sharp-pointed cusps for crushing weak-bodied prey. The piscivorous toothed whales have largely lost all differentiation in their teeth, which are simple, conical, grasping structures. The teeth of the carnivorous dogs and cats are high-crowned and tubercular, well fitted for shearing flesh. Herbivorous ungulates and rodents have teeth that are flat-crowned, suited to grinding harsh grasses and other vegetation. Their jaws are capable of considerable lateral motion. Omnivores may have both grinding and pointed teeth. Saprovores have rather blunt teeth. The ant-eating sloths and their relatives have no teeth, and the mouth is almost tubular in shape. The tongue has become long and prehensile for lapping up tiny ants.

The bills of birds display great variety in shape and size, adaptations to feeding in numerous quite specialized niches in the environment. The tongues of birds are variously modified to serve as long probes or spears (woodpeckers and nuthatches), as a strainer (ducks), as a long capillary tube for obtaining nectar from flowers (hummingbirds), as a rasp (hawks and owls), as a finger for manipulating the food in the mouth (parrots and sparrows), and as a tactile organ (sandpipers and herons) (Gardner 1925).

The mouth parts of insects are adapted primarily either for biting and chewing or for piercing and sucking. Among marine invertebrates, adaptations for feeding on detritus (Blegvad 1914) include pseudopodia (Foraminifera); ciliated epithelium that maintains a flow of water through the animal (sponges, clams); prehensile, often ciliated arms (various polychaetes; holothuroideans); and soft eversible gullets (various polychaetes, sipunculids). Those that are herbivorous or carnivorous, as well as detritus feeders, have prehensile tentacles armed with nematocysts (hydroids, actinians), radulae in the mouth (mollusks), eversible stomachs (starfish), and masticatory structures in the mouth or stomach (crustacea, diptera larvae).

In addition to mouth part adaptations, there are many modifications in other parts of the digestive tract for handling particular types of food. These adaptations occur throughout the animal kingdom, but are especially evident in birds. A crop is present in some species but not in others. The walls of the stomach are more muscular in seed-eating birds than in flesh-eaters. Owls and some other species form and regurgitate from the stomach pellets of indigestible matter. Gallinaceous birds are able to retain or shift the supply of gravel or grit in the stomach as an aid to grinding seeds. The length of the intestine varies with the type of food consumed; the caeca are longer in browsing and seed-eating gallinaceous birds for digesting cellulose.

Associated with these anatomical and histological adaptations are adjustments in function and behavior. Obviously, if an animal has morphological adaptations for ingesting and digesting flesh, it must behave as a carnivore and not as an herbivore. The possession of these adaptations and adjustments means that animals are generally restricted to the particular types of food that they can use most efficiently. The kinds of food eaten by animals is of fundamental ecological and economic importance.

METHODS OF STUDY

A common procedure for analyzing kinds of food consumed by organisms is to identify the contents of the crop, stomach, cheek pouches, or other parts of the digestive tract (Hartley 1948).

The diet may be described in terms of number of items of each kind of food found in one specimen, or percentage of specimens containing a particular item, but it is usually more satisfactory to measure in one specimen the percentage volume of each food item against the total contents (McAtee 1912).

This procedure has the advantage of showing accurately what an animal has actually ingested, but has the disadvantage that the animal must usually be killed; thus, the information obtained is on only one meal, or portion of a meal. It also gives no information on where or how the food was obtained. Nevertheless, considerable information on the food habits of animals has been obtained in this manner (Henderson 1927, McAtee 1932, Davison 1940, Martin *et al.* 1951). Improved techniques make it possible to secure the stomach or crop contents without killing the animal. This is done by manual manipulation of the crop (Errington 1932), or by use of flushing tubes (Vogtman 1945, Robertson 1945). Artificial beaks with open gapes placed as decoys among nestlings have been used to collect food brought by the parents (Betts 1954).

There are usually indigestible parts in all kinds of food, and these indigestible or undigested parts are eliminated from the body. The contents of fecal droppings or regurgitated pellets can often be identified by differences in shape, size, color and texture, or by histological techniques (Dusi 1949). Collection of droppings is not practicable for aquatic animals, or for more than a few of the terrestrial invertebrates. Moreover, the droppings must be relatively fresh, as they quickly disintegrate in wet weather. The analysis of owl pellets is very fruitful, for owls swallow all parts of their mammalian or avian prey, and then regurgitate the hair, feathers, and skeleton. Hawks, gulls, and shrikes also produce pellets. The considerable advantage of pellet analysis is the possibility of continuous diet analysis on the same individual, or species, through long periods of time, without disturbance to its normal behavior (Dalke 1935, Errington 1932).

Whatever method is used, field observation of the feeding behavior of animals in the natural environment is desirable. For instance, one series of stomachs of the house sparrow contained a large number of May beetles, which would suggest that the bird was important for the control of this insect pest. Observations disclosed, however, that the sparrows were picking up dead beetles littering the pavement under street lights. Field observation itself often furnishes considerable information concerning the kinds of food consumed, but the results are usually not quantitative, do not disclose the less conspicuous kinds of food taken, and may be inaccurate if not carefully formulated. A hawk visiting a game farm may take not game animals but undesirable rodents that are also present (Kalmbach 1934).

Food chains can be determined by correlating the food eaten by different species in the community. Radioactive elements incorporated metabolically into an organism are taken into the predator of that organism; radioactivity-tracing technique gives promise of more direct tracing of how matter flows through the ecosystem. A number of radioactive elements may be used; among them, phosphorus-32 and iodine-131 (Odum 1959). Interesting studies in this connection are being conducted at the Oak Ridge National Laboratory in Tennessee.

CHOICE OF FOOD

The kinds of food eaten by animals depend on factors of their genetic heritage, parental training, or conditioning while young. Involved in the evolution of the food habits of a species are the animal's physical adaptations for ingesting and digesting particular types of food, the nutritional values of the food, its palatability, the size of it, its availability or abundance, and its ease of procurement which depends in large part on the various protective devices that it possesses.

Nutritional values

Animals generally require proteins, carbohydrates, fats, vitamins, minerals, and water. Proteins are used as the basic substance in the composition of protoplasm; carbohydrates and fats are oxidized to furnish energy for the body; vitamins serve as catalysts for specific metabolic processes; minerals are needed to regulate osmotic pressure and as constituent elements of various body organs; and water is used as a general solvent, lubricant, and circulatory medium. Species differ, however, in their needs for particular substances. The beetles, *Tribolium, Lasioderma,* and *Ptinus,* for instance, grow slowly but nonetheless satisfactorily on diets lacking carbohydrates. Hence, they may be distributed more widely than are species which require carbohydrates in their diet (Fraenkel and Blewett 1943).

Foods differ in composition. Foods *staple* to an organism's diet are those easily digested, and of high caloric and protein content. They are adequate to sustenance of the weight and vigor of the animal, but usually need to be supplemented with vitamins and minerals. The bobwhite and ring-necked pheasant, for example, eat certain cultivated grains and weed seeds, such as corn, sorghum, barley, wheat, rye, soy beans, pigeon grass, and lesser ragweed as staple foods, at least on a mixed diet.

Non-staple or *emergency* foods are not in themselves sustentative, and animals limited to them gradually lose weight and die. Such foods are, however, often abundant and easily procured in emergencies, when staple foods are covered with snow or ice, and furnish sufficient energy to tide the animal over the critical period. In emergencies, the bobwhite and ring-necked pheasant eat black locust beans, fruits of the bittersweet and sumac, rose hips, dried wild grapes, and sweet clover seeds (Errington 1937).

During good acorn years, squirrels, deer, and raccoons feed extensively on the acorns of white and black oak, but almost completely ignore northern red oak. Experiments with fox squirrels show that the animals gain weight on an exclusive diet of white oak acorns, scarcely maintain weight on acorns of the black oak, and lose weight rapidly on acorns of the red oak. The percentage of tannin in red oak acorns is twice that in white oak acorns, and animals are probably able to distinguish red oak acorns by a bitter taste (Baumgras 1944).

Vitamins are necessary for the maintenance of good health in wild animals, just as in domestic animals or man. The symptoms of vitamin deficiency, induced experimentally, are similar. Evidence has been difficult to secure, however, that animals suffer from vitamin deficiencies in their natural environments (Nestler 1949, House and Barlow 1958).

Animals obtain most of their required minerals from their food and water. Additional salt must sometimes be given caged animals to prevent cannibalism. The gnawing of castoff deer antlers by rodents is apparently for additional salts. The use of certain soil deposits and springs as natural "licking sites" by deer and other ruminants is apparently for sodium salts lacking in their general diet (Stockstad *et al.* 1953). Some birds, such as the evening grosbeak, are also attracted to sources of salt supply. There is some disagreement as to the need for grit in the stomach as an aid for the grinding of seeds and hard vegetable matter in gallinaceous and other birds (Nestler 1949); this grit may be instead a source of minerals.

Animals appear to become aware of nutritional deficiencies in their diet through physiological and neurological mechanisms. Experiments with rats show that when the body lacks some necessary element such as sugar, salt, or a vitamin, the animal consumes more of that particular substance than usual. Discrimination and selection are apparently made by taste, and a special need for a particular substance sharpens the taste for that substance so that it can be detected even when present in food or water in but very small quantities (Richter 1942). Nutritional needs are neither the sole nor necessarily the most important factor involved when animals show preference for one type of food over another. Many other factors condition the choice (Dethier 1954).

Palatability

Different species of animals vary considerably in efficiency of digestion and utilization of particular food substances. Thus, clothes-moth larvae can digest cloth and bird lice can digest feathers, because among other things they have an exceptionally high hydrogen ion concentration in their intestines.

Digestive enzymes occur generally throughout the animal kingdom although less is known about them in the Protozoa. In the lower phyla the enzymes are generalized in respect to the kinds of foods on which they act; in the higher phyla, they become highly specialized (Prosser *et al.* 1950). A specific enzyme, however, does not differ greatly from one animal group to another. Carnivores have strong proteases and weak carbohydrases, correlated with their meat diet. Herbivores, on the other hand, have weak protein, but active carbohydrate, enzymes. Herbivorous mammals and birds possess a bacterial flora in their digestive tracts that makes possible digestion of cellulose. Omnivores have a full complement of enzymes and can utilize a wide variety of foods.

Practically all food contains some indigestible matter; ordinarily, that is passed through the digestive tract and eliminated in the feces. If the indi-

TABLE 13-1 Quantitative comparison of food organisms eaten by the brown trout, a carnivore, with those present in the fauna of an English fishpond (data from Frost and Smyly 1952).

		Spring			Summer		
Common name	Classification	Per cent eaten	Per cent in fauna	Forage ratio	Per cent eaten	Per cent in fauna	Forage ratio
MUD-LIVING ORGANISMS							
Midge fly larva and pupa	Chironomidae	36	66	0.5	36	48	0.8
Alderfly larvae	*Sialis lutaria*	10	1	10.0	4	1	4.0
Mayfly naiads	*Caenis* sp.	+	6	+	20	+	20.0
Fingernail clam	*Pisidium* sp.	17	16	1.1	5	27	0.2
Worms	Oligochaeta	0	1	0	0	2	0
	Totals	(63)	(90)	(avg. 0.7)	(65)	(79)	(avg. 0.8)
WEED-LIVING ORGANISMS							
Caddisfly larvae	*Leptocerus* sp.	21	+	21.0	21	1	21.0
Caddisfly larvae	Limnophilidae	3	+	3.0	1	1	1.0
Caddisfly larvae	Polycentropidae	1	1	1.0	2	1	2.0
Mayfly naiad	*Leptophlebia* sp.	7	4	1.8	0	+	0
Damselfly & dragonfly naiads	Odonata	3	1	3.0	2	5	0.4
Beetle adults	Coleoptera	+	+	1.0	+	+	1.0
Water-boatman	Corixidae	1	3	0.3	2	9	0.2
Snail	*Lymnaea pereger*	1	+	1.0	5	+	5.0
Water mites	Hydracarina	+	1	+	+	3	+
	Totals	(37)	(10)	(avg. 3.7)	(35)	(21)	(avg. 1.7)

gestible material is excessive, or if it contains toxic substances, regurgitation or vomiting may result.

Size of food item

The size of the food in relation to the animal is not of major importance to many herbivores or saprovores as they normally feed in or on the organism or substance. With carnivores, the size of the prey must be within their power of conquest. Ordinarily the size of prey is less than that of the carnivore that feeds on it, but a high degree of ferocity and audacity, or pack hunting in the manner of wolves, often enables the carnivore to take prey larger than itself. On the other hand a predator cannot profitably prey on species so small that the energy derived from its consumption does not equal the energy expended in its capture. Some very large aquatic animals, however, have become adapted to feed with a minimum of effort on very small organisms occurring in dense concentrations through the evolution of a filtering apparatus in their mouth parts. A good example is the feeding of baleen whales on plankton.

Availability

In order to determine if a species is fed upon in proportion to its abundance (McAtee 1932), it is necessary to find out what animals have been eating of that which is available in a habitat. The relation between the two may be shown graphically (Hamilton 1940a) and expressed as *forage ratio:* per cent of species in animals' food divided by per cent of species in habitat (Hess and Swartz 1941). A value of unity indicates that the food item is taken in proportion to its abundance; a value greater than unity indicates that it is taken more frequently; values of less than unity indicate that the item is either inaccessible, of the wrong size, too difficult to obtain, or is actually avoided. Table 13-1 is an example of such a study conducted upon a carnivorous species. It is apparent that while there is a relationship between the relative abundance of various species and the degree to which they were taken as food, there are also several discrepancies. Weed-inhabiting organisms, more accessible to fish than organisms buried in the mud, are accordingly fed upon heavily, in disproportion to their relative abundance in the total fauna. The fingernail clam is fed upon heavily in spring, since it lies on the surface of the mud. But there is no explanation of why it is fed upon less heavily during the summer. Water boatmen and water mites, however, are generally not acceptable. Although the alderfly larva is a mud dweller, it is fed upon in large numbers, suggesting that there may be something in its behavior that makes it especially vulnerable, or that brown trout have evolved special methods for securing it. The caddisfly larva *Leptocerus* also appears to be easily taken, as it is devoured in numbers greatly disproportionate to its relative abundance. The mayfly naiad *Caenis* is not much fed upon in spring, at which time it is buried in the mud, but it is fed upon in large numbers in summer, at which time it comes to the surface of the water to emerge. Midge flies also become more vulnerable during the process of emergence. Zooplank-

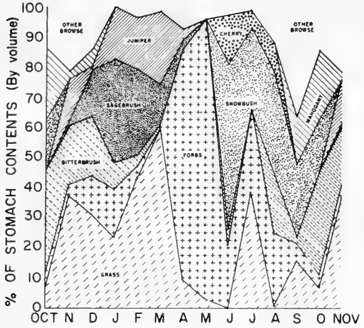


FIG. 13-2 **Monthly variation in kinds of food consumed by an herbivore, the mule deer, in California and Oregon (Interstate Deer Herd Committee 1951, courtesy California Division of Fish and Game).**

ton is of very minor importance in the diet of the fish. Forage fish were not present.

The vulnerability to a predator of a prey species is directly proportional to its relative abundance among the other species available. Voles are preferred by the red fox over white-footed mice, but both mice and voles are preferred over moles, shrews, and snakes. Predator preferences among them, however, occur only when all are abundant. When prey species are reduced in numbers and difficult to get, little or no predator preference occurs (Scott and Klimstra 1955).

There is some evidence that predators—particularly insectivorous birds—when searching for prey concentrate on one or a few species at a time. By a kind of learning, they acquire what may be called specific searching images for these species and thereby mostly disregard other species. When a new species becomes numerous in an area, they feed on it at first only as the result of chance encounters. To obtain a preference for the new species, they must become conditioned to it gradually and must learn the proper cues of where and how to search it out (Tinbergen 1960).

The importance of availability is illustrated by seasonal variations in the kinds and amounts of food consumed by animals. Predator species that remain in one habitat throughout the year must adjust their feeding to the kinds of food available in each season. Species that are unable to do this are compelled to migrate, hibernate, or make other adjustments to survive the unfavorable seasons. Thus birds that are strictly insectivorous may occur in a given area only during the warm part of the year, leaving it before insects disappear. Omnivorous species commonly change from an insect diet in summer to a diet of seeds and fruits in the autumn and are often nonmigratory.

Seeds and fruits are most abundant and easily obtained in the autumn. During the winter they decompose, become buried in the snow or softened ground, or are consumed. In Michigan, the weed seeds available on agricultural lands in March are only nine per cent of those available in October (Baumgras 1943). The most critical time of the year, as far as food supplies are concerned, is early spring, the time before new vegetation and hibernating prey animals appear. Abundance of seeds also varies with fertility of soil, which thus influences survival, density, and distribution of animal populations.

Animals are subject to considerable variation in the abundance and kinds of food available to them from year to year. In a four-year study of the yield of fruit and seeds from 27 species of trees and shrubs in West Virginia, only 33 per cent of the species produced a crop every year, 29 to 33 per cent failed to produce a crop in three of the four years, and 22 per cent failed twice within the four years (Park 1942). When herbivorous species vary in abundance, because of variation in food supply or other factors, carnivorous species that prey upon them often vary in direct proportion.

Protective devices

Few kinds of plants are well equipped with defense mechanisms against the grazing and browsing of animals. Trees and shrubs may be deformed or killed by excessive browsing because the tender terminal twigs and buds are destroyed. Grasses are not, for they grow from the base of the leaves; they may even be benefited by moderate cropping. Some species of trees, shrubs, and cacti are protected from browsing by prickles or thorns. This protection is important to the plants for survival in deserts and in grazing subseres of humid regions. Some plants are noxious or toxic, and animals quickly learn to avoid them.

When coloration renders it inconspicuous in its normal environment, an animal is said to have *concealing* or *cryptic coloration* (Cott 1940). When the coloration or markings reproduce the general tone or characteristics of background, it is called *protective resemblance; disruptive,* when the markings break up the outlines of an animal and replace it by some irregular configuration so that the animal is not recognized as prey. The white collar of the killdeer, observed casually from a distance, tends to the human eye to separate the head as a distinct object from the rest of the body. *Obliterative coloration,* or *counter-*

FIG. 13-3 **Protective resemblance of an incubating ruffed grouse to her surroundings (courtesy U.S. Forest Service).**

shading, describes the condition where the upper side of the body, exposed to the brighter illumination, is heavily pigmented and the lower side of the body, which is in the shadow, is lighter in color. This coloration obliterates the effect shadows have of making a body stand out from its surroundings (Thayer 1910). *Aggressive resemblance* is where the animal closely resembles some particular object rather than the general environment. The *Kallima* butterfly of the Orient and the preying mantis of Central America match the shape, markings, and color of leaves when the insects repose with wings folded. The familiar walkingstick resembles a twig. Several insect species look like bird-droppings. Such resemblances doubtless serve the animals to escape the attention of predators only as long as they remain motionless. Even slight movements quickly call attention to animals, regardless of any concealing coloration that they may have. Behavioral orientation is well shown by those caterpillars that are lightly colored dorsally and darkly colored ventrally. They bring their counter-shading into proper position by coming to rest upside-down along

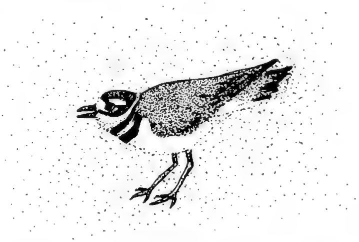


FIG. 13-4 **Disruptive coloration of a killdeer. The white color obscures the connection between head and body.**

FIG. 13-5 **Countershading. (a) the caterpillar, last instar of *Dicranura vinula,* in normal upside-down position on a willow twig in natural diffuse light. The back of this animal is lighter than the underparts, annulling the shadow. (b) the same caterpillar, inverted, is much more conspicuous, for the countershading effect is lost. This caterpillar has second and third lines of defense: when touched, it turns a kind of grotesque "face" toward you; when pressed, it squirts acid (courtesy N. Tinbergen).**

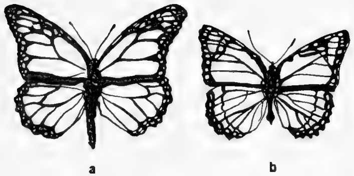


FIG. 13-6 **Mimicry of (a) the monarch by (b) the viceroy butterfly.**

plant stems (Ruiter 1955). The tell-tale shadows cast by animals may be eliminated when the resting animal lies lengthwise, rather than crosswise, to the sun, or when they lie pressed close to the ground.

Some animals, on the other hand, are vividly marked with strikingly conspicuous patterns or bright colors, and this *aposematic* or *warning coloration* is accompanied by unpalatableness in certain butterflies, bugs, beetles, ants, and birds; stings, in wasps and bees; a disagreeable odor in skunks; or some other offensive feature (Poulton 1887). There is experimental evidence that such animals are actually avoided by predators (Finn 1895–97, Jones 1932, Cott 1947). However, a hungry predator is less selective in its choice of food than one that has recently fed. Apparently each individual carnivore must have a personal experience with an animal so marked before it learns to avoid it by associating the coloration with the disagreeable feature.

There are many examples of *mimicry* among insects (Goldschmidt 1945). *Batesian mimicry* is the resemblance of a palatable species in external features to an unpalatable one that in turn possesses warning coloration and is the more abundant of the two species. The palatable species derives benefit from the relation, since predators, especially birds, avoid them as well as the unpalatable ones. The viceroy butterfly mimics the disagreeable monarch butterfly and differs strikingly from other members of its own genus (Brower 1958). There is considerable controversy about mimicry, however, and even the classical example of the butterflies is disputed (Urquhart 1957a). In *Mullerian mimicry,* both model and mimic are unpalatable. Pooling of numbers between the two species gives more chances for inexperienced birds to learn to avoid them and reduces the losses per species during the learning process (Sheppard 1958).

Some animals possess bright spots or colors so placed on the body as to be *deflective.* The attention of a pursuing predator is drawn to less vulnerable parts of the body; for instance, eyespots on the fins or tail of a fish. Eyespots on the wings of some butterflies and moths are concealed at rest, but when flashed out by spread wings may frighten away an attacking bird or other predator.

Concealing coloration and resemblance to other objects are apparently also useful to animals aggressively. A carnivore that matches its background can approach its prey undetected more easily than can a conspicuously marked one. Some predators have *directive markings* to confuse their prey as to the location of their mouths or to allure them in various ways.

There has been considerable controversy about the value of concealing coloration. McAtee (1932) minimized its importance because he found both protectively colored and conspicuously colored species in the stomach contents of the birds he examined. Probably few species are entirely immune to predation, but if coloration to match the surroundings, mimicry of some other avoided species, or peculiarities of form or structure render predation even slightly less frequent than it would otherwise be, it can well have survival value and evolve as characteristic of a species.

A number of experiments in regard to concealing coloration have been performed by exposing different kinds of insects (Carrick 1936, Isely 1938), fish (Sumner 1935), and mice (Dice 1947) to bird predators, with the result that those individuals that most closely matched the color of their background were taken less frequently than those that did not do so. In a black aquarium in which equal numbers of black and white mosquitofish were exposed to the predation of a penguin, 27 per cent of the fish eaten were black and 73 per cent were white, but in a white aquarium 62 per cent of the fish eaten were black and only 38 per cent were white.

RANGE OF FOOD SELECTION

There is considerable range in the variety of foods eaten by most species. Outside of parasitic forms, few animals are restricted to a single species for their food. Herbivorous species are often more specific in their feeding habits than are carnivorous forms. However, even herbivorous forms have various degrees of restriction, as shown in the following analysis of 240 species of plant-juice sucking aphids (Clements and Shelford 1939):

	Percentage
Species restricted to a single plant species	27
Species restricted to a single genus but feeding on more than one species	40
Species feeding on several different genera	33

One may argue with considerable justification that animals such as aphids, gall wasps, some bugs, and others that show host specificity are really parasitic rather than herbivorous in their feeding behavior, and hence are not good examples of free-living animals of restricted diet. Actually it is very difficult to find proven cases of animals that confine themselves to a single species of food. It is more common to have an animal feeding on a small group of related species, as do aphids. The potato beetle originally fed chiefly on the sand-bur *Solanum rostratum* in the Rocky Mountains until about the year 1859, when it began to infest the potato *Solanum tuberosum* and spread across the country. There may be a biochemical reason for the preference of animals for related plant species, recognized by similarity in taste, odor, or nutritional values.

Herbivorous species may be classified in respect to the diversity of their food into:

Monophagous:	restricted to a single food plant
Oligophagous:	restricted to a few very definite food plants
Polyphagous:	feed on many species.

The restriction of animals to particular foods may be the result of chemicals affecting odor or taste, or to structural adaptations. Chemical stimuli are especially important with insects (Dethier 1947). The crossed bills of certain birds (*Loxia* sp.) are well fitted for prying seeds from between the bracts of coniferous tree cones. The Siberian nutcracker has special structures in its bill for cracking the nuts of the Siberian cedar on which it depends almost exclusively for food (Formosof 1933).

In spite of the monophagy exhibited by some species, many herbivorous species have a wide choice of food; the bobwhite quail in Georgia is known to feed on 927 different food species, 107 of them regularly. These are mostly seeds and fruits, although about 14 per cent of the food of this species consists of insects and spiders taken chiefly during the summer months (Stoddard 1931). Restriction of feeding to a single or a few species is a specialized behavior. Feeding on a wide variety of substances or prey usually represents the more generalized primitive condition (Dethier 1954).

FOOD CHAINS

A single food chain should have at least three links to be complete: plant⟶herbivore⟶carnivore. Very often, however, a small carnivore or omnivore may be preyed on by a larger carnivore, and so on until four or five links are involved. Rarely are food chains longer than five links. An example of a three-link chain occurring on the North American Great Plains is: grass⟶pronghorn⟶coyote. A four link chain common to deciduous forest communities might include tree foliage⟶leafhopper⟶vireo⟶hawk. A five-link chain would have to involve a number of small species as bacteria⟶protozoan⟶rotifer⟶small fish⟶large fish. A food chain does not need to start with a living plant; consider, for instance: detritus⟶snail⟶shrew⟶owl. A strict predator need not necessarily be the last link, it could be an omnivore: flowers⟶bees⟶bear. Saprovores do not fit into food chain diagrams very well because they feed on all links of the chain. Food chains occur in all kinds of habitats and communities, even with the micro-organisms of the soil: detritus⟶nematodes⟶mites⟶pseudoscorpion.

The feeding coactions between the many species that constitute the community are seldom as simple as the food chains just described. The rotifer feeds not only on protozoans but on bacteria. The small fish feeds on insect larvae and many other plankton species besides the rotifer. The shrew in the forest feeds not only on snails but on a variety of insects, and is fed upon in turn not just by owls but also by hawks, foxes, weasels, and others. If all of these feeding relations between species in a community were diagrammed, a complicated web would be formed—the so-called *food web*.

BALANCE OF NATURE

Charles Darwin explained, a hundred years ago, that there was a balance in nature between the abundances of plants, herbivores, and carnivores. Were carnivores for some reason to increase unduly in numbers, they would soon exhaust their food supply and die of starvation. On the other hand, were food plants or herbivores to fluctuate excessively, then predators would vary in a similar manner. There is no doubt that marked variations in abundance in one link of a food chain will cause variations in the other links. Rodent plagues in a local area will bring an influx of foxes and hawks; a spruce budworm oubreak will result in an increase in the bird population; increases and decreases in soil bacteria are correlated inversely with decreases and increases in soil amoebae that feed upon them (Russell 1923).

As a case in point, the relation between the mule deer population and its predators on the Kaibab Plateau in northern Arizona is worth citing in detail (Rasmussen 1941). When this area was made a game preserve in 1906, killing of deer for sport was prohibited. At the same time, there was a marked decrease in grazing by domestic sheep. During the period from 1906 to 1939, there were 816 mountain lions, 863 bobcats, 7388 coyotes, and 30 wolves trapped or shot, mostly by government hunters.

The wolves were exterminated, and the other predators were markedly reduced. The deer increased from an estimated 4000 animals in 1906 to an enormous herd of nearly 100,000 in 1924. The deer's habits and the topography of the country prevented a scattering of animals to adjacent ranges. The over-populations of deer consumed all new growth of young trees and browsed the foliage of mature trees as high as they could reach, yet the population could not secure enough food to keep it in good physical condition. The population far surpassed the carrying capacity of the range. In September 1923, it was estimated that 30,000 to 40,000 animals were on the verge of starvation and during the winters of 1924–25 and 1925–26, an estimated 60 per cent of the population died. Plainly the balance of nature was upset in this instance, with dire results. Hunting was again permitted in 1924, and the herd was reduced to about 10,000 by 1939. This history of the Kaibab deer herd is not unique; similar cases have been reported in about a hundred other areas (Leopold, Sowls, and Spencer 1947). Over-populations in all areas have followed reductions in the number of predators, although other factors were involved.

Constancy of balance

When populations of species with differing food habits are in equilibrium, the surplus of prey species resulting from reproduction is destroyed and consumed by the predators. If predation does not destroy the total yearly surplus, the prey population increases in size; if predation takes more than the surplus the population of the prey decreases in size. Actually, even in entirely natural communities undisturbed by man, a strict balance of nature is probably never maintained for any appreciable period of time. It is characteristic for populations to vary in size, but these fluctuations tend to vary rather closely around a certain constant population mean. Depending on the length of its life cycle, a species population in an area may fluctuate from day to day, from season to season, or from year to year.

Many factors other than food coactions cause fluctuations in the abundance of animals, and predation is not always the most important (see Chapters 16, 17). Close interdependency between populations of prey and predator species occurs most commonly when a prey species has only one or two important species preying upon it, while the predator species is largely restricted to that one species of prey (Pennington 1941). It is obvious, however, that an equilibrium of a sort exists between different species, and this is what is referred to by the concept of balance of nature.

TROPHIC LEVELS

In order to analyze the intricate coactions involved in the food web and balance of nature, it is desirable to simplify the relationships into nutritional or *trophic levels* (Λ) (Thienemann 1926, Lindeman 1942, Allee *et al.* 1949, Odum 1953). The lowest level (P) is composed of photosynthetic plants that are able to use solar energy for the manufacture of food, and certain types of bacteria that use either the free energy of unstable inorganic compounds or are activated by light to synthesize a limited amount of new organic matter. These are the *producers*. At the second level (C_1) come the herbivores, or *primary consumers;* at the third level, the smaller carnivores, or *secondary consumers* (C_2); and at the fourth level, the larger carnivores, or *tertiary consumers* (C_3). Occasionally there may be *quarternary consumers* (C_4). The terms "producer" for plants and "consumer" for animals were used, and the essential relationship understood by Dumas in 1841. These two groups are also distinguished as *autotrophic* and *heterotrophic,* respectively.

The levels in subdivision of consumers are not sharply defined, as the feeding behavior of some species involves them simultaneously in several levels. Actually, the more remote an organism is from the initial source of energy (solar radiation), the more likely it is that it will prey on two or more levels. This need not confuse the essential relationships involved (Lindeman 1942). Omnivores overlap between levels C_1 and any of the higher levels. Large saprovores, the heterotrophic bacteria, and fungi derive their nourishment from the excreta and dead bodies of organisms from all trophic levels. Since they are reducers or decomposers, they may for simplification be grouped with the autotrophic bacteria, and be called *transformers* (T), since their total effect is to convert dead organic matter into nutrients that green plants can again absorb.

Figure 13-7 illustrates how a complicated food web may be simplified, somewhat arbitrarily, into trophic levels. Detritus, derived from the disintegration of dead organisms and excreta from organisms, is worked over by the bacterial transformers, and the detritus and bacteria represent an independent base of the food web separate from the green plants.

A characteristic of trophic levels in most communities is that the nearer a level is to the source of energy, the greater the diversity of species involved. Thus in Fig. 13-7, the primary consumers (C_1) include some twelve taxa; the secondary consumers (C_2), four; the tertiary consumers (C_3), three; and the quaternary consumers (C_4), but one. Species in the lower trophic levels have a higher rate of reproduction than those in the higher levels to compensate greater predation.

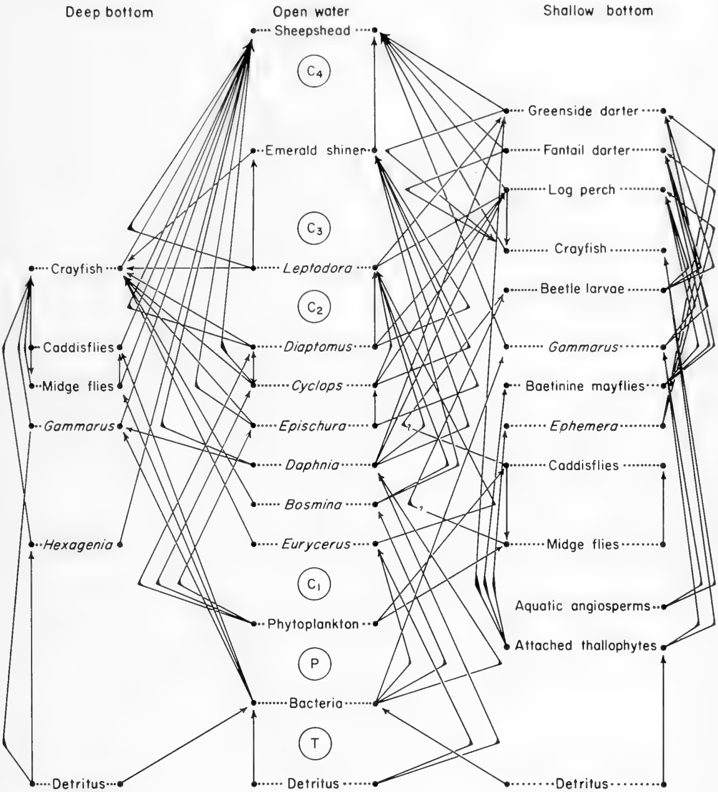


FIG. 13-7 **Food web in western Lake Erie, leading to the sheepshead fish. Species are separated into their different trophic levels. The diagram would be even more complicated if other fish species in the C_4 trophic level of the community had been included. Although adult sheepshead are not preyed on by other animals, young during their first year serve as food for three or four other fish species (considerably modified from Daiber 1952).**

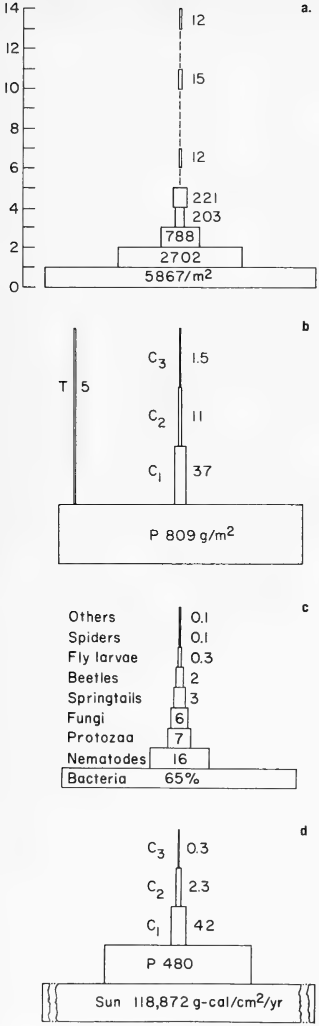


FIG. 13-8 **(Left) Ecological pyramids of (a) numbers by size classes (soil animals of tropical broad-leaved forest, Williams 1941); (b) dry biomass, Silver Springs stream (Odum 1957a); (c) per cent total metabolism by different taxa of a hypothetical soil population in a meadow (Macfayden 1957); (d) gross productivity, Lake Mendota (Lindeman 1942).**

PYRAMID OF NUMBERS AND BIOMASS

When the total animals in a community are grouped according to an arbitrary series of size ranges (Elton 1927, Allee *et al.* 1949), there are always a larger number of small individuals present than large ones. Plotting these data gives a pyramid of numbers.

Pyramids of numbers arranged by trophic levels, rather than size, have special interest in respect to food coactions. In a bluegrass field, the number of green plants at the producer level (P) was over 8 times the number of herbivorous invertebrates in the level of primary consumers (C_1); the number of primary consumers was 2 times the number of spiders, ants, and predatory beetles at the secondary consumer level (C_2); and the number of secondary consumers was over 100,000 times the number of birds and moles among the tertiary consumers (C_3), because of the great difference in size of individual animals at these two levels (Odum 1959). In Michigan, the ratio between numbers of rodents and their hawk and owl predators was found to be approximately 1000:1 (Craighead and Craighead 1956).

In evaluating the importance of trophic levels in the community, biomass is a more important index than number of individuals. Of 13 ratios of fresh weights between different trophic levels (Lindeman 1941, Juday 1942, Turček 1952, Birch and Clark 1953), the majority fall between 2:1 and 12:1. These early studies furnish no certain evidence that the ratio varies between different trophic levels; this needs further investigation. Although these are not given as established limits, as far as we now know, it is expected that biomass ratios falling far outside these will represent inadequate or incomplete sampling of populations, populations out of balance, or quite special situations. Thus the 23:1 ratio between P and C_1 trophic levels in Cedar Lake Bog in Minnesota (Lindeman 1941) is correlated with large annual accumulations of vegetation in a very old pond where winter stagnation under the ice kills off much of the animal life that might otherwise consume the plant material. The ratio of 22:1 in dry weight between P and C levels in Fig. 13-8b is due, in part, to a significant fraction of the produce level being exported downstream. In balanced communities, total biomass of plants must ordinarily be larger than the biomass of herbivorous animals that feed upon them; in turn, the biomass of each consumer level must ordinarily be greater than the biomass of the succeeding level that feeds on it.

Metabolism is even more accurate than biomass, for it represents the rate at which energy is being utilized and work performed. Figure 13-8c evaluates a hypothetical soil population on this basis; we need actual measurements of this factor in every community.

Finally, a pyramid may be drawn to show the rate at which new organic matter is produced through reproduction and growth at each trophic level (Fig. 13-8d). The basic principle in this pyramid, fundamental in all types of pyramids, is that *the rate of production cannot be less and will almost certainly be greater than the rate of primary consumption, which in turn cannot be less and will almost certainly be greater than the rate of secondary consumption, etc.* (Lindeman 1942: p. 408).

SUMMARY

In respect to feeding behavior, animals are herbivores, carnivores (predators), omnivores, or saprovores, and have special adaptations for securing particular kinds of food. Various methods have been developed for analyzing the kinds of food that animals consume. Animals discriminate in their choice of food depending on its nutritional values, palatability, size, abundance and availability, and the protective devices that the food possesses. Relatively few species, however, are restricted to feeding upon a single species of plant or animal prey.

Concealing coloration is of various types: protective, disruptive, obliterative, and aggressive resemblance. Bright coloration may be warning of some disagreeable feature that the animal possesses, be mimicry of another species that possesses such features, or be deflective or directive.

Food chains commonly contain three to five links: a plant, an herbivore, and one or more carnivores. In each community the large number of food chains inter-connect in various ways to form a food web. The relative number of organisms in the different links tends to be constant to give a balance of nature.

All organisms making up a link in the food web may be considered together as constituting a trophic level, of which there may be five: producer; and primary, secondary, tertiary, and quaternary consumers. Transformers work over the excreta and dead organisms from all levels. In lower trophic levels, there is generally a greater variety of species, larger number of individuals, higher rates of reproduction, and individual animals are usually but not always smaller in size. A plot of the number of individuals in different size classes or the number of individuals, biomass, or productivity in different trophic levels takes the form of a pyramid. The relationships shown in these pyramids are fundamental to an understanding of community structure and dynamics.

14

Energy Exchanges, Productivity, and Yield

The food coactions of organisms are important since animals can obtain energy only from consumed food. All activities of organisms constitute work and require energy. The amount of work performed depends on the amount of energy the organism can mobilize. Hence the flow of energy through the ecosystem and the manner and efficiency with which it is used is an important ecological process.

ENERGY FLOW THROUGH THE ECOSYSTEM

Unlike nutrients, energy does not circulate indefinitely through the ecosystem. Energy is continuously and rapidly lost, although a certain amount of energy may pass through the ecosystem more than once before it is entirely dissipated. Hence energy must continuously enter into the ecosystem from the outside.

Acquisition

The basic source of energy for all trophic levels is solar radiation. A surface exposed normal to the sun's rays, and outside the earth's atmosphere, would receive energy at the rate of 1.94 g-cal/cm^2/min. This is the solar constant. On the earth's surface, solar energy is effective only during the daylight hours and, because of absorption in passing through the atmosphere, scattering by smoke, dust particles, and cloudiness, only about 46 per cent of daylight radiation reaches the earth's surface (Fritz 1957), although this varies with latitude, season, and locality. At Columbus, Ohio, located at latitude 40° N, the average amount of solar energy is estimated as follows (Shaw 1953):

	Kcal/m²/day
Summer	6263
Spring and autumn	3628
Winter	1604
Average	3781

The basic means by which solar energy is trapped is the formation of sugar by plants that contain chlorophyll (Rabinowitch 1945–46). In terms of moles (Brody 1945):

Photosynthesis —

$$6\ CO_2 + 6\ H_2O + 709\ \text{Kcal} \longrightarrow 6O_2 + C_6H_{12}O_6$$

Respiration —

$$C_6H_{12}O_6 + 6O_2 \longrightarrow 6\ CO_2 + 6\ H_2O + 674\ \text{Kcal}$$

Respiration is going on at all times to furnish energy for the plant's activities, and this energy is derived from oxidation of the sugars formed in photosynthesis. Under ordinary daytime light intensities, the amount of sugar formed by photosynthesis greatly exceeds the amount oxidized in respiration. Photosynthesis ceases during darkness, but loss of sugar at night, because of respiration, continues. Sugars may be converted to starch or fat or upon combination with nitrogen, sulphur, and phosphorus be changed into proteins. The amount of sugar resulting from photosynthesis represents the *primary production* of the ecosystem. Accurate measurement of the rate of primary production is one of the most important problems of trophic ecology, for the activities of all plant and animal organisms in the community depend on the energy thus supplied. It is necessary to distinguish between *gross production*, the total amount of energy captured, and *net production,* the amount that remains after that used for respiration. Primary production is commonly expressed in terms of glucose or carbon, or indirectly in the amount of oxygen released or carbon dioxide absorbed, all of which can be converted into calories of energy.

Use

Net energy at the producer level becomes available for use of animals when it becomes transferred to the higher trophic levels through predation, here considered also to include consumption of plants (Riley 1940, Lindeman 1942, Clarke 1946, Clarke, Edmondson, and Ricker 1946, Birch and Clark 1953, Macfadyen 1957). In order to measure the transfer and use of energy at each trophic level (Λ), it is desirable to know the size of the *standing crop or biomass (B)* at each level. Energy is acquired by animals only through the consumption of food, which may be indicated as the *gross energy intake (I)*.

A good portion of the energy ingested is used for existence, that is for basal metabolism, temperature regulation, procurement and digestion of food, and other normal activities. There is almost continuous loss of heat energy from the body and in homoiotherms this must be compensated for by increased heat production. Energy is used for the production of eggs and sperm, reproductive behavior, and other activities in the normal life of the individual animal. Even the process of converting raw food into protoplasm is work and requires energy. In transfer of energy from one form to another, there is always loss of free energy. No transfer is 100 per cent efficient. This is the second law of thermodynamics. The total energy that is utilized to perform work and to produce heat is called *respiratory energy (R)*.

Transference

The gross energy intake, *I*, less the respiratory losses of energy, *R*, gives the net production of the consumer levels, the same as at the producer level. The rate at which net production accumulates is net productivity or simply *productivity* (λ). Net production may be lost to the trophic level in the decomposition of excreta and dead animals; it may become evident in the growth and increase of population; or it may be transferred to a higher trophic level.

FIG. 14-1 Isolines of average solar radiation (g-cal/cm²/day) received in July on a horizontal surface in the United States during days of average cloudiness. In December, isolines run nearly straight and parallel across the country, and are of values less than 100 in the North and over 250 in the South (Fritz 1957).

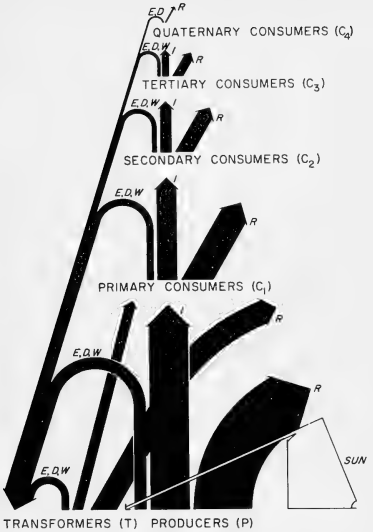


FIG. 14-2 **Energy flow through an ecosystem the trophic levels of which are in balance with each other; symbols are explained in text. The weights of the arrows are intended to suggest the relative proportions of energy flow in the various directions, but this is schematic because the proportions vary widely in different ecosystems.**

Certain of the food taken in, *I,* is indigestible or may simply be undigested, or if digested and absorbed is not completely metabolized in the tissues, so that it is eliminated in feces and excreta. This is designated *excretory energy, E. Assimilated energy* is the energy of the food actually absorbed and utilized $(I - E)$. These terms may also be applied to the producer level when I represents the total solar radiation reaching the plant, and E is that portion of the radiation not used.

Aside from being killed by predators, organisms die from a multitude of other factors such as disease, extreme weather, starvation, combat, old age, and accident. In order for the populations of the different trophic levels to be maintained at a more or less constant level, organisms that die *non-predatory deaths, D,* must be replaced by the reproduction and growth of new individuals.

For energy to be transferred from one trophic level to a higher one, organisms must be killed and eaten by predators of the higher trophic levels. When predators consume their prey completely, as do fish feeding on plankton, there is no wastage, but with many predators, the prey killed is so large it must be eaten piecemeal, and much is not used. Predatory kill must therefore be separated into the *energy consumed* by the higher trophic level $(I_{\Lambda+1})$ and the *energy wasted, W.*

Energy lost from a trophic level through excreta, non-predatory deaths, and wastage from kills is used by saprovores or transformers, T. This allows for the decomposition and conversion of nitrogen and other compounds into nutrients suitable for reabsorption by plants. Energy from the transformer level recirculates into higher trophic levels when detritus and the transformer organisms, bacteria, fungi, protozoans, and the like, are consumed, as indicated in Fig. 14-2.

When populations of different trophic levels are in balance, the total net production of each trophic level, after losses from excreta, non-predatory deaths, and wastage from kills have been subtracted, is consumed by predators of the higher trophic levels. In unbalanced populations, predatory consumption may not equal the available net production, so that the population of that trophic level increases. If the predatory kill exceeds the available net production, the population decreases. A *change in the biomass, b,* of a population may, therefore, be either plus or minus. An entire ecosystem is in balance when the total exchange of oxygen and carbon dioxide between consumers and producers is equal.

Increase in biomass comes with the growth of individuals. When an individual organism grows, it increases in size and weight by adding organic matter. When reproduction takes place there is an increase in number of individuals, but not necessarily an increase in biomass, which takes place only if the offspring increase in size. Since individuals of most species have limits of growth increase, reproduction increases the potential productivity of a community by adding to the number of individuals capable of growth.

MEASUREMENT OF PRODUCTIVITY

Productivity may be measured during any reasonable period of time. Because of essential metabolic differences between day and nighttime, however, the 24-hour day is the smallest practicable unit. Similarly, because of seasonal changes in the environment and in community populations, the measurement of annual production is probably most useful. Production is commonly expressed in terms of individuals, biomass, or preferably calories per unit area per unit time. The basic problem is that of analysis of how energy is obtained, how efficiently it is used, what portion of it is available for reproduction and growth, and how much of it is passed on to higher trophic levels through predation. These many factors may be brought together in the following equation to show what happens to the gross energy intake, I_Λ at any trophic level:

$$I_\Lambda = E + R + D + W + I_{\Lambda+1} + b$$

One can make a number of derivations from this equation; but what is of particular interest and importance is the amount of energy of each trophic level that is transferable to the next. This is represented by the equation:

$$I_{\Lambda+1} = I_\Lambda - E - R - D - W - b$$

Each factor in the equation must be measured at each trophic level, and for each species. Since primary production is basic and concerns the capture of energy by plants, it will be considered first.

Primary production

Various methods are employed for measuring primary productivity, each procedure having certain advantages and disadvantages (Ryther 1956). Further work in evaluating and improving these methods or developing new ones is desirable.

A common procedure for analyzing aquatic habitats is to take equal samples of green phytoplankton, ordinarily inseparably mixed with bacteria and zooplankton, and suspend during daylight hours in both transparent and blackened bottles at the same depth at which obtained. Photosynthesis of course does not occur in the blackened bottle, and there is a *loss* of oxygen, resulting from respiration, R, and decomposition, $E + D + W$. In the transparent bottle, photosynthesis occurs in addition to respiration and decomposition, bringing a production of carbohydrates. There will either be an *increase* in oxygen concentration, or the loss of oxygen will not be so great as in the blackened bottle. The difference in the final oxygen content of the two bottles will be a measure of *gross production:* I_Λ.

If the oxygen content of the water is measured at the beginning of the experiment, then the loss of oxygen in the blackened bottled subtracted from the difference in oxygen content of the two bottles at the end of the experiment will represent the net productivity. This net productivity may also be determined from the difference in the oxygen content of the transparent bottle between the beginning and the end. To obtain net production for an entire daily cycle, the consumption of oxygen for respiration and decomposition over 24 hours must be subtracted from the gross photosynthetic output during daylight hours. The use of black and white bottles for measuring productivity has been criticized because of a possible difference in the amount of oxygen utilized by bacteria in the two bottles (Nielsen 1952, Pratt and Berkson 1959), but the occurrence of a significant difference has been denied (Ryther 1956).

One may use the amount of carbon dioxide, rather than oxygen, absorbed during a period of time as a measure of photosynthesis, if correction is made for the carbon dioxide given off in respiration and decomposition. Changes in the amount of CO_2 in the water may be calculated from the differences in pH, the hydrogen-ion concentration (Verduin 1956). Net production during daylight hours may be measured by introducing a known amount of $C^{14}O_2$ into a volume of water where the amount of carbon dioxide already present is known. The amount of C^{14} absorbed by the phytoplankton can be accurately determined by use of counters applied to phytoplankton collected and dried at the end of the period. Then the proportion of the radio-active carbon absorbed to the amount introduced can be applied to the total CO_2 initially present to get the total amount absorbed (Nielsen 1952).

In fertile eutrophic lakes there is a continual sinking of dead organic material, derived chiefly from the plankton, from the epilimnion into the hypolimnion. The decomposition of this material absorbs oxygen from the hypolimnion and liberates CO_2 to produce a stagnation period during the summer months. The amount of oxygen deficit, or carbon dioxide increment, and the rate at which it forms can be measured to furnish a rough index of the lake's net productivity during the period between spring and autumn overturns (Hutchinson 1938, Ruttner 1953). Such estimates are in error by the amount of organic material brought in by streams, and they will vary in comparative usefulness depending on the volume ratio of hypolimnion to epilimnion (Hutchinson 1957).

Since nitrogen and phosphorus are metabolized more rapidly by plants in the manufacture of food during the growing season than they are regenerated from decomposing material, the rate and extent of the depletion of nitrates and phosphates in freely circulating bodies of water or in the epilimnion of stratified lakes serve as an index of the amount of organic matter produced (Hutchinson 1957). The rate of accumulation and regeneration of these substances in the hypolimnion from the dead organisms that sink into it may also be used to get an approximation of primary production (Waldichuk 1956). These measurements are not exact since they do not account for the repeated regeneration and reutilization of the substances in the photic zone during the season nor their transference to and storage in the bodies of animals.

The rate of photosynthesis varies in relation to the amount of chlorophyll present and to light intensity

(3.7 gC assimilated/hr/g chlorophyll in marine phytoplankton at light saturation) (Ryther and Yentsch 1957). The amount of chlorophyll in the plankton may be determined photometrically for all depths and calculated in terms of unit area of surface.

Measurement of productivity in flowing waters, such as streams, presents special problems. Most of the vegetation is benthic rather than planktonic. Determination of the rates of photosynthesis and oxygen use are best made by direct measurement of changes in the concentration of oxygen in the water as between day and night. Because of photosynthesis, there is a net increase in oxygen concentration during the daytime.

At night, photosynthesis ceases, but oxygen use continues, so the oxygen loss gives a measure of the rate of respiration and decomposition, and this presumably remains the same throughout the 24-hour daily cycle. Adding the average hourly night loss to the average hourly gain during the day and multiplying by the hours of daylight gives the total gross production for the 24-hour day. To obtain the net production for the entire day, the hourly loss at night must be multiplied by twenty-four, and subtracted from the total gross production. Corrections need to be made, however, for the greater diffusion of oxygen from the air into the water at night, when oxygen concentration in the water is lowered, than during the day, when it is higher. There may actually be diffusion of oxygen out of the water during the daytime when the photosynthetic rate is high. Additional corrections will also be necessary for import of oxygen from ground water and surface drainage and transportation of oxygen and carbon dioxide downstream by swift currents (Odum 1956, 1957).

On land, the annual net production of herbaceous plants that grow from seed or underground parts is approximately equivalent to the biomass of the vegetation at its maximum stage of growth, provided no appreciable amount has been lost or consumed by animals. Exclosures may be erected to prevent grazing by larger animals. The measurement of total production is inexact when the maximum standing crop occurs before the terminus of the growing season. The annual crop divided by the length of the growing season gives net productivity in terms of average daily increment. Daily productivity varies, however, with the stage of growth. At one site, the cumulative productivity of common cat-tail, from March 29 to July 2, when the largest crop was reached, averaged 8.17 grams carbon per square meter per day, but for a short period of maximum growth, May 4 to 28, was 23.48 (Penfound 1956). Seasonal biomass production of grasses is increased by a moderate amount of grazing, so in measuring primary productivity under natural conditions, the stimulating or inhibiting effect of animal consumption should be given proper evaluation.

The annual woody increment of trees and shrubs is proportional to the increase in diameter or width of growth rings. Mature trees may be felled, unit samples of branches, trunk, and roots dried and weighed, and the annual woody production since germination calculated (Ovington 1957). Attempts have been made to measure respiratory losses (Moller *et al.* 1954), and the annual production of foliage, seeds, acorns (Downs and McQuilken 1944), and nuts, but measurement methods need to be improved (Baldwin 1942).

Secondary production

When an animal species is represented by a low overwintering population, or an immature stage, the maximum biomass obtained in each generation is the approximate net production for that generation. However, this does not account for continued reproduction and growth of individuals after the maximum biomass of the population is attained, nor does it account for excreta, natural deaths, or the kill of predators. If the population of the species is maintained at a more or less uniform level throughout the year, then the mean biomass times the number of generations gives the net production, with again the exception of the factors mentioned above. Lindeman (1941) considered the phytoplankton turnover, or the production of a new generation, to occur every week from May through September and every two weeks through the rest of the year, the zooplankton to replace itself bi-weekly through the year, *Chaoborus* to have three generations per year; midge flies, two; and various aquatic beetles and bugs, one generation per year. Juday (1940) estimated that the mean standing crop of both phytoplankton and zooplankton replaced itself every two weeks throughout the year. To obtain gross productivity, the respiratory rates of these animals must also be measured.

Although shortcut methods may often be practicable, we need more accurate data, based on careful field observations and experiments, of food requirements, reproductive rates, growth rates, mortality, and so on, for individual species. The energy intake and requirements of individual species can often be measured under experimental conditions by presenting a known amount of food to one or several individuals and determining the amount consumed during a period of time. This is preferable to measuring the oxygen intake of resting animals. The influence of various environmental factors, size and age of the animals, density of populations, etc., on the food consumption can be ascertained and often also the proportion utilized for existence, growth, and other activities (ground animals, Bornebusch 1930; *Tubifex*, Ivlev 1939; grasshoppers, Smalley 1960; rotifers, Edmondson 1946; *Daphnia*, Richman 1958; fish, Ricker 1946, Gerking 1954; birds, Kendeigh 1949; mammals, Golley 1960). Occasionally, the amount of food required by a species can be determined under natural conditions. Beavers in Michigan cut 216 poplar trees, averaging 5.25 cm in diameter, per year per individual, in order to use the bark and cambium as food. With 3750 such trees per hectare (1500 per acre), one hectare (2.5 acres) could support a pair of beavers for about 9 years (Bradt 1938).

Mortality from non-predatory causes, D has rarely been measured. Combined rates of mortality from predatory and non-predatory causes may be computed from the size of populations of different age groups, or from recaptures of marked animals. If one knows the population of predators in an area and their average food requirements, non-predatory deaths may be calculated.

PRODUCTIVITY VALUES

The photosynthetic efficiency of plants in the use of solar radiation under natural conditions is very low, in terms of calories. Only a small percentage of the available radiation is actually absorbed and used. The growing season of plants is limited to only a portion of the year. Much radiation is reflected back from ground and water surfaces, or is absorbed by the ground or water or other non-living material, and later radiated back into the atmosphere. Some wavelengths of the spectrum are relatively ineffective in photosynthesis, and complete utilization of even the effective portion of the spectrum may be limited by temperature, available moisture, concentration of carbon dioxide, and amount of chlorophyll present.

The utilization of solar radiation received at Lake Mendota, Wisconsin, has been apportioned as follows (Juday 1940), last two figures corrected:

Melting of winter ice	2.9%
Annual heat budget of water	20.4
Annual heat budget of bottom	1.7
Evaporation	24.7
Reflection	24.0
Conduction, convection, radiation	25.9
Gross biological intake	0.4

The extent to which solar radiation is used depends considerably on the luxuriance of the vegetation. Deserts and short-grass plains have a gross primary productivity in dry weight of less than 0.5 g/m²/day; ocean, fresh-water communities, forests, and prairie from 0.5 to 5.0; coral reefs, estuaries, mineral springs, semiaquatic communities, and evergreen forests may produce up to 20 (Odum 1959). Miscellaneous data on secondary productivity are given in Chapters 5–9.

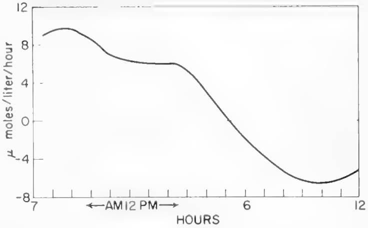


FIG. 14-3 **Rate of carbon dioxide removal, photosynthesis, at different times of day in western Lake Erie. Negative values at night mean that carbon dioxide is being added rather than removed (after Verduin 1957).**

In both freshwater (Verduin 1957) and the sea (Shimada 1958), maximum rates of photosynthesis occur in the early morning. Monthly variations show a relationship between photosynthesis and solar radiation, although it is observed that maximum photosynthesis occurs in June rather than in July for reasons that are not clear. Photosynthesis in the sea increases proportionally with light intensity until saturation intensity is attained (Ryther 1959).

The consumer trophic levels derive energy from transformers, T, as well as from green plants, P. The number or biomass of bacteria, fungi, saprovores, and detritus feeders depends on the amount of organic matter that accumulates from non-predatory deaths, D, excreta, E, and waste from predatory kills, W. The ratio between predatory consumption ($I_{\Delta+1}$) and E, D, W doubtless varies in different ecosystems. Adult lions in Africa kill, on an average, 20 kg (44 lb) of food per day, although they require only about half of this amount for existence. The unused

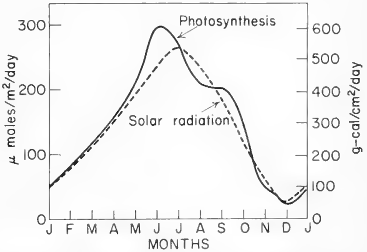


FIG. 14-4 **Rate of carbon dioxide removal, photosynthesis, in different months of the year in western Lake Erie correlated with intensity of solar radiation (after Verduin 1956a).**

portion of the kill supports a large population of bird, mammal, and invertebrate scavengers (Wright 1960). Harvestmen are predaceous on insects. Males waste nearly three-fourths of their prey, females about one-third. Of the food ingested, about 46 per cent of the energy is assimilated; the remainder is eliminated in the feces (Phillipson 1960).

From measurements made at Lake Beloe, natural mortality of *Tendipes plumosus* and other bottom fauna is reported to be twice predation (Ricker 1946). In a Massachusetts spring-pool, however, non-predatory deaths of another species of midge and of planarians amounted to one-fourth predation (Teal 1957). In a small Indiana lake, non-predatory deaths of bluegills amounted to 64 per cent of the average protein content of the standing crop during the year, but only 29 per cent of the total turnover of protein (Gerking 1954). In an Arctic lake not in trophic balance, the net productivity of the entire community, as shown by the accumulation of bottom deposits, averaged something less than 2 mg organic matter/cm^2/yr during the 6000 years since recession of the Pleistocene glacier, compared with 8 mg/cm^2/yr in a Connecticut lake during a comparable period of time (Livingstone *et al.* 1958).

The food chain or food web thus has a double base, although this useful energy, made available by the transformers, disappears as it recirculates into higher trophic levels. In balanced communities it is continuously replenished from the producers. Feeders on detritus and transformers are important both in aquatic habitats and in the soil. Mud flats on the California coast contain at least 39 g/m^3 dry weight of bacteria. Assuming that this biomass increases only 10 times per day, there would be 390 g/m^3 produced per day available for nourishment of the animal population (ZoBell and Feltham 1942).

Some of the most intensive and accurate studies of productivity are being carried out with phyto- and zooplankton in marine waters (Riley *et al.* 1949, Riley 1952, Deevey 1952). It is calculated that the total annual fixation of carbon by photosynthesis in Long Island Sound is about 470 g/m^2. Over half of this amount (265 mg) is used in the respiration of phytoplankton (56 per cent). Of the 205 g/m^2 net production, 26 per cent appears to be used by the macro-zooplankton, 43 per cent by the micro-zooplankton and bacteria, and 31 per cent by the benthic fauna and flora (Riley 1956). In the sea off Plymouth, England, it has been estimated (Harvey 1950) that the zooplankton is required to assimilate daily an equivalent of 4 per cent of its dry weight in vegetable matter just to meet respiratory needs, and 7–10 per cent for growth and to offset the amount consumed by other animals. Thus, of the energy intake at this level, approximately 30 per cent was used for respiration and 70 per cent for growth. On the other hand, pelagic fish, at a higher trophic level, used 90 per cent of assimilated food for respiration and converted only 10 per cent into body tissue.

Primary productivity of coral reefs is far greater on an areal basis, 1800–4200 grams carbon per square centimeter per year, than for most marine habitats, 28–912, but 4650 in an eelgrass bed off Florida. This high productivity is probably due to the luxuriant benthic algae on the reef platforms (Kohn and Helfrich 1957).

There are difficulties in obtaining accurate measurements of all factors for complete ecosystems. In his pioneer study of lakes, Lindeman (1942), and later also Dineen (1953), found that the percentage of gross energy intake that became transferred through predation to the next higher trophic level became progressively greater (Table 14-1). He also found that the percentage respiratory loss increased at each higher trophic level, and this has been confirmed for a terrestrial food chain involving plants, mice, and weasels (Golley 1960).

In a Montana reservoir, of the total gross production of the phytoplankton during the summer months, 17 per cent was dissipated in respiration, 4.5 per cent was converted into increase of phytoplankton, 71 per cent was consumed by macro-zooplankton, and 7.6 per cent utilized by bacteria, micro-zooplankton, and bottom fauna. The energy intake of the macro-zooplankton was divided 90 per cent for respiration and 10 per cent for population increase (Wright 1958). Effort should be made to investigate these relations more accurately, especially in ecosystems in which all trophic levels are in equilibrium.

Analyses of energy relations in complete ecosystems have been made by Odum and Odum (1955) for a coral reef community in the Pacific Ocean, and Odum (1957) and Teal (1957) for spring-fed streams and pools. These studies of flowing waters are complicated by the export of energy downstream with the current.

SUCCESSION

When trophic levels are in balance within an ecosystem, all the net production of one level is consumed by other levels, and there is neither a surplus nor a deficit in the total annual production. The biomass of annual plants, the foliage of perennial plants, and the populations of animals with one or more generations per year reach large size at the end of a growing season, far beyond possible immediate consumption by predatious animals at higher trophic levels. Yet this biomass does not accumulate. With

TABLE 14-1 Gross productivity (I_Λ) and efficiencies ($I_\Lambda + 1$)/ (I_Λ) in lakes and ponds.

Trophic level	Cedar Bog Lake, Minnesota Lindeman (1942)		Lake Mendota, Wisconsin Lindeman (1942)		Minnesota pond Dineen (1953)	
	g-cal/cm²/yr	Efficiency	g-cal/cm²/yr	Efficiency	g-cal/cm²/yr	Efficiency
Radiation	118,872	--	118,872	--	118,872	--
Producers	111.3	0.10	480	0.40%	49.9	0.04
Primary consumers	14.8	13.3	41.6	8.7	9.2	18.4
Secondary consumers	3.1	22.3	2.3	5.5	3.4	36.9
Tertiary consumers	---	--	0.3	13.0	---	--

the onset of winter these organisms die, and during the following season their dead bodies are worked over by the transformers so that the nutrients and surplus energy that they contain recirculate through the ecosystem until all energy is dissipated. Measurements of CO_2 exchange between plants and animals in western Lake Erie indicate that photosynthesis of the producers and respiration of the total aquatic community are approximately equal (Verduin 1956a). In a coral reef community in the Pacific Ocean, the balance in the ecosystem was reached at a level of energy exchange between producers and consumers of approximately 96 Kcal/m²/day (Odum and Odum 1955).

Such an equilibrium of energy exchanges is found only in some climax communities. It is more characteristic of seral communities for the total net production of all trophic levels to be greater than can be utilized during the course of the year. On the death and decomposition of these organisms, more organic matter is added to the substratum than can recirculate through the ecosystem. This increases the fertility of the soil. In marsh and bog areas this surplus accumulation of organic matter may be considerable. Fixation of nitrogen commonly exceeds denitrification in seral communities; there is absorption of minerals from underlying rock; and in ponds and lakes there is an influx of nutrients from the surrounding drainage basin. All these processes increase the carrying capacity of the habitat so that progressively larger standing crops can occur.

As fertility increases, changes also occur in the species composition of the community. Species that formerly were unable to occur because of low energy resources or other intolerable situations now find conditions favorable. Their invasion forces those resident species that cannot withstand competition to disappear. Oligotrophic lakes become eutrophic, and then marsh. Bog mats change to bog forests and eventually to the climax (Lindeman 1942). Sandy and rock habitats accumulate greater fertility with each succeeding stage. These changes persist until the climax stage is reached, where respiratory loss of energy balances the energy gain of the producers.

YIELD

In such applied fields of ecology as wildlife management, forestry, animal industry, and agriculture, the objective is to harvest the available net production for human benefit rather than to let it accumulate in the natural habitat or be used by other organisms. Crops of game animals, timber, or food are removed periodically to give a *yield*. Man is an animal consumer and removes the net production that would ordinarily be taken by the herbivore or carnivore plus whatever additional growth, *b*, occurs. If man takes his yield as a primary consumer he will obtain more energy in food per unit area than if this yield is obtained at higher trophic levels (Fig. 13-8d). Since excretory and respiratory losses and nonpredatory deaths bring an accumulative dissipation of energy at progressively higher trophic levels, the potential yield of game or food animals decreases the higher the position of the species in the trophic level of the community. The fewer the links present in the food chain, the greater the yield of game or fish. More plankton-eating cisco or herbivorous carp can be harvested in a given area than fish-eating bass, more muskrats than mink, and so on. In human economics, a land will support larger populations of people if they are content with eating rice, wheat, or corn than if they require the extravagance of beef, pork, and lamb.

Yield should never exceed net production, lest with reduction of the standing crop the productive potential become exhausted. On the other hand, human economics make it desirable to harvest the maximum yield that the ecosystem can supply without jeopardizing continued production year after year. The determination of *maximum sustained yield* or *optimum yield* in harmony with the productivity and maintenance of a steady state in the ecosystem is one of the most vital and complicated problems in applied ecology (Russell 1931). Maintenance of maximum productivity is also of importance to the organisms themselves as it permits attaining of large populations in each species.

There is a point in the growth curve of all populations at which the species is making the greatest use of the energy resources of the ecosystem and growing most rapidly without the depressing effects of intra- and inter-specific strife, predation, and disease becoming excessive. This is the point of inflection between the accelerating and inhibiting phases of the growth curve, the point at which the increment curve reaches its highest point. In most species investigated, this occurs at a population size approximately half that of the asymptote. Theoretically if the yield were so great that the population is kept below this point, total production would be reduced because of the small parent breeding stock that is left. If the population were allowed to go beyond this point of inflection, fewer offspring would be brought to maturity because of increased competition and other factors. It appears that the optimum yield should be such as to maintain the population continuously at this level, and thus balance maximum annual production (Hjort *et al.* 1933, Ketchum *et al.* 1949, Scott 1954). The problem of optimum yield of animal and plant species for human use seems to reduce, then, to determining the point of inflection in the population growth curve of the species concerned, keeping in mind that productive capacity varies between different species and habitats.

It may well be that balanced ecosystems have evolved under natural conditions so that predation is of such intensity as to maintain populations of prey at this level of maximum productivity. In a small pond in southern Michigan, in which no predatory fish were present, the benthos biomass increased two- or three-fold during the season to an upper asymptote, after which there was no net productivity. In another similar pond with fish present, the benthos biomass eaten by fish never reached this asymptote, and productivity was maintained continuously at such a high rate that the production during the growing season amounted to 17 times the standing crop (Hayne and Ball 1956).

Experimental work has not so far demonstrated a relation between optimum sustained yield and the point of inflection in the population growth curve. In laboratory cultures of flour beetles, productivity increased progressively with rates of exploitation that brought the surviving population far below the point of inflection (Watt 1955). With *Daphnia pulicaria*, maximum sustained yield occurred over a period of time when 90 per cent of newborn animals were removed at regular intervals (Slobodkin and Richman 1956). In experimental populations of guppy fish, the standing crop was reduced but the yield was greatest when the tri-weekly exploitation removed 30–40 per cent of the individuals, and the population mass was at one-third its asymptotic level. An exploitation rate of 75 per cent brought extinction of the population (Silliman and Gutsell 1957).

The lack of agreement between experimental results and theory may be due in part to the fact that the age distribution of the population after such harvests is not the same as under conditions of normal population growth. In an attempt to keep a natural population of Norway rats in Baltimore at the inflection point, it was found necessary to remove one and a half times as many animals as expected from an analysis of the growth curve. After a few months, however, the populations collapsed, probably because the average age of the females was reduced until they were too young to breed (Davis and Christian 1958).

Certainly much more study is required to determine practical means of estimating optimum yield, to understand the factors involved, and to put proper harvesting procedures into operation (Beverton and Holt 1957, Ricker 1958). In North America, several species have been exterminated through overuse; the passenger pigeon, for instance. On the other hand, there is evidence that in some localities the yield annually taken of fish, muskrats, and deer is not as great as populations of these species could support.

With organisms that have no specific adult size but continue growth throughout life, such as fish, yield should be calculated in terms of biomass. With these animals there is the additional problem of determining the minimum size limit of individuals which would provide the greatest sustained yield in weight for the population as a whole (Saila 1956, Ricker 1958).

In undisturbed ecosystems, non-predatory deaths and excreta at all trophic levels return both organic and inorganic nutrients to the substratum in amounts sufficient, when completely regenerated, to maintain the standing crop, and input of solar energy replaces respiratory losses. With the harvesting of plant and animal crops by man, however, there is removal of nitrogen, phosphorus, calcium, and many other minerals from the ecosystem that can be replaced only very slowly by natural processes. Artificial fertilization is ultimately necessary, therefore, when yields are taken. Artificial fertilization is often also desirable in early stages of succession, when the natural supply of nutrients in the soil or water is a limiting factor. Addition of nitrates and phosphates to sterile ponds usually results in a sudden bloom of phytoplankton. This bloom is later followed by increases in animals at the consumer levels and greater yields of fish.

SUMMARY

Energy, unlike nutrients, does not circulate indefinitely through the ecosystem. It is continuously dissipated to perform work and produce heat, and hence must be continuously replaced. The chief source of energy is solar radiation. This energy is captured by green plants in photosynthesis. Some of this energy is transferred to higher trophic levels through predation, but the amount that is transferred decreases at each higher trophic level in spite of the greater efficiency of predation, until none remains.

Gross productivity is the total energy intake per unit area and unit time at any trophic level. It is called primary productivity at the producer level and secondary productivity at the consumer levels. Gross energy intake minus respiratory losses is the net production.

Net production may be lost to the trophic level in excreta and dead animals, produce growth and increase of populations, or be transferred to a higher trophic level. Energy lost in excreta, non-predatory deaths, and wastage of predatory kills is utilized by the transformers to activate the nutrient cycles (Chapter 11), and some of it recirculates again through the ecosystem. A variety of methods are being developed to measure quantitatively the various uses and flow of energy through the ecosystem.

In seral stages, annual production exceeds total utilization so that accumulation of energy and nutrients results. This increases the fertility of the substratum. In climax communities total utilization may balance total production so that the ecosystem is at an equilibrium.

Productivity of populations is sustained at a faster rate over a longer time if the surplus production above a certain level is removed by predators, or man. Theoretically, the population level giving greatest absolute productivity should come at the point of inflection in the growth curve of the population, but disturbance of age ratios or other conditions may place the level of optimum sustained yield at some other point.

In this chapter we have been primarily concerned with basic principles and methods rather than with results. Data are not available to permit broad generalizations about the total energy relations within ecosystems. Much more work needs to be done. The need for a better understanding of productivity and yield has both theoretical and economic incentives and provides one of the main challenges in the future research of ecologists.

15

Reproductivity and Population Structure

In the previous chapter, we dealt with the productivity of communities; in this chapter, we will be concerned with the productivity of single species or *reproductivity.* The rate at which a species reproduces and the frequency of its population turnover can affect the speed with which it occupies new areas, becomes adapted to new niches, or evolves into new races. In order to analyze the population dynamics of a species, it is necessary to know its life history. This involves the stages in its life cycle, mortality rates of each stage, longevity, sex and age ratios, age at which individuals become sexually mature, fecundity, factors causing mortality, and so forth (Cole 1954). The proportion of different ages and sexes gives the population a definite structure. All these essential data may be conveniently summarized in the form of life-tables.

FECUNDITY

Species vary greatly in the characteristic number of generations, broods, or litters produced per year, and in the sizes of them. Protozoans often divide so rapidly that they produce a new generation every few hours. Plankton organisms, less fecund, may produce a new generation every few days. Many vertebrates breed but once a year; some large animals only once every two or three years. Several species of small birds and mammals have two or more broods per year. The female woodland white-footed mouse in Michigan may produce three litters between early April and early June, and two more between middle August and early October (Burt 1940). Under favorable environmental conditions, rodents may continue to breed throughout the winter so that their reproductive potential is enormous (Kalabukhov 1935).

Innate capacity

The maximum size of a litter is determined by the physiological and morphological characteristics of the species. With mammals which produce viviparous young, the size of the uterus and body cavity as well as the number of mammary glands for suckling the young after birth are limiting factors. With birds there is a limit on the number of eggs that one individual can cover and successfully incubate. In species that do not take care of their eggs after laying, the number produced may be limited only by the energy resources of the parent. This is indicated in part by the inverse relation between number of eggs produced and their average size (Lack 1954).

Parental care

The number of eggs or young produced per litter is correlated inversely with the amount of attention that they require. When parental care is altogether lacking, invertebrates may lay 1,000 to 500,000,000 eggs at one maturation; where there is some protection afforded by brood pouches, 100 to 1,000 eggs may be laid; with a high degree of brood protection, 10, or less, to 100 eggs may be laid. Mammals seldom have more than a dozen young in a single litter and, in larger species, usually only one. Characteristic clutch size among birds varies from 1 to 15; rarely, 20.

There is a limit on the size of the brood or litter that adult warm-blooded animals can successfully feed and raise to maturity. There is no advantage, for instance, for starlings to have broods larger than five (Table 15-1). In larger broods, each individual receives less food, and hence has less vigor and weight on leaving the nest. Mortality increases either before fledging or in immediately subsequent months. The larger broods raised during years of abundance further indicate that food is a critical factor (Lack *et al.* 1957). The variability in clutch and litter size for most species allows them to take advantage of temporarily improved conditions. There is some evidence that in the tropics the number of young raised may be limited not by food but by increased predation on the larger sized broods (Skutch 1949).

Weather

Clutches laid by birds during periods of hot weather are usually smaller than those laid when temperature is moderate (Kendeigh 1941). Clutches laid by related species in temperate latitudes tend to be larger than those laid in the tropics (Moreau 1944, Lack 1947–48). The fecundity of white-tailed deer is higher with good forage than with poor forage (Cheatum and Severinghaus 1950). Reproduction is generally more successful after periods of high mortality than during years of abundance.

The mobilization of energy, usually within a definite period of time, is a limiting factor in warm-blooded organisms. The house wren, for example, lays 5, 6, or 7 eggs per clutch, the total weight of which is 7.0, 8.4, or 9.8 g respectively; yet the adult female herself weighs only 11.5 g. It is estimated that under average conditions about one-third of the daily energy intake of the bird, above its needs for existence, is deposited in the eggs being produced. Any appreciable change in temperature or rate of feeding thus affects the size of the egg, the number laid, or whether laying is undertaken at all (Kendeigh 1941).

TABLE 15-1 **Reproductivity in the starling in relation to litter size (from Lack 1948).**

Brood size	Number banded	Per cent recovered after 3 months	Brood size × per cent recovered
1	65	0	0
2	328	1.83	3.7
3	1,278	2.03	6.1
4	3,956	2.07	8.3
5	6,175	2.07	10.4
6	3,156	1.68	10.1
7	651	1.54	10.2
8	120	0.83	
9	18	0	0
10	10	0	0

Among invertebrates, clutch size also varies under different conditions and in different localities. The copepod *Eudiaptomus gracilis* commonly carries 11 eggs in April, 3 in early August, 9 in early November, and 5 or 6 over the winter. There is a decrease between spring and summer in the number of eggs carried in its brood pouch by the cladoceran *Daphnia*. *Diaptomus siciloides* carries but 4 eggs in mountain lakes of California, as many as 18 in the Illinois River. These variations appear to be correlated with differences in temperature and food supply (Hutchinson 1951).

Death rate

Death rates vary between species and are correlated with rates of reproduction (Table 15-2). The death rate of a species is influenced by a number of factors, but of fundamental importance is the number of young that are born in relation to the carrying capacity of the habitat. When more young are born than the habitat can support, the surplus must either die or leave the area. When populations are stabilized at a constant level, the death rate must fluctuate with the birth rate. Evolutionary adaptation tends to lower the frequency at which the population replaces itself and to raise reproduction to the highest rate compatible with the energy resources both of the species (Table 15-1) and of the habitat (Lack 1954).

SURVIVAL OF YOUNG

Success in raising young depends not only on the ability of the adults to care for the young, but also on the vitality of the embryo and on the chance

TABLE 15-2 **Relation of reproductive to mortality rates per year (Lack 1954).**

A. Local differences in same or related species.

Species and locality	Young produced per pair	Adult mortality rate
Starling		
Switzerland	5.8	63%
England	4.7	52
Blue tit		
Britain	11.6	73
Spain and Portugal	6	41
Canary Isles	4.3	36
Wall lizard		
Italian mainland	24	40
Italian islands	11	20
California fence lizard		
Plains	8.5	80
Mountains	3.3	30

B. Species differences in same locality

White-footed mice in California	Young produced per pair	Average further life of half-grown young in days
Peromyscus californicus	6.2	275
Peromyscus truei	11.7	190
Peromyscus maniculatus	20.0	152

destruction of nests, eggs, or young by storms, wind, floods, predators, accidents, and desertion of the parents. Considerable data are available in this connection with birds.

Nest failures in birds are most frequent early in the nesting cycle and decrease progressively as follows as nesting proceeds: 2.4 per cent per day during nest-building, 2.2 per cent per day during egg-laying, 1.2 per cent per day during incubation, and 0.5 per cent per day while the young are in the nest (Kendeigh 1942). Location of the nest is a factor in the successful raising of young (Table 15-3).

The relatively low percentage of nests that produce young successfully in many species is not a true index of annual reproductivity, since birds commonly make a second or even a third attempt if earlier nestings were failures. The ring-necked pheasant in Iowa has maximum nesting success averages of only 41 per cent; yet, before the season is over, by making repeated efforts, between 70 and 80 per cent of the hens are successful in raising broods. Full reproductive success is not assured, however, in raising the young to the stage of leaving the nest. In the study of the ring-necked pheasant, the average number of young hatched in successful nests was 8.7; after 1 to 3 weeks the average size of the brood was reduced to 6.7; after 4 to 5 weeks to 5.9; after 6 to 7 weeks to 5.3; and after 8 to 10 weeks to only 4.9 (Errington and Hamerstrom 1937).

TABLE 15-3 **Correlation between type of nest or nest location in birds and percentage of fledglings raised from eggs laid (Kalmbach 1939, Nice in Spector 1956: 93–94).**

Category	Number of studies	Per cent successful
Precocial gallinaceous species nesting on the ground	17	44
Open nests of altricial species	27	46
Waterfowl in aquatic habitats	22	60
Hole-nesting altricial species	32	66

LIFE TABLES

Species differ widely in the number of young produced each year, in the average age to which they live, and in their average rate of mortality. When sufficient facts about a species are known, a *life table* that tabulates the vital statistics of mortality and life-expectancy for each age group in the population may be formulated (Table 15-4, Pearl 1923). Age is usually represented by the symbol x and is some convenient fraction of a species' mean life span, such as a year or stage of development. The life table is set up on the basis of an initial cohort of 100, 1000, or 100,000 individuals; and the number living to the beginning of each successive age interval is symbolized as l_x. Plotting these data gives a *survivorship curve* for the species. The number dying within each age interval is designated as d_x and gives a *mortality curve*. The rate of mortality during each age interval is commonly expressed as the percentage of the number at the beginning of the interval $100(d_x/l_x)$ and as indicated as q_x. Survival rate is the difference between the mortality rate and one hundred per cent $(100 - q_x)$ and is expressed as s_x (Hickey 1952). Life expectancy (e_x) is the mean time that elapses between any specified age and the time of death of all animals in the age group.

Life tables are also useful for computing the average longevity of a population, for showing the age composition of a population, for indicating critical stages in the life-cycle at which mortality is high, for showing differences between species, for showing the success of the same species in different communities, for furnishing information of value in game and fish exploitation (yield), and in control of pests (Quick, in Mosby 1960).

Information for constructing life tables may be obtained from a knowledge of age at death of a random but adequate sample of the population; informa-

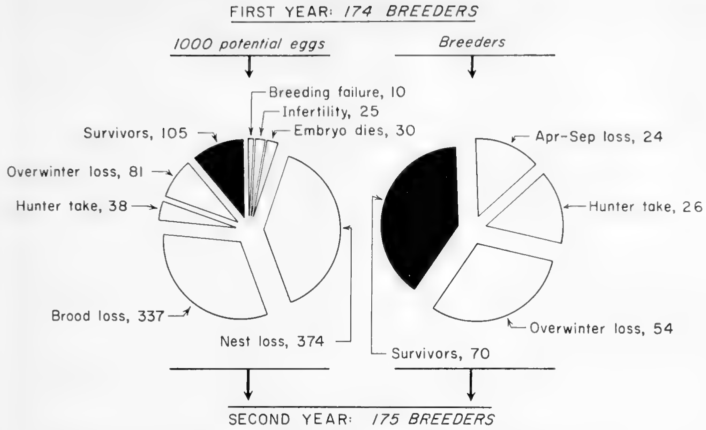


FIG. 15-1 Average life equation of a stabilized ruffed grouse population in New York State (Bump *et al.* 1947).

tion on the age ratios of the living population, provided it is stabilized; or from data on a single cohort, adequately identified, followed throughout its life's span (Farner 1955).

Curves of survival plotted from life tables may be of three types (Pearl and Miner 1935, Deevey 1947). In type I, a cohort finds environmental conditions ideal; all members born at the same time, live out the full physiological life span characteristic of the species, and all die at about the same time. In type II, the rate of mortality is fairly constant at all age groups so that there is a more or less uniform percentage decrease in the number that survive. Type III shows extremely heavy mortality early in life, but

x	l_x	Factor responsible for d_x	d_x		q_x	
Eggs	1000	Parasites	17		2(-)	
		Predators	86		9(-)	
		Others	6		1(-)	
		Totals		109		11
Instar I	891	Dispersal, etc.		428		48
Hibernacula	463	Winter		79		17
Instar II	384	Dispersal		242		63
Instars III - VI	142	Parasites	51		36	
		Disease	3		2	
		Birds	20		14	
		Others	61		43	
		Totals		135		95
Pupae	7	Parasites	0.6		8	
		Predators	0.7		10	
		Others	1.3		18	
		Totals		2.6		36
Moths	4.3	Totals for generation		995.7		99.5

TABLE 15-4 Life table for the 1952–53 generation of the spruce budworm in New Brunswick, Canada (after Morris and Miller 1954).

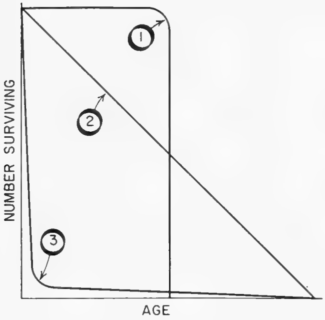


FIG. 15-2 Schematic representation of different types of survivorship curves. The vertical scale may be graduated, arithmetically or logarithmically. If graduated logarithmically, the slope of the line will show the *rate* of change; a straight line is indicative of a mortality rate equal at all ages (Deevey 1947).

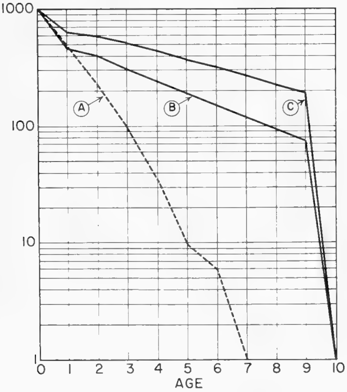


FIG. 15-3 Survivorship curves for (A) the American robin, zero age at November 1 (Farner 1945a), and for female mule deer (males only are hunted) in (B) shrubland and (C) chaparral in California (Taber and Dasmann 1957).

those few individuals that survive have a high life expectation thereafter. Types I and especially III are not often observed under natural conditions. Nearly all survival curves so far obtained are of type II, although they seldom approach a straight line. Probably more curves approaching type III would be found if data could be secured beginning with the fertilized egg, as mortality in early life is often high, especially in aquatic species that spawn many eggs. Evolution of parental care in higher animals gives greater protection and efficiency in raising the young. This evolutionary trend should change survivorship curves from type III towards type I.

SEX RATIO AND MATING BEHAVIOR

The *primary* sex ratio at the time the eggs are fertilized should be approximately 50 ♂♂ : 50 ♀♀ in most species, although it has seldom been measured. This ratio may be displaced in one direction or the other by differential mortality of the two sexes during the period of growth, become manifest in the *secondary* sex ratio at the time of hatching or birth, and even more pronounced in the *tertiary* sex ratio of the adults (Mayr 1939). Protozoa, some coelenterates and flatworms are potentially immortal. Recognition of sex and age in living animals is often difficult, although criteria have been worked out for many species (Taber, in Mosby 1960).

The sex ratio of the adults is especially important in understanding mating relations and reproduction potentials. For instance, the adult sex ratio in ducks is often in the neighborhood of 60 ♂♂ : 40 ♀♀ (Johnsgard and Buss 1956). Since these birds are largely monogamous under natural conditions, a population of 100,000 birds does not furnish 50,000 breeding pairs but only 40,000. In polygynous species, such as pheasants, some grouse, turkeys, deer, and fur seals, breeding potential is probably not diminished under natural conditions if there are two, three, or even ten times as many females as males. On the other hand, polyandry has become characteristic of some tinamous and bustards, and this is correlated with a preponderance of males (Kendeigh 1952).

The tertiary sex ratio is not a constant factor. In the California quail it was found to vary monthly from 51 ♂♂ : 49 ♀♀ in early autumn to 53 ♂♂ : 47 ♀♀ during winter to 56 ♂♂ : 44 ♀♀ in June (Emlen 1940). Game birds that are monogamous or only slightly polygynous in the wild may become highly polygynous after hunting seasons or in captivity, situations in which there is a preponderance of females over males. Yearly variations in the ratio of males to females in the house wren are correlated inversely with tendencies toward polygyny, and positively with tendencies toward polyandry (Kendeigh and Baldwin 1937). Mating behavior is therefore to some extent adaptable in order to compensate for lopsided sex ratios and to maintain high reproductive capacity.

BREEDING AGE

The age at which young animals first attain the ability for reproduction affects the reproductive capacity and rate of growth of populations. Planktonic entomostracans are sexually mature in a few days; insects, often in a few weeks. Among birds, a tropical sparrow is known to reach full reproductive level in six to eight months (Miller 1959). Small non-tropical song birds commonly nest during spring and summer of the year following that in which they hatched, but banding of nestling house wrens indicated that 12 to 18 per cent failed to do so until the second or third year (Kendeigh and Baldwin 1937). Upland game birds probably nest as yearlings; geese and wild turkeys do not nest until they are two years old; common terns, commonly only after three years. Some lizards and snakes require two to three years to reach sexual maturity; turtles much longer.

Females of the European voles may mate at 13 days, even before they are weaned, and give birth to their first litter when only 33 days old (Frank 1957). Woodland white-footed mice born in spring may produce young late in summer; but most small and medium-sized mammals do not breed until one year old. Beaver, wolf, lion, and whale breed when two years old. Big game mammals, such as deer, bison, and bear, reach maturity only after three years. The elephant is said to require 8–16 years, and the rhinoceros 20 years (Spector 1956: 115, 119).

NON-BREEDING POPULATIONS

Although the breeding population of a particular mammal, bird, or other animal is the only fraction of the total population of a species concerned with its reproductivity, there is often present in an area a substantial, though inconspicuous, non-breeding population that must be considered in any understanding of community dynamics (Zimmerman 1932). In a 16-hectare (40 acre) tract of spruce-fir forest in northern Maine, there were, in 1950, 308 individuals (154 pairs) of nesting birds present during the first half of June. By the use of fire-arms the population was reduced to 21 per cent by June 21, and held at this level until July 11. This involved a removal of not only 228 breeding birds plus 49 of uncertain status, but also of 250 new birds appearing to take over the territories and places of the nesting birds that were removed (Hensley and Cope 1951). This surprisingly high non-breeding reserve may not be typical of all species of birds (Bendell 1955). Other studies have shown that the non-breeding population, especially of birds, consists principally of young animals that have been slow to reach sexual maturity, of surplus individuals of either sex in monogamous species, and of adults which, for one reason or another, have lacked reproductive vigor or have been unsuccessful in establishing proper breeding relations.

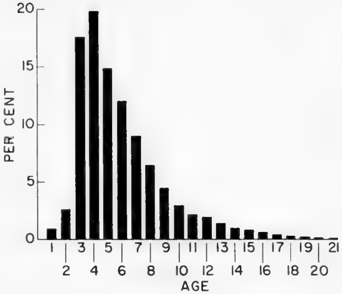


FIG. 15-4 **Age composition of a breeding population of common terns (Austin and Austin Jr. 1956).**

LONGEVITY AND MORTALITY RATE

When protected in captivity, animals are capable of living surprisingly long periods (Spector 1956: 182). Definite physiological limits of life are characteristic of each species and are occasionally realized under natural conditions (Cooke 1942), but invariably the potential longevity of a species is many times greater than the mean longevity actually attained by wild populations (Bourlière 1946).

Finding the mean length of life for wild populations requires the working out of life tables, accomplished for only a few species. In birds older than the juvenile stage, it commonly varies from one to five years (Farner 1955), although in some large species it is considerably longer. In rodents, usually not more than 6 per cent of the population reaches one year of age (Blair 1953). The larger Dall mountain sheep has a mean length of life of 7.09 years. Adult barnacles have a mean life of 12.1 months (Deevey 1947), and different species of rotifers variously from 3 to 35 days (Edmondson 1946). Longevity may often differ between the sexes. Thus in the male flour

TABLE 15-5 Relation between annual mortality and longevity in birds (after Lack 1951).

Bird species	Average longevity, years	Average annual mortality, per cent
Starling	1.1	63
California quail	1.5	50
Song sparrow	1.7	45
Lapwing	2.0	40
Barn swallow	2.8	30
European swift	5.1	18

beetle, *Tribolium madens,* it is 199 days, in the female, 242 days; in the male *T. confusum,* 178 days and in the female, 196 days (Park 1945).

The rate of mortality in many species varies from one age level to another; thus, a mean death rate has only general significance. In birds, however, the death rate is nearly constant once they become adult, and it is then apparent that it varies inversely with adult longevity (Table 15-5). In adult penguins, pelicans, shorebirds, gulls, and swifts, the annual mortality rate is commonly between 12 and 30 per cent; in herons, hawks, and owls it is about 30 per cent; in ducks, doves, and song birds it is between 40 and 68 per cent, while in gallinaceous birds it is the highest, 60 to 80 per cent. These rates for game species include mortalities from hunting (Farner 1955).

TABLE 15-6 Theoretical age composition of stabilized populations with three different survival rates, assuming that the rate of mortality is the same for each age group. The figures are the percentage or number of animals (lx) in each age class in a population of 100 (from Nice 1937).

Age (x) in time intervals	Survival rate		
	75	50	25
1	25	50	75
2	19	25	19
3	14	13	5
4	11	6	1
5	8	3	0
6	6	2	0
7	5	1	0
8	4	0	0
9	3	0	0
10	2	0	0
11	1	0	0
12	1	0	0
13	1	0	0
Totals	100	100	100
Average lifespan	3.8	2.0	1.3

AGE RATIOS

The life-table gives the number or percentage of individuals in a brood or litter surviving to the next age level. From such data, as well as by occasional direct observation, it is possible to determine the age structure of a population at any one time. Table 15-6 gives the percentage of each age class in populations of adults having three different mean survival rates in all age classes. It is at once apparent that the number of age classes in a population is greater when survival rates are high than when they are low. It is also evident that there is less difference between number of individuals in succeeding age classes when survival rate is high than when it is low.

The exact age of the sexually mature adult is usually at best difficult to determine unless one can band or mark the young when they first appear, or unless there are growth rings, such as in the scales and otoliths of fish and in the shells of clams, or other criteria of age that can be used. Immature animals are often distinguishable from adults (Thompson 1958) so that adult-young ratios are usually obtainable, and often yield important information. The proportion of immature to adults is highest at the end of the breeding season, and then usually declines until the beginning of the next period of reproduction, because of the higher mortality rate of the young compared with that of adults. In the California quail, the ratio of immature to adults in October was 70:30. During the following months the ratio progressively decreased as follows: November and December, 62:38; January, 58:42; February, 56:44; March, 54:46; and the breeding season, April to June, 50:50 (Emlen 1940).

Age ratio is of practical value in wildlife management (Alexander 1958). A low ratio of immature to adults indicates a poor reproductive season and should caution against excessive take or yield, as the population is declining. The precarious state of the whooping crane is indicated in that the entire population of the species wintering on the Aransas Wildlife Refuge in Texas from 1949 to 1953 has consisted of only 3 to 4 young birds each year compared to 21 to 34 adults annually present. Low ratios of young to adults also occur with overpopulation, but overpopulation is usually easily detected. Bag limits may ordinarily be increased if the ratio of young remains consistently high. Here again, however, high ratios of immature to adults are characteristic when populations are recovering from catastrophes. When a population of rusty lizards in Texas was reduced by drought in 1954, the percentage of one-year-olds changed from 63 in the relatively stabilized population to 85 in the subsequent expanding population (Blair 1957). When a population is stabilized, the

Species	Intrinsic growth rate per day *(r)*	Average longevity in days *T*	*r·T*	Net production rate
Short-tailed vole	0.0125	141.75	1.772	5.90
Norway rat	0.0147	217.57	3.198	25.66
Flour beetle	0.101	55.6	5.616	275.00
Rice weevil	0.109	43.4	4.731	113.56
Human louse	0.111	30.92	3.432	30.93

TABLE 15-7 **Comparison of intrinsic growth rates and other data on the populations of different species (compiled from various sources by Evans and Smith 1952).**

young and middle-aged classes are more or less equal in numbers, the decline in size occurring progressively throughout life.

ADAPTATION TO NICHE

In the stabilized population of any species, whatever the number of eggs or young produced per pair of adults, the number of offspring reaching reproductive status can never be greater than two in sexual forms, which is the number required to replace the parents on their death. With each new generation there is, therefore, a *population turnover,* with newly born individuals replacing the adults that die. In a stabilized population, the rate of increase of a population through the course of several reproductive cycles must equal the death-rate, so that the value of one factor is also a measure of the other. Either factor is indicative both of the rate of population turnover and of the intensity of environmental resistance.

The intrinsic growth rates for populations of several species under optimum conditions is given in Table 15-7 by the factor r, which represents the mean rate of increase per individual per day. There is a general inverse relation between growth rate and longevity, T. However, if growth rate were dependent only on the longevity of the species, then rT would equal a constant. Obviously this is not true. It appears that different growth rates may correlate with various intensities of environmental resistance in the different habitats occupied by different species. If there were a habitat offering no environmental resistance, and all offspring therefore survived, then a female would need to produce only one female offspring to replace herself when she died. This would be the net production rate of Table 15-7. Actually, the number of female offspring that must be produced to offset mortality caused by the environment is always more than one, attesting the rigor of the natural environment in spite of the species' adaptations for life in it. The method used in calculating the net production rate, $\sum l_x \cdot m_x$, the sum of number alive at age x, l, times rate of reproduction at age x, m, for all age groups, is explained by Evans and Smith (1952). It is interesting that as a result of long evolutionary processes, the low net reproduction rates for the herbivorous vole, the omnivorous rat, and the parasitic human louse indicate that they are in much better balance with what to them are optimum environments than are the graminivorous flour beetle and rice weevil. The vole and rat are viviparous; the other three, oviparous. It would be very interesting to have similar data on other species to show the degree to which adjustments to particular environments have become perfected and the reproductive strain imposed upon related species for occupying different habitats.

SUMMARY

Reproductivity is the rate at which a species reproduces. The number of offspring raised to maturity per unit of time is generally characteristic of a species, and varies with fecundity and survival of the young. Fecundity depends upon the morpho-

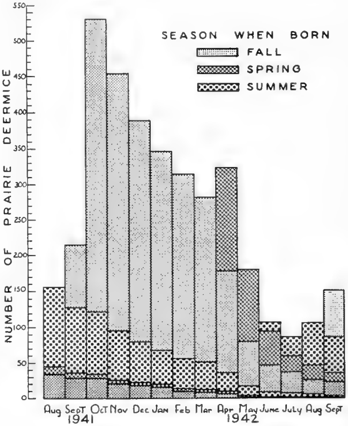


FIG. 15-5 **Monthly changes in the density and age-structure of a population of prairie deer mice in Michigan. As one population dies out a new one takes its place, and there is a population turnover (Howard 1949).**

logical and physiological capacities of the species, the amount of parental care that the offspring receives, and weather conditions. Death rates correlate directly with the number of young produced. Reproduction cannot be considered successful unless the young reach sexual maturity.

Life tables tabulate, in condensed form, the vital statistics of survival and mortality by time intervals. They provide essential data for calculating longevity and age composition of populations. Survivorship curves show three characteristic survival patterns, but most populations exhibit a relatively high death rate early in life and a lower, more constant death rate thereafter.

Sex ratios are often correlated with mating behavior. The age of full reproductive maturity varies widely between species. Young birds, surplus adults of either sex, and birds unsuccessful in establishing breeding relations sometimes constitute a relatively large non-breeding population in addition to the more conspicuous breeding one. Perhaps this is true also for other animals, but evidence is scanty.

Ratios of young animals to adults often indicate whether a population is expanding, contracting, or is stabilized. In stabilized populations the number of offspring reaching reproductive maturity can never be greater or less than the number of adults themselves. The number of young that must be produced to permit such a population turnover gives a measure of the rigor of the environment, and how well adapted a species is to its niche.

16

Ecological Processes and Community Dynamics:

Regulation of Population Size

It is seldom possible to measure the total worldwide population of any species, unless it is one of restricted distribution and is readily accessible to censusing. The gannet, a sea bird, nests in only 22 island and sea cliff colonies. From 1819 to 1929 the annual population level of this species was about 340,000 birds. Because of molestation by man, the population dropped to about 106,000 in 1894, but, after some protection of the colonies was established, rose to about 165,600 in 1939 (Fisher and Vevers 1944). For most species population can only be expressed in terms of number per unit area (population density).

The abundance of a species in a geographic region is termed the *average* or *regional density* of it. A region, however, usually includes unfavorable habitats, from which the species is absent, as well as suitable niches in which it is populous. The abundance of a species within its niche is called its *economic* or *niche density,* never less and almost always higher than its regional density.

The regional density of a species depends on the prevalence of its favored niche in the area and the density which the species maintains within its niche. Muskrats may be very numerous in a marsh, but if there are few marshes in the region, their average density will be low. We will here be primarily concerned with why an animal species attains a particular level of abundance within its niche.

Species obviously vary in the level of abundance that they attain. Springtails may occur in hundreds per square meter, large mature snails as one per square meter, and white-footed mice as only one individual per 400 m^2. Principles involved in understanding these differences in population levels are the size classes of the animals and their position in food chains, pyramids, and trophic levels.

The population of any one species may be said to be *stabilized* when it fluctuates in an irregular but restricted manner from the mean. If environmental conditions temporarily become unusually favorable or unfavorable, population size may fluctuate accordingly, but with stabilization there is always the tendency to revert again to the average level when the unusual conditions have disappeared. The dynamic resiliency of populations is evident in the high rates of increase that occur with the beginning of recovery after a population has been depleted, and the progressive diminution in the rate of increase as the population approaches its characteristic level. Although at the beginning of the population growth curve, increasing numbers may sometimes bring a cooperative effect evident in increased rates of growth and reproduction (Odum and Allee 1954), cooperation is soon replaced by disoperation in that the reproductive rate then varies inversely and the mortality rate varies directly with the density of the population in

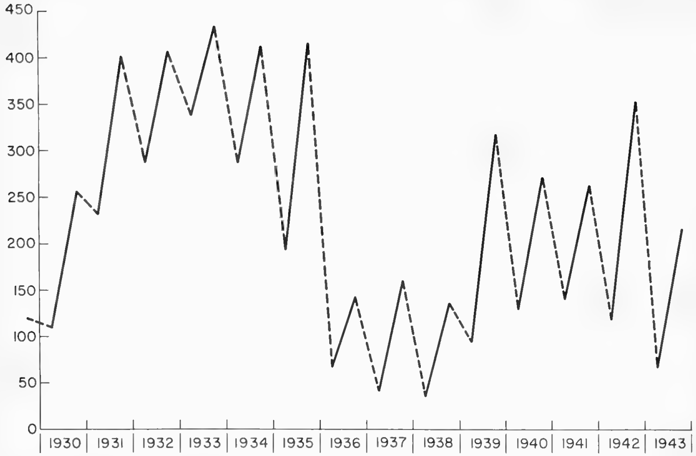


FIG. 16-1 **Seasonal and yearly changes in the population of bobwhite on 1800 hectares (4500 acres) in Wisconsin. The solid line shows the net reproductive increase each year from spring to autumn; the dashed line, the mortality over winter (from Errington 1945).**

terms of mature offspring raised. As a necessary corollary, the mean longevity of a population also varies inversely with its density (Davis 1945).

DENSITY-STABILIZING FACTORS

The intrinsic growth rate of a population, is limited to the early stages in the sigmoid growth curve of the population. Very soon, environmental resistance restrains the rate of growth more and more sharply until, at the asymptote, the environmental resistance equals the biotic or reproductive potential and the population is stabilized.

We need now to take a closer look at the processes that produce these effects and determine the levels at which populations reach their asymptotes. These processes may be conveniently divided into two groups; those that are density-stabilizing, and those that are density-limiting. The first group of factors are biotic in that they depend on coactions between individuals within the same population or between populations of different species. Limiting factors, which determine the level at which populations become stabilized, are basically physical and vary in intensity because of influences outside or largely independent of the population or community. All factors taken together are commonly considered to constitute the environmental resistance, a convenient if not entirely accurate term.

Density-dependent factors (Howard and Fiske 1911: p. 107, Nicholson 1933, 1954, Smith 1935, Solomon 1949, Ricker 1954) are those that vary in the intensity of their action with the size or density of the population, but not all density-dependent factors are density-stabilizing. Only if the *percentage* of a prey species destroyed by predators, for instance, increases with the size of the population and decreases as the population declines, is natural control preventing indefinite population expansion, yet preventing extinction, too. This action then tends to *stabilize* the population size (Table 16-1). If, however, the percentage of prey taken remains approximately the same at all population levels the effect is *proportional*. If the percentage of prey or host affected actually decreases as the population increases, the effect is *inverse*. This happens occasionally (Tothill 1922). Obviously the proportional or inverse effects of a factor cannot inhibit the continuous expansion of a population. Complete quantitative data are required in order to classify and evaluate the effect of any factor. The density-dependent factors that will be considered in respect to their stabilizing effect on population size are competition, reproductivity, predation, emigra-

TABLE 16-1 Different effects of density-dependent factors on the size of animal populations, assuming number surviving is composed equally of males and females, and each pair gives birth to six young. The size of the prey population each generation includes both the young and adults. Thus, of 3 individuals surviving, the number of young produced (1.5 × 6 = 9) plus the 3 adults totals 12.

Factor	Generation 1	2	3	4	5	6	7
Stabilizing (assuming an increase of 10 per cent mortality each generation until the population becomes stabilized)							
Size of prey population	4	12	32	72	128	180	180
Number destroyed	1	4	14	40	83	135	135
Percent mortality	25	35	45	55	65	75	75
Number surviving	3	8	18	32	45	45	45
Proportional (assuming a constant rate of mortality)							
Size of prey population	4	12	36	108	324	972	2,916
Number destroyed	1	3	9	27	81	243	729
Percent mortality	25	25	25	25	25	25	25
Number surviving	3	9	27	81	243	729	2,187
Inverse (assuming a decrease of 2.5 per cent mortality each generation)							
Size of prey population	4	12	36	116	384	1,304	4,564
Number destroyed	1	3	7	20	58	163	456
Percent mortality	25	22.5	20	17.5	15	12.5	10
Number surviving	3	9	29	96	326	1,141	4,108

tion, and disease. The effect of density-dependent factors has been much studied from a mathematical viewpoint, but the present approach will be largely introductory and non-mathematical.

Competition

The definition and basic principles of competition have already been considered. We are here concerned with how competition helps to stabilize a population at a particular level. In this respect competition is primarily for space, cover, and food.

Every terrestrial green plant requires a volume of soil for its root system and a volume of air in which it can display its foliage to receive solar radiation. In a dense forest the individual tree grows tall because of competition with its neighbors. Trees unable to keep up with this competition become overtopped by other trees and, lacking sunlight, die. Sessile marine animals, such as corals, mussels, and barnacles, may crowd into close physical contact, even growing on top of one another, but there is undoubtedly a limit to the number that can survive and carry on normal activities in an area of restricted size.

Competition for space is well demonstrated in those species that defend territories; birds, for instance. With increase in number of birds in an area there is, at first, some accommodation as the size of territories varies inversely with the size of the popula-

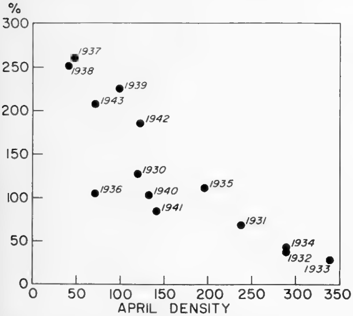


FIG. 16-2 Per cent yearly increase in population size of bobwhite in relation to April densities (Errington 1945).

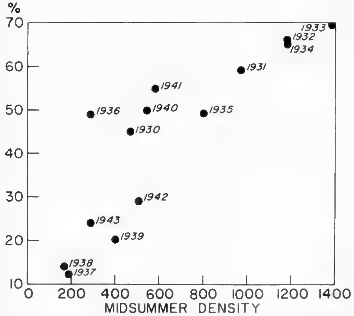


FIG. 16-3 Per cent loss rates of bobwhite from midsummer to early winter in relation to midsummer densities (Errington 1945).

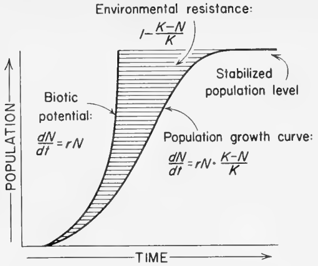


FIG. 16-4 **Relation between biotic potential and environmental resistance in determining the population level attained by a species.**

tion and amount of competition involved. With 7 pairs of bay-breasted warblers on a 10-hectare plot (25 acres), the average size of territories was 3157 m^2 (0.78 acre). On another plot with 18 pairs the territories averaged 1740 m^2 (0.43 acre); on a plot with 25 pairs, 1497 m^2 (0.37 acre); and on a plot with 42 pairs, only 1174 m^2 (0.29 acre) (Kendeigh 1947). With decrease in size of territories, however, comes intensification of competitive singing, scolding, chasing, and fighting. On a 6-hectare (15 acre) area there were no instances of destruction of nests, eggs, or young in the six years through which the population of male house wrens did not exceed 11, but during the 13 years when such acts of destruction did occur, the male population had ranged from 11 to 16 (Kendeigh 1941b). A pair of birds requires a specific minimum territory for successful nesting. When an area becomes saturated with territories compressed to this limited size, disturbances occur in nesting and other individuals attempting to invade the area are forced to go elsewhere. Thus the population density becomes limited by the space available. On the other hand, with species possessing only undefended home ranges, competition for space is of less critical importance in regulating population size.

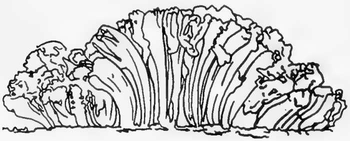


FIG. 16-5 **Competition for space by barnacles; a median longitudinal section through a hummock (after Barnes and Powell 1950).**

Related to the competition for space is the competition for the most favorable portions of the niche, those offering maximum food and protection. In Holland, three species of tits (*Parus major, P. coeruleus, P. ater*) prefer mixed woods to pine woods. In years when they are scarce, the species are mostly confined to the mixed woods; when populations increase in size, they do so first in the mixed woods until the birds become intolerant of further crowding. Then they spill over into pine woods to nest but never become as abundant (Kluijver and Tinbergen 1953).

Food supply is an important determinant of the carrying capacity of any area. When large numbers of animals are present there is, of course, less food available to any one than when there are few individuals present. Competition for food therefore becomes intense in large populations. Population size is as limited as food is available sufficient to supply the minimum needs of the individuals already present.

For fish, the number of individuals may continue to increase in the presence of a limited food supply but each individual becomes stunted in size. There is a tendency for the biomass of a species to be regulated by the food supply, with size or weight of individuals varying inversely with number. Thinning the population artificially usually results in increased growth of remaining individuals (Parker 1958). Body size in *Daphnia* (Frank *et al.* 1957) and in several species of mammals also appears to be to a certain extent density-dependent in that smaller-sized individuals are characteristic of larger populations (Scheffer 1955).

The role of competition in regulating population size is thus directly effective by causing mortalities through fighting, nest destruction, and loss of food supplies. It also results, as will be seen in the discussion that follows, in lowered rates of reproduction, increased predation, dispersal into other regions, and decreased health and vigor.

Reproductivity

A study of the reproductive rate of a species in relation to population density requires separate studies of the number of eggs or young produced, called *fecundity* or *natality*, and the number reaching sexual maturity or *survival*.

In cultures of *Paramecium*, a decrease in the volume of culture fluid for the same initial number of individuals, or an increase in the initial number of individuals for a given volume of fluid, decreases the rate at which cell fission occurs (Myers 1927). Birth rate and growth rate in cultures of *Daphnia magna* vary inversely with the density of population even when a surplus of food is present (Pratt 1943, Frank *et al.* 1957).

Female *Drosophila* fruit flies crowded into small bottles do not lay as many eggs as they do when not crowded. This has been attributed to the competition of females for space, and to frequent disturbing contacts with other flies, so that they do not feed adequately. It could also be attributed to their energy being dissipated and to their ovipositing being too often interrupted (Pearl 1932, Bodenheimer 1938, Chiang and Hodson 1950). On the other hand, the reduction in fecundity may not be so much a result of disturbance as one of reduction both in the quantity and quality of food that is available per individual (Robertson and Sang 1945).

Experimental studies of populations of the flour beetle *Tribolium confusum* show that, as they increase in size and modify the flour in which they live, there is a decrease in the number of eggs deposited, an increase in the length of the larval period before pupation, an increase in larval and pupal mortality, and a decrease in the weight of both the pupae and adults. Apparently these effects are produced partly by decreased fecundity of the individual females and partly by cannibalism of larvae and adults upon the eggs and pupae, presumably induced by accumulation of excreta and deterioration of the food supply. When the modified flour is replaced by fresh flour at 48-hour intervals, the rate of reproductivity rises, even when the beetle populations become very large (Park 1934, 1938, Park and Woollcott 1937, Hammond 1938–39, Rich 1956). Similar effects of crowding on weight, length of developmental period, and mortality have been demonstrated in sheep blow-flies (Ullyett 1950) and in *Drosophila* (Sokoloff 1955). In the sheep blow-fly, artificial destruction of a large per cent of emerging adults brings an increased length of adult life, increased fecundity rate per female, and an increased total number of offspring produced (Nicholson 1954).

Overcrowding of pink salmon in small impoundments causes retention of many eggs within the female at spawning, and perhaps also mechanical injury to the eggs already deposited from excessive stirring of the gravel (Hanavan and Skud 1954).

A study of the European bird, the great tit, carried on for five years in 16 different areas, revealed a striking inverse relation between density and fecundity (Kluijver 1951). The average number of eggs laid per pair of birds per season varied from 13 to 20 at population densities of 8 to 12 pairs per 40 hectares (100 acres), to only 7 or 8 at population densities of 9 to 19 pairs per 40 hectares. The percentage of pairs having second clutches during a year varied between 40 and 100 at population densities of less than 16 pairs, but decreased to less than 10 at higher densities. Similar results have been obtained on the North American house wren (Kendeigh and Baldwin 1937). Apparently the lowered fecundity at high population densities in these cases is in part the result of frequent disturbance and conflicts resulting from the crowding of territories and in part to less food available per pair on the smaller-sized territories (Lack 1952). The non-breeding population of birds is doubtless high only when the breeding population is sufficiently dense that it occupies all of the most favorable territories.

TABLE 16-2 **Relation of reproduction to density of laboratory mice during a four-month period (after Retzlaff 1939).**

Groupings	**Number of groupings**	**Litters per female**	**Offspring per litter**	**Offspring per female**
1♂, 1♀	12	4.7	7.8	35.2
2♂, 2♀	6	4.3	7.2	31.1
4♂, 4♀	3	4.0	6.6	26.2
8♂, 8♀	2	3.6	7.4	26.8
12♂, 12♀	1	3.4	6.4	21.9

In the vicinity of Ithaca, New York, during three years of population increase, the average number of embryos per pregnant female in the meadow vole was 6 to 6.2, but in the year of decline following the peak only 4.5 to 5.5 (Hamilton 1937a). In California, the litter size of the montane vole declined as the population increased, and small litter sizes continued, as in New York, during the following decline in the population (Hoffman 1958). There is evidence that as snowshoe rabbit populations build up in the upswing of a cycle, litters are larger and more frequent than during the ensuing downswing (MacLulich 1937, Rowan and Keith 1956, Green and Evans 1940).

Experimental studies of populations of the laboratory mouse lend support to high population as a curtailing influence on reproduction (Table 16-2). With an increase in the number of mice crowded into cages of uniform size there was a decrease in the number of litters produced, in the size of each litter, and in the total number of young. At the higher densities there was considerable fighting, resulting in serious wounds and even death for some individuals. A social hierarchy was established, and it appeared that only the despots at the top of the bite order were able to reproduce at a normal rate. Those at the bottom of the order produced few young or none at all (Crew and Mirskaia 1931, Retzlaff 1939, Crowcroft and Rowe 1957). It has been shown that in the coccid insect *Lepidosaphes ulmi* a decrease in fecundity at high population levels was not a result of a decrease in number of eggs laid by fertile females but of an increase in the percentage of females that were sterile (Smirnov and Polejaeff 1934).

An experimental population of house mice was established in a large enclosure with cover and water supplied in excess but with food allotments held to a constant daily amount. The population increased in

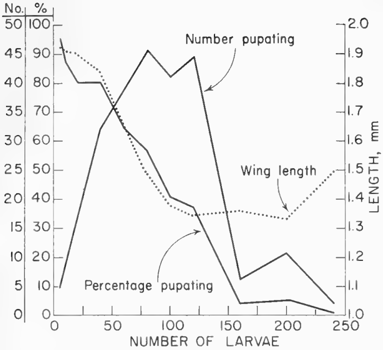


FIG. 16-6 **Effect of density of larval populations of *Drosophila melanogaster* on number pupating, percentage pupating, and wing length of resulting female adults (after Chiang and Hodson 1950).**

size until the per capita consumption of food was cut by one-fourth as a result of the increased number of animals, and then reproduction stopped altogether. It appears that in times of stress the limited energy resources of animals are diverted from reproduction to individual survival (Strecker and Emlen 1953). In another experiment, food was supplied in excess but space and cover were restricted. Population increase was finally limited by litter mortality from cannibalism and desertion. In some of the populations there was a decline in fecundity. This appeared to be the result of a social hierarchy becoming established so that subordinated individuals failed to get adequate amounts of food, even though a surplus of food was available, and were prevented from completing their mating behavior (Southwick 1955). Reproductivity has also been found to decline in the short-tailed meadow vole in large populations, because of chasing and fighting, when there was a surplus of food and water present (Clarke 1955).

Fertility of eggs appears to be high as they are laid under natural conditions. Egg viability, the capacity to hatch, has been shown in *Drosophila* cultures to be modified by the same factors that affect fecundity, particularly the amount of food available to the adult (Robertson and Sang 1945).

The survival of young is greatly affected by the number of animals present. When larvae of *Drosophila* are reared at different densities in containers of equal size and with equal amounts of food, the percentage that succeeds in pupating drops in an almost straight line with increase in density of the larvae. However, because of the larger initial numbers of larvae present, the actual number pupating is greatest at intermediate densities. The size of the adults emerging from the pupae decreases abruptly as density increases. It has been shown experimentally that effects produced were due to the exhaustion of food at progressively earlier growth stages as the population densities increased. The continued growth of some individuals even after the original food was gone was apparently because they devoured dead larvae (Chiang and Hodson 1950).

The average growth rate of tadpoles in a limited volume of water is inversely proportional to the number of individuals. However, some individuals grow at normal rates at all densities; the decreasing average growth rate at higher densities is due to the larger number of individuals that become stunted (Rose 1960). This effect of overcrowding is produced through water conditioning.

For the grain weevil there is an optimum intermediate density for rate of population increase even though the progeny raised per female decreases progressively as the population increases (Table 16-3). There is a similar relationship among fish (Herrington 1947).

The amount of disturbance of females with suckling young in crowded experimental populations of the house mouse decreased the number of litters successfully weaned. Females abandoned or devoured their young, and when the disturbance factor became sufficiently severe, all successful weaning of litters ceased (Brown 1953).

The snowshoe rabbit cycle in Minnesota reached a peak of 200 per 100 hectares (500 per square mile) in 1933 and dropped to a low of only 13 per 100 hectares (32 per square mile) in February 1938. Mortality percentage of the adults, duration of the reproductive season, proportion of females pregnant, and the average number of embryos per pregnant female remained relatively constant throughout this period. The significant variable that appeared to determine the cycle was the mortality of the young after birth. At the peak of the cycle, yearling rabbits constituted 60 per cent of the entire spring population, but at the bottom of the cycle in 1937 they constituted only 44 per cent. As the cycle began to swing upwards again in 1938 and 1939, the proportion of young reached 80 per cent (Green and Evans 1940).

It is desirable, when considering reproductivity as a density-stabilizing factor, to distinguish clearly between fecundity and success in raising young to maturity. Changes in fecundity are density-dependent, at least in some species, but are not usually sufficiently great to be of major importance in stabilizing the numbers of a species at any definite level (Lack 1954a). However, mortality of the immature

TABLE 16-3 **Reproductivity of the grain weevil at different densities (Maclagan 1932).**

Grain Weevil	Density							
Weevils per gram of grain	0.25	0.50	1	2	4	8	16	32
Number of grains per weevil	100	50	25	12.5	6.25	3.12	1.56	0.78
Population size after 64 days	69	95	138	167	192	77	51	29
Progeny per weevil	17.2	11.8	8.6	5.2	3.0	1.2	0.4	0.1

stages induced by intraspecific competition, predation, and conditioning of the habitat becomes extensive with overcrowding and is usually much more important.

Predation

It is well known that variations in the population level of predators coincide or often follow closely after variations in the population of prey species, but it is not always certain whether the number of predators depends simply on the abundance of prey serving as food, or whether the predators by their feeding regulate the number of prey animals. Experimental studies amply demonstrate that under certain conditions, at least, both true predators and parasitoids greatly affect the numbers of the species on which they feed, and hence similar relationships may be looked for under natural conditions.

A study made in California shows clearly that while the long-tailed mealybug increases rapidly on the citrus trees from March through May, their populations are reduced by June or July by the action of three insect predators, two lacewings and a lady beetle. The predator populations are low compared with the prey, but each predator destroys many mealybugs (DeBach 1949).

Quantitative determination of the significance of predation in controlling vertebrate populations under natural conditions is difficult to make, since it requires accurate measurement of the number of prey per unit area, the number of predators in the same area, and the number of prey taken by the predators. In one of the best such studies (Errington 1937a), carried on in Wisconsin and Iowa between 1930 and 1935, the population of the prey, the bobwhite quail, was expressed in percentage of saturation or carrying capacity of the area, and the extent of predation by the great horned owl was given in terms of percentage of owl pellets containing quail remains. Although there is considerable variability evident, the general trend is for the percentage of predation to increase with the density of the prey population in the manner of a density-stabilizing factor (Table 16-4). It appears that at densities of prey below the carrying capacity of the area, when the bobwhite can find plenty of cover and food close at hand, predation is very low, but as soon as populations reach densities above the carrying capacity so that surplus individuals are forced to make use of inferior cover or go greater distances in search of food, predation intensifies.

Some excellent studies of predator-prey coactions, especially in vertebrates, have been concerned with the relations between a single predator and its various prey species (Tinbergen 1933, Errington *et al.* 1940, Errington 1943, Murie 1944, Tinbergen 1946, Fitch 1947, Dunnet 1955, Craighead and Craighead 1956), or between a particular prey species and all its predators (Errington 1945, 1946, Bump *et al.* 1947, Koford 1958), but a complete understanding of the role of predation in regulating population levels requires a knowledge of coaction between all prey species and all predator species within community limits, since interrelations between any two species are affected by the interrelations of each species with others in the community. Thus when meadow voles are abundant an owl will feed largely on that single species, but when populations of meadow voles be-

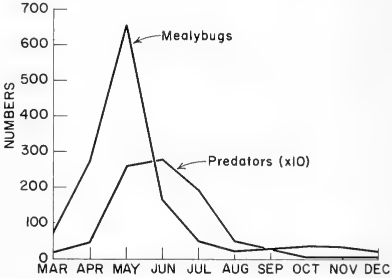


FIG. 16-7 **Relation of changes in the populations of long-tailed mealybugs and their predators, both living on citrus trees in California during 1946 (DeBach 1949).**

TABLE 16-4 **Evaluation of horned owl winter predation on bobwhite (from Errington 1937).**

Number of locality-winter records	Density of prey in per cent of carrying capacity	Intensity of predation in per cent of owl pellets containing quail remains
9	36-100	1.9 (0.0-6.3)
10	106-123	6.7 (0.0-16.0)
3	133-150	14.6 (10.4-19.0)
4	155-197	11.0 (0.0-20.0)

come reduced, the owl will prey to a greater extent on other species if they are available (Table 16-5). Other species that take the brunt of predation when a perferred species becomes reduced in availability are called *buffer species* (Bump *et al.* 1947).

Not only is there variation in the food of predators dependent on the availability of several potential prey species, but with any one prey species there is variation in the number and kinds of predators affecting it, dependent on its density and vulnerability. During outbreaks of insect or mouse plagues, predator species of many kinds converge on the easily obtainable food supply (Piper 1928, McAtee 1922, Kendeigh 1947). Predatory pressure is therefore very flexible, shifting its major impact from species to species and from one locality to another. This makes the evaluation of predation as a density-stabilizing factor particularly difficult, but there can be no doubt that the application of predation pressure from all sources often exerts an important regulatory influence on prey populations. There are too many cases on record of prey species developing disastrous overpopulations when predatory species are artificially eliminated to think otherwise (Ball and Hayne 1952).

When only a small number of species are involved in the food web, as in arctic communities or with insect pests infecting cultivated crops, stability of population levels is difficult to attain. An increase or decrease in the abundance of any one species produces changes in all other species. On the other hand, when a large number of species are involved, as in tropical communities or in complex stands of temperate zone vegetation, each predator has so much choice of prey and each prey species is subjected to attacks from such a variety of predators that a sudden change in the population level of any one species is absorbed without greatly affecting the stability of the community as a whole (Voûte 1946, Craighead and Craighead 1956, MacArthur 1955). Cycles of population are much more prevalent, therefore, in far northern communities where the variety of species is scanty than in the highly complex communities of southern latitudes.

TABLE 16-5 **Percentage of different prey species taken by wood owls, during a winter (1930–1931) in which populations of European meadow voles were high, compared with the following winter (1931–1932) when vole populations were reduced (from Tinbergen 1933).**

Species	Winter 1930-1931	Winter 1931-1932
Rodents:		
European meadow-mouse	88.0	52.0
House mouse, European woodland mouse	5.8	14.2
European red-backed mouse	1.1	2.1
Norway rat	0.5	1.9
Birds	4.1	27.1
Miscellaneous	0.5	2.7

The importance that predation may have to maintenance of health and vigor in prey populations, aside from regulating their numbers, is of significance. In careful observations of 688 attacks by hawks on other birds, only 7.6 per cent were successful in the capture of the prey, but of these successful captures, over 19 per cent of the victims had previously shown injuries, abnormalities, or unusual behavior (Rudebeck 1950–51). In another similar study, the abnormal individuals among the victims varied from 14 to 33 per cent (Burckhardt 1953). Wolves have great difficulty catching healthy adult caribou, and even calves are not often overtaken except in the confusion of a large herd. Over 50 per cent of the kills that wolves make are of crippled or sick caribou, although the incidence of such individuals is less than 2 per cent (Crisler 1956). Water boatmen with one or more legs artificially amputated were destroyed by fish in an experimental setup at a faster rate than were normal individuals (Popham 1942). Apparently predation exerts a selective force and less fit individuals are eliminated in greater proportion than are the fit.

The ultimate result of parasitoids is the death of their hosts. They function in curtailing over-populations of host species in nearly the same manner as do true predators. The relations between host and parasitoid may, however, be more varied and complex (Nicholson 1933) than between a true predator and its prey.

The normal relation between host and parasitoid is one of equilibrium where neither becomes overly abundant or overly scarce. This means that the abundance of parasitoids must also be controlled by density-stabilizing factors. Parasitoids may in turn be infected with hyperparasitoids, and the relations between the two are similar to those between the pasasitoid and the original host (Nicholson and Bailey 1935).

At low host densities, the reproductivity of the parasitoid tends to vary proportionally with the density of the host (Varley 1947). However, it has been shown experimentally that with increase in population density of the parasitoid, there is decreased reproductivity for it, increased difficulty in finding individual hosts not already infected (DeBach and Smith 1941), and increased competition between duplicate infestations in the same host individual (*super-parasitism*) so that neither parasitoid survives (Fiske 1910). Of interest in this regard is that in one experiment 50 parasitoids during a limited period of time were able to find and eventually kill 80 per cent of the hosts, but that it required 100 parasitoids to find 95 per cent of the hosts and 200 parasitoids to find them all. This phenomenon is comparable to the law of diminishing returns and is doubtless one reason why a parasitoid rarely exterminates a host (DeBach and Smith 1947). In order for a particular parasitoid to regulate the numbers of a particular host species, it ordinarily needs to have a high intrinsic rate of increase, at least equal to its host (Muir 1914), and to have high searching ability for locating host individuals (Andrewartha and Birch 1954).

Even though the density of host or prey population greatly affects the success with which a parasitoid or predator finds its victim, searching is not random as far as the individuals are concerned. Predators in general have evolved many adaptations in sense organs, methods of attack, and special behavior patterns designed to facilitate the finding of specific prey, avoid unsuitable objects, save time, and increase efficiency (Thompson 1939). However, searching is largely at random as far as the area covered by the entire population is concerned since the individuals mostly hunt independently of each other and may cover the same or different areas indiscriminately. Many parasitoids avoid placing their eggs inside the bodies of prey that are already infected, but this behavior tends to break down when the ratio of number of parasitoids to number of uninfected prey is high.

The coaction between host and parasitoid may be complicated by differential effect of environmental conditions, such as temperature, on the two species. Experimental studies have shown that the greenhouse whitefly, a homopteran, at temperatures below 24°C lives longer, lays more eggs, has a higher rate of oviposition, and consequently increases more rapidly in abundance than does it chalcidid parasitoid. At 24°C, the rate of population increase is about the same in the two species, but above 24°C, the parasitoid population increases more rapidly than does the host species. The result is that the percentage of hosts infected increases markedly with rise in temperature (Burnett 1949). Similar relations have been demonstrated for other species of hosts and parasitoids (Payne 1934).

Buffer species may be as important with parasitoids as with true predators. Prior to 1925 in the Fiji Islands, the zygaenid moth *Levuana iridescens* was a serious pest of coconuts, defoliating trees over extensive areas. Outbreaks terminated only when its supply of food became exhausted. In 1925, the tachinid fly *Ptychomyia remota* was introduced from Malaya and within a year reduced *Levuana* to a rare species, a status which it has had ever since. However, *Ptychomyia* requires alternate hosts to maintain its existence when *Levuana* becomes reduced in numbers. Such alternate hosts, or buffer species, occur on most of the Fiji Islands, but on one island from which they are absent the death rate among the predators became so high that *Leuvana* has been able again to increase in numbers (Andrewartha and Birch 1954).

There are several known cases where crop pests in agricultural regions have been controlled or virtually extirpated by introduced parasitoids and predators (Fleschner 1959, Varley 1959). In the Hawaiian Islands, the sugar cane leafhopper is controlled by the capsid bug *Cyrtorhinus mundulus*, and the sugar cane borer by the tachinid fly *Ceromasia sphenophori*. The black scale in California is successfully controlled by the chalcidid *Scutillista cyanea* imported from South Africa. The silk industry of Italy was apparently saved by importations of *Prospaltella berlesi* which controlled the scale that was destroying mulberry trees, on the leaves of which the silkworm feeds (Thompson 1928). Not all cases of supposed control of pests by parasitoids and predators can be substantiated in critical study. Pests most adequately controlled are usually scale-insects, mealybugs, aphids, and leafhoppers of the order Homoptera which are sedentary, gregarious, and limited in the number of host species that they attack. Beneficial parasitoids and predators belong chiefly to the Hemiptera, Diptera, Coleoptera, and Hymenoptera (Sweetman 1952).

The relations between some insect herbivores and plants are somewhat similar as between parasitoids and hosts. *Cactoblastis* and *Dactylopius*, introduced from California, are credited with destruction of large areas of tree cactus in the Hawaiian Islands (Huffaker 1957).

Attempts at artificial control of pests with insecticides often bring disorder and unexpected results. Elm trees on the University of Illinois campus were sprayed with DDT to control *Scaphoideus luteolus*, a leafhopper vector of phloem necrosis which was causing considerable destruction of the trees. But the spray also caused a high mortality of *Aphytis mytilaspidis*, a hymenopteran parasitoid of the scale *Aspidiotus*, and allowed the scale to increase and do damage in turn to the trees (Tinker 1957).

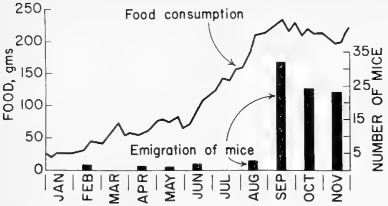


FIG. 16-8 **Relation between population size of house mice, as expressed by average amount of food consumed per day, and emigration of mice away from the colony. The colony was started with five pairs of mice in January (Strecker 1954).**

Emigration

The pressure of overpopulations can be relieved by mass emigrations of individuals from particular localities as well as by their death. It has been shown experimentally that such emigrations will actually occur under conditions of crowding in a mouse population. It is of interest that those individuals which remained continued their normal rates of reproduction. This contrasts with the drastic reduction, even cessation, of reproduction in other colonies from which emigrations were prevented.

Two species of aphids placed in their optimum niches, one at the top, the other at the bottom of a single barley plant, multiplied to saturation and dispersed downward and upward on the plant until both species came to exist side by side. Continued reproduction and overcrowding forced surplus individuals to emigrate to surrounding plants over 7.5 cm away, leaving the two populations in equilibrium on the original plant. In another experiment where plants were within 3.0 cm of each other, the aphids spread to the preferred sites on the second plant rather than to less favorable spots on the first plant (Ito 1954).

Emigrations under natural conditions occur when there is overcrowding in the migratory locust, lemming, grouse, snowy owl (Gross 1947), snowshoe rabbit (Cox 1936), Arctic fox (Braestrup 1941), gray squirrel, and occasionally in other species (Heape 1931, Dymond 1947). The emigrations of the European lemming in the Scandinavian countries are spectacular (Elton 1942). Emigrations on a reduced scale are known to occur also with lemmings in North America (Thompson 1955).

Lemming emigrations do not invariably lead to death of whole armies as popularly believed, but to settlement of new areas, leaving the original area populated with reduced numbers. Emigration must have survival value for the species or otherwise the tendency for emigration would have been a weakening factor and disappeared in the course of evolution.

It is, of course, population pressure that is responsible in large part for the dispersal of young and extension of ranges into new areas. Under normal conditions adult animals, especially among the higher vertebrates, are well established on their territories and the young are forced to seek homes elsewhere. Among insects, there is a relation between emigration and inherited behavior tendencies. Individual tent caterpillars, both larvae and adults, differ innately in the extent to which they show activity even within the same colony. In the development of populations of excessive size, spread of infestations of the insect into new regions is largely by the more active individuals. The outbreak finally terminates when the proportion of sluggish individuals comes to predominate in the population (Wellington 1960).

Disease

Although *infectious disease* in some form is a common cause of mortality, it is less important as a stabilizing factor than the others already considered, because it reduces the population size in an important manner only when epidemics, or more accurately *epizootics*, occur. The mortality may then be extreme so that the population falls way below the level of stabilization, and a period of recovery follows.

Whether or not epizootics occur, depends on the virulence of the disease-producing organism, the rapidity with which it is transmitted from individual to individual, and the resistance of the hosts. Worm and protozoan parasites, bacteria, and viruses may be transmitted through body contact of host individuals, by the host ingesting contaminated food or water, or by vectors which are commonly external parasites themselves. It is obvious that ease and rapidity of transmission increase with the size of host populations. Overcrowding often also lowers the vigor of the hosts so that they become more susceptible.

In the course of time, natural selection tends to evolve tolerable relations between hosts and the disease organisms that they harbor. Mutations of disease organisms to greater virulence result in more rapid or extensive die-offs of the host with the consequence that the mutant strains disappear. During upswings in host populations, extra virulent mutations may persist for a time, because of the abundance of host individuals to which they can spread, but when the host population declines, only those host individuals will survive that are not infected with the virulent strain or that develop immunity to it.

Epizootics among wild animals are often severe, and they usually break out when population densities are high. Among mammals, epizootics have been observed in voles, lemmings, mice, rats, beavers, squirrels, rabbits, moles, foxes, deer (Elton 1942), birds, fishes, and reptiles. Incidence of them is often sporadic in that they do not always appear with high densities of host populations nor with declines in cyclic species so that their importance as a regulating factor on animal populations has been difficult to evaluate (Chitty 1954).

Physiological stress is not infectious but becomes pathological when extreme and may bring considerable mortality in the population. States of stress have been produced experimentally by allowing confined populations of albino and house mice and meadow voles to increase to high levels of abundance, even with a surplus of food and water present. Evidence that a state of stress exists is demonstrable in experimental populations by increase in the weight of the adrenals, by decrease in the weight of the body, testes, thymus, preputial glands, and seminal vesicles; by decrease in the number of circulating eosinophils in the blood; and by aberrant maternal behavior (Clarke 1953, Christian 1956, Louch 1956, 1958). An increase in adrenal weights, especially the adrenocortical tissue, as population rises, has also been shown in wild populations of the Norway rat (Christian and Davis 1956), and the behavior symptoms usually associated with high physiological stress have been observed in wild populations of European meadow voles (Frank 1953).

It seems probable that *shock disease* as it occurs in snowshoe rabbits is a manifestation of the stress syndrome (Green and Larsen 1938) and occurs when the liver degenerates leaving inadequate reserves of glycogen available for emergencies. Under these conditions, any undue exertion or excitement may cause normal animals to go suddenly into convulsions, sink into a coma, and die.

Relaxation of density-dependent effects

With so many decimating factors acting on populations, one wonders why species do not become extinct more often than they do. The explanation is that there is relaxation in the intensity of action of the factors as the affected population becomes reduced in size. This relaxation is brought about by the heterogeneity of the environment so that at least some individuals escape the full force of the factor; hyperparasitoidism or overcrowding reducing the population of parasitoids and predators themselves; development of immunity to or tolerance of the factors involved; change in behavior so that the decimating factor is avoided: survival of dormant eggs, pupae, or encysted stages after the active stages in the life-cycle perish (Solomon 1949).

DENSITY-LIMITING FACTORS

Variations in space or cover, favorable weather, and food occur independently of population densities and may cause drastic changes in the abundance of animals. Heavy silting of estuaries along the coast from erosion of the surrounding upland may smother oyster spat and reduce the amount of hard surface available for setting quite independently of the number of oysters already there, or variations in oyster abundance from year to year. The amount of solid surface available also determines the population density reached by sessile rotifers (Edmondson 1946). Variations in water level of a stream affects the availability of suitable spawning areas for fish, and consequently their abundance (Starrett 1951). A drought may dry up a marsh, making it unsuitable for muskrats and waterfowl. A severe winter freeze may kill all but a few hardy individuals of any species regardless of the size of the original population. Failure of a food crop, from weather, flooding, or some other physical factor, may deplete populations that depend on it for subsistence. On the other hand, agriculture has provided food, and allowed some species to become abundant that once were scarce; for instance, many insect pests of crops.

Although fluctuations in space, weather, and food may directly affect the abundance of animals in an obvious manner, their average or prevailing condition determines the level at which density-stabilizing factors bring populations into equilibrium. With abundant food, cover, and favorable weather, populations will be high. When food is scarce, competition for it becomes acute at a lower population density. It

FIG. 16-9 **The 1932 emigration of sharp-tailed grouse from northern Ontario and Quebec (Snyder 1935).**

TABLE 16-6 **Effect of different combinations of temperature and humidity on the levels attained by populations of flour beetles in experimental cultures (Park 1954).**

Temperature	Relative humidity	Mean ± S.E.
34°C	70%	38.25 ± 1.53
34°C	30%	9.61 ± 1.07
29°C	70%	50.11 ± 3.40
29°C	30%	18.79 ± 1.32
24°C	70%	45.15 ± 2.77
24°C	30%	2.63 ± 0.35

has been demonstrated experimentally, for instance, that the density attained by the cladoceran *Daphnia obtusa* is directly proportional to the food supply (Slobodkin 1954). This principle was known to Thomas R. Malthus back in 1798, and influenced the theory of evolution as developed by Charles Darwin. If cover is deficient, animals become exposed to predation and bad weather earlier so that the population becomes stabilized at a low level. Likewise, differences in temperature and humidity affect the level attained by experimental cultures of flour beetles (Table 16-6).

Differences between species in their relative demands for space, food, and shelter affect the population levels that they attain. Species of small body size require less space than those of large size. In similar fashion, species that get along in small territories will be more numerous than those requiring large territories. Herbivorous species find more food available in a limited area than do species higher in the food chain and hence will be the most numerous. Hardy species will flourish in climatic areas where less tolerant species are scarce.

The limiting effects of space, weather, and food are properly considered to be *density-independent*. However, some actions of these factors are *density-responsive*. The amount of space available for additional individuals is, of course, inversely proportional to the space already occupied, so that the greater the population density, the less space there is available per individual. If all favorable cover is occupied, additions to the population are forced into inferior cover where they receive less protection in inclement weather and where they become more exposed to the attacks of predators. Voles feeding in grassland may, when abundant, consume so much of the vegetation that they destroy their cover as well as their food supply. When populations of brown lemming are low over winter, they utilize less than one per cent of the annual production of the grasses and sedges which are their favorite food. At peak populations however, they use nearly 100 per cent of the growth, become greatly exposed to predation, and are subsequently forced to shift to the less palatable forage and poorer cover of moss. The lack of adequate winter forage and cover, concurrent with a reduction in reproduction and increase in predation, results in a rapid decline in population level (Thompson 1955a).

Outbreaks of spruce budworm do not occur in the coniferous forests of Canada until the succession to white spruce and especially balsam fir develops a sexually mature evergreen canopy overtopping the aspen and birch. Insect larvae newly emerged from hibernation feed on the flowers, especially the male flowers, before the leaf buds open; then they move down to consume the current foliage, eventually defoliating and killing the trees. Millions of dollars worth of timber is destroyed. Native parasitoids are incapable of preventing outbreaks. The outbreak dies out in a few years by which time all the mature trees are destroyed and the insects' food supply is exhausted. Another outbreak will not occur in the locality until another generation of spruce and balsam matures in the area (Prebble 1954).

In stored grain infested with insects the heat produced by the insects may raise the temperature beyond their limit of tolerance and prevent further increase in population density (Solomon 1953). Insects and rodents at high populations tend to have reduced vigor and health and to be affected by weather conditions which at low population levels are easily tolerated (Chitty 1960, Wellington 1960). It is thus apparent that even the climatic environment may be density-responsive in its effects in special situations. However, it is well to distinguish between density-responsive effects that are relatively passive and limiting and density-dependent effects that are dynamic and stabilizing.

INTERCOMPENSATIONS

The difficulty of evaluating, under natural conditions, the role of any factor in regulating the size of animal populations is in large part a result of the fact that it seldom acts alone. The *time* in the life-cycle of an organism at which a factor takes effect influences the importance of it. Normally, the earlier in the life of the organism at which a factor is effective, the more nearly its apparent controlling role is a real one. Thus 60 per cent of the mature larvae of an insect may be fatally infested with parasitoids, but if 82.9 per cent of the original output of eggs have already failed to reach this stage for other reasons, the influence of these parasitoids must be evaluated at only 10.2 per cent, 0.60 × (100 — 82.9), instead of the full 60 per cent (Table 16-7). On the other hand, a 10 per cent apparent mortality resulting from egg parasites which comes at an early stage in the life cycle may produce a nearly equal real mortality (9.5); but a 10 per cent parasitization of pupae late in the cycle may cause only 0.47 per cent real mortality.

Stage	Factor	Apparent mortality per cent	Real mortality per cent
Eggs at deposition	Sterility	5.0	5.0
Eggs after deposition	Egg parasites	10.0	9.5
Young larvae	Intrinsic factors	80.0	68.4
Mature larvae	Larval parasites	60.0	10.2
Mature larvae	Agricultural factors	30.0	2.05
Pupae	Pupal parasites	10.0	0.47
Adults	Meteorological factors	54.86	2.30
	Total		97.92

TABLE 16-7 **Evaluation of mortality factors effective at different stages in the life cycle of an insect (Thompson 1928).**

The *variability* of a factor also affects its importance. If a factor consistently produces, say, a 60 per cent mortality year after year, it will influence the size of the population any particular year less than will another factor that varies from, say, 20 to 30 per cent. However, a variation of 10 per cent in a factor that averages 60 per cent mortality is more important than the same variation in a factor that usually produces only 20 per cent mortality. An increase in mortality from 60 to 70 per cent reduces the surviving population 25 per cent (40 — 30)/40, but an increase from 20 to 30 per cent reduces the surviving population only 12.5 per cent (80 — 70)/80 (Morris 1957).

Aside from time and variability, the influence of any factor is dependent on the level of population size at which it first comes to exert an effective or critical role. This level represents a *threshold of vulnerability* of the population for that particular factor. The threshold of vulnerability varies between species and within the species, depending on the amount of protective cover that is present, the movements and activities of the species, its protective coloration, and the aggressiveness and capabilities of the predators themselves (Craighead and Craighead 1956).

There is also an *upper limit of vulnerability* or *escape phase* (Voûte 1946) above which a factor no longer exerts effective control over a population increase. With increase in the number of cocoons of European pine sawfly, predation by small mammals rises to a peak at a density of 2,000,000 cocoons per hectare (800,000 per acre), at which level about 50 per cent of the prey are destroyed. With further increase in density of cocoons, the percentage of prey taken by mammals decreases in a density-inverse relation. The prey has escaped the stabilizing influence of predation or gone beyond the upper limit of vulnerability to this factor (Holling 1959).

Competition or fighting between individuals appears at rather low population levels among vertebrates. With crowding, a social hierarchy may become established with disadvantages to those in the lower positions, or territories may become seriously compressed in size. When fighting becomes intense, individuals are forced to leave the area (emigrate); failing this, their reproductive activities are disturbed. In other species, for instance insects, competition may not be sufficient to control the increase in population, so that the population reaches a level at which predation becomes significant. Populations of vertebrates become especially vulnerable to predation when all suitable cover becomes crowded and surplus animals are forced to accept inferior cover or are driven into the open. Once an outbreak surpasses a certain level in spite of predation, predation can on longer take any significant percentage of the species. In fact, bird predation on insects may even become a hindrance at high population levels in that it destroys parasitoids that then become the most effective regulating factor (Strickland 1928, Thompson 1929, Betts 1955). Emigation and epizootics ordinarily do not occur unless competition and predation fail to hold down the increase in population and very high population thresholds are reached (Severtzoff 1934, MacKenzie 1951). Populations occupying inferior habitats usually never reach densities that render them vulnerable to epizootics, and they ordinarily escape the violent fluctuations in size that occur with the species in habitats of higher carrying capacity (Evans 1942).

These various regulating factors affect species differently. Song birds with well defined territories seldom reach densities at which reduced reproductivity or predation becomes important. They are, however, subject to reduced reproductivity in high populations. Game birds, which do not defend nesting territories, ungulates, and insects, in which group competition is relatively ineffective, commonly have their population levels controlled by predation. If predation, reduced reproductivity, and competition do not curtail population expansion, lemmings undergo emigrations, and all animals become subject to epizootics or physiological stress. For many species the effect of density-dependent factors is cumulative; that is, several factors are involved to varying degrees (Milne 1957). For some insects, no density-dependent force is effective; the population is never stabilized, and it continues to increase until there is exhaustion of space or food or curtailment by bad weather.

A good example of a population that never becomes stabilized is the rose thrip, that inhabits rose blossoms. Rapid multiplication of the thrip is possible only during a limited period, during spring and early summer. In this period the insect increases rapidly,

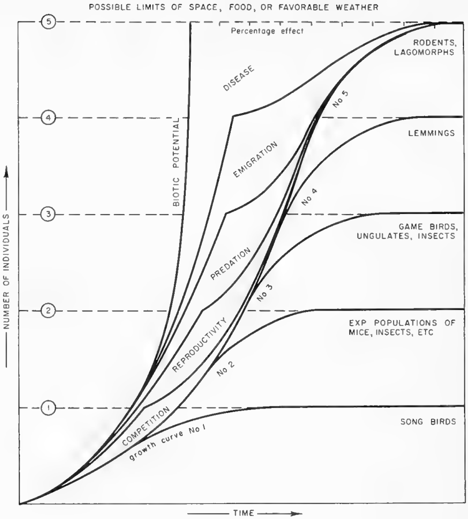


FIG. 16-10 Interrelations of various density-stabilizing and density-limiting factors ("environmental resistance") in the regulation of population size at various possible levels. Considerable variation occurs between species in the relative importance and position of the different factors. Note that the limits of population growth set by space, food, or favorable weather may occur for different species at 1, 2, 3, 4, or 5.

but so does the number of roses available to them. The favorable period normally ends long before the thrips have time to saturate the niche. Summer drought brings high mortality and a decline to the low densities of the species characteristic of late summer and winter. The rise of the thrip population is a race against time, the increase in density greatest in those years when the favorable period lasts longest; but it never reaches the point where competition becomes important. Annual variations in maximum densities in this species are almost entirely the result of density-independent climatic factors (Davidson and Andrewartha 1948). What is true for thrips may apply also to many other kinds of insects and invertebrates having annual life cycles; that is to say, climatic factors appear more important than biotic ones in determining the yearly size of the populations (Uvarov 1931, Bodenheimer 1938, Thompson 1939, Andrewartha and Birch 1954).

The various stabilizing and limiting factors act in an *intercompensatory manner.* All stabilizing factors, for instance, are in temporary abeyance following catastrophes of weather, drought, floods, or other factors until there is recovery of normal population levels again (Nicholson 1954a).

One of the most thorough studies of stabilizing factors has been made on the muskrat (Errington 1946, 1951). This species is subject to such density-dependent mortality factors as intraspecies competition or fighting; predation, especially by mink and foxes; emigrations from overcrowded habitats; and epizootics. Overpopulations may be reduced by one of these factors singly, or by two or more working simultaneously. If fighting or predation keeps the population at a low level, disease is unimportant; but if fighting or predation is negligible some one particular year, then disease may reduce the numbers of animals. Emigration to other areas occurs when a marsh becomes overcrowded or drought reduces the carrying capacity. If freezes, violent storms or floods, drought, or trapping reduces the population excessively, there is compensation by increased breeding activity, and for a time all other regulating factors are held in abeyance. The fur yield of a muskrat marsh cannot, therefore, be increased simply by destroying the predators, for other controlling factors become proportionately more effective. Trapping for fur, if not excessive, is economically profitable and can be carried on year after year, if the animals eliminated through trapping are restricted to the numbers that would be destroyed anyway by natural factors. The general trend is to maintain the population at the carrying capacity of the habitat. Improvement of yield is brought about only by increase in the carrying capacity in respect to food, cover, and space. These concepts are fundamental not only to an understanding of population dynamics, but also to wildlife management.

RELATION TO DISTRIBUTION

Variations in abundance of a species are closely related to distribution. Three zones of abundance may be recognized. There is an inner *zone of normal abundance*, where climatic and other conditions are ordinarily favorable and high populations of the species are characteristic. Surrounding this inner area is a *zone of occasional abundance,* where climatic or other conditions are usually severe enough to hold populations at a low level, but where occasional years occur in which high populations may be reached. On the outside is a *zone of possible abundance*, where the normal environment is such that the species cannot maintain a permanent population but where the species may occur during favorable years by emigration from the inner zones (Cook 1929). Populations can become stabilized only in the innermost zone. Where climate, suitable space or cover, and food continually vary from year to year, as in the middle and outer zones, stabilization is never attained for any appreciable length of time (Swenk 1929). Ordinarily, therefore, one may expect a species to maintain a stabilized level of abundance only in the center or optimum habitat of its range, and to decline and fluctuate in abundance to an increasing extent towards the limit of its distribution.

SUMMARY

The regional density of a species depends on the prevalence of its favored niche, and its habitat density within this niche. Populations become stabilized by density-dependent factors whose effects increase in intensity as the population level rises and decrease as the population level declines. The most important density-stabilizing factors are competition, fecundity, survival of young, predation, emigration, and disease and physiological stress.

The level at which populations become stabilized is determined by such density-limiting factors as space or cover, prevailing weather, and food supply. These factors are largely density-independent, since their magnitude is primarily determined by the physical conditions of the environment. However, their action is responsive to the size of the population as the amount of space, protection from weather, and food available per individual decreases as the population increases.

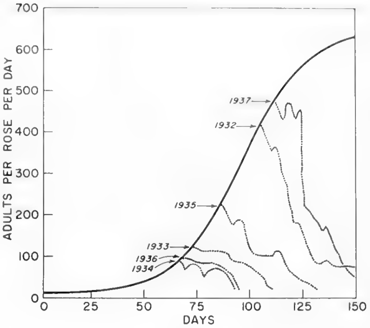


FIG. 16-11 **Control of population size of thrips inhabiting rose blossoms by density-independent factors. The total population tends to increase each year, as indicated by the sigmoid curve, but never reaches saturation of the available niches because of the onset of summer drought. The dotted lines indicate decline from the maximum population size for each of the years 1932–1937 (Davidson and Andrewartha 1948).**

The influence of any factor upon a population is determined by the time in the life-cycle of the organisms at which it is effective, its variability, and its threshold and upper limit of vulnerability for the population. Intercompensations occur so that when one factor becomes ineffective in controlling the density of a population, another factor becomes more effective.

A species normally attains a stabilized level of density only in the center of its range, where physical conditions are optimum. Towards the periphery of its range, its population density becomes increasingly unstable and fluctuating.

17

Ecological Processes and Community Dynamics:

Irruptions, Catastrophes, and Cycles

Abundance may change continuously and progressively in one direction over a long period of time, or variations in abundance may take the form of irruptions, catastrophes, or cycles. An understanding of how and why such changes in abundance occur is of considerable academic interest, and is of the utmost importance for the economic management of fish and game, preservation of wildlife, and in animal husbandry, agriculture, and forestry.

Minor fluctuations of less than 2:1 or 3:1 are often the result of sampling errors in estimating the true size of the population. When the ratio of population sizes from one period to another is greater than can be explained by errors of sampling, the fluctuations have meaning for which we should know the causes. Population ratios from one year to another are commonly of the order of 10:1, 100:1, or in insects, up to 10,000:1 or more (Solomon 1949).

PROGRESSIVE CHANGE

Populations that continue to increase or decline over a period of years are said to change progressively. The phenomenon is demonstrated as a species invades a new habitat or region or is becoming extinct. Progressive change in numbers also occurs with seasonal growth of populations. Long-time climatic change may produce gradual changes in abundance and distribution. Thus the amelioration of winter temperatures in northern Europe since the mid-nineteenth century correlates with the northward dispersal and increase in abundance of several species of birds and mammals (Kalela 1949).

IRRUPTIONS, OUTBREAKS, PLAGUES

The phenomenon of a population suddenly exploding to supersaturate an area is called an *irruption, outbreak,* or *plague.* These terms are considered here to be synonymous and to represent the time when an animal is abundant or injurious enough over an appreciable area to be noticed and recorded by untrained observers (Carpenter 1940b). The number of rodents may be in the hundreds or thousands per hectare, of insects in the millions. Outbreaks are known to have occurred since the beginning of recorded history in Europe, Africa, and North America, especially in insects and rodents. Plagues of European meadow voles were recorded 18 times in France between 1792 and 1931 (Elton 1942).

The cause and control of plagues have concerned man since civilization began. Biological control of these outbreaks by introducing parasitoids, parasites, bacteria, and viruses to infect the species concerned has been attempted. Once a foreign insect has be-

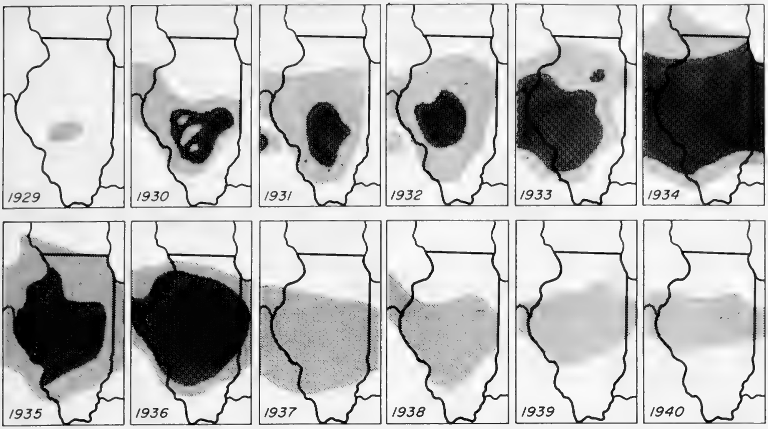


FIG. 17-1 **Onset and subsidence of an outbreak of chinch bugs in Illinois during the 1930's. Areas supporting the densest populations are indicated by the darker pattern (Shelford and Flint 1943).**

come an important crop or fruit pest in the United States, investigators are sent to its place of origin, to discover its natural parasitoid or predator enemies and introduce them into the area of infestation. On the whole, this procedure has been successful (Sweetman 1958).

About the turn of the century several attempts were made in Europe, especially in France, to suppress plagues of meadow voles by starting epizootics of typhoid. This bacterium was found present in dying voles, was cultured and distributed through the fields on food that the voles would eat. The success of the various attempts was always controversial, and when it was appreciated that the disease was also dangerous to man, these procedures were generally abandoned (Elton 1942). Considerable study is being made at the present time of the use of bacteria and other micro-organisms in the biological control of insects (Steinhaus 1960).

Myxomatosis has been used for the suppression of the rabbit population in Australia. Caused by a filterable virus, it is highly contagious among the introduced European rabbits, but apparently not transmissible to man or other animals. The virus is carried between rabbits principally by mosquitoes in Australia, and by fleas in England. Death occurs about 15 days after exposure. In 1950, extensive field trials with the myxoma virus were undertaken in eastern Australia, and by the end of the year mortalities locally as high as 99.8 per cent occurred. Epizootics have continued in later years but with somewhat lower virulence. The virus was introduced into France in 1952, where it spread rapidly; it reached England in 1953. The prognosis of the disease is uncertain. In some regions of Australia, rabbits have recovered from less virulent strains of the virus, or there has been selection of genetically more resistant individuals, so it is possible that some degree of immunization may arise. The disease, however, may be successful in keeping the population at a low level (Bourlière 1956).

Irruptions may occur with almost any kind of animal in any habitat. Irruptions of the bean clam occurred several times between 1894 and 1955 in the intertidal zone at La Jolla, California. The abrupt decline of the last outbreak in 1951–52 was the result of an epizootic associated with a minute unicellular organism of uncertain identity, found in the tissues of the clam (Coe 1955).

CATASTROPHES

Catastrophes occur at more or less widely spaced intervals and bring marked depressions in the population level of a species. Figure 17.2 shows annual populations of the house wren over 41 years, first in Ohio, then in Illinois. Decidedly low points

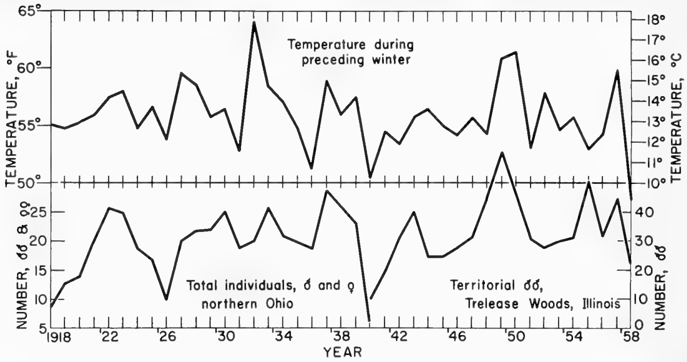


FIG. 17-2 Yearly variations in populations of the house wren. The data for northern Ohio are for total males and females on a 15-acre estate, most of the males being banded and captured at their nest-boxes. The data for Trelease Woods, in central Illinois, are for territorial males censused on a 55-acre tract by the spot-map method. Mean temperatures are for the wintering range only, based on monthly weather data for Tampa and Jacksonville, Florida; Savannah, Georgia; Montgomery and Mobile, Alabama (Kendeigh and Baldwin 1937, Kendeigh 1944).

in this curve occur in 1918, 1926, 1940, and 1958. Information from observers indicated that low populations were widespread in eastern North America both in this species and in many other song and game birds during these years. There is considerable evidence that these conspicuous variations in abundance, as well as some less pronounced, were the result of severely low winter temperatures. It is of interest that, in England, severe winters causing high mortality among such song birds as thrushes, blackbirds, and tits were recorded in 1111, 1115, 1124, 1335, 1407, 1462, 1609, 1708, 1716, 1879, 1917 (Elton 1927). To birds that feed on the ground, the depth of snow is as critical a factor as low temperature in determining the number that survive.

Among mammals, fluctuations in the population of the common hare in Denmark have been correlated with the varying effects of summer rainfall, spring temperatures, and the number of days of frost during the winter (Andersen 1957).

Catastrophes may occur with practically any type of animal life. The severe winter of 1917–18, for instance, produced a marked reduction in the numbers of many species of marine invertebrates in the

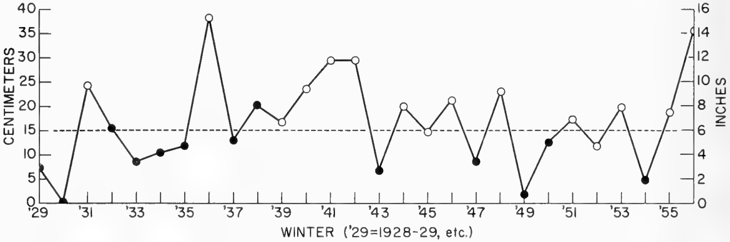


FIG. 17-3 Fluctuation in the average snow depth in the winter in southwestern Finland and population fluctuations of the partridge during the autumns following. The dotted line shows the critical snow depth, below which increases (solid circles) and above which decreases (open circle) in population usually occur (Siivonen 1956).

region of Woods Hole, Massachusetts (Allee 1919). In seeking correlations between catastrophes and weather or other environmental conditions, one needs to determine the period in its life cycle during which the species is most vulnerable, and the weather conditions coincident with that period that exert greatest effect.

CYCLES

Populations are cyclic or oscillatory when they vary in a more or less uniform manner between high and low levels of density.

Types

Although cycles of different duration have been postulated for many species at different times, the best established cycles are those of periodicities of 3–4 years and 9–10 years (Speirs 1939, Elton 1942, Dymond 1947, G.R. Williams 1954, Siivonen 1957).

The best known 3–4 year cycles are demonstrated in the following species:

Birds	*Mammals*
Snowy owl	European lemming
Willow ptarmigan (northern Europe)	Siberian lemming
	Brown lemming
Capercaillie	Collared lemming
Blackgame	European meadow vole
Hazel grouse	Arctic fox

Other species that may also vary in a 3–4 year cycle are rough-legged hawk, northern shrike, North American meadow vole, short-tailed meadow vole (England, Scotland), red fox (far North), marten (far North), and sockeye salmon (Pacific coast of North America). Species well recognized as showing the 9–10 year cycle are:

Birds	*Mammals*
Ruffed grouse	Snowshoe rabbit
Sharp-tailed grouse	Muskrat
Willow ptarmigan (North America)	Canada lynx

In addition, a number of other species may have a 9–10 year cycle: rock ptarmigan, goshawk, great horned owl, red fox (South), marten (South), fisher, mink, and Atlantic salmon.

Fluctuations in populations, commonly of 5–6 years (Mackenzie 1952), occur in the British Isles in red grouse, rock ptarmigan, black game, and capercaillie, but there is question as to whether they are regular and definite enough to be truly cyclical. Among invertebrates, insect pests of coniferous forests in Germany fluctuate in periods variously from 6 through 18 years (Eidmann 1931); grasshoppers in Manitoba, 7 through 16 years (Criddle 1932); chinch bugs in Illinois, from about 3 through 16 years (Shelford and Flint 1943). Subjective estimates of damage by the starfish *Asterias forbesi* on mollusk fisheries between New York and Cape Cod suggest a periodicity of 14 years for this marine species (Burkenroad 1946).

It is possible to demonstrate mathematically that an apparent cycle or a series of irregular fluctuations may actually be compounded of several distinct periodicities, each of different duration (Wing 1953). Cycles can thus be postulated in the population fluctuations of many species, in the migration of birds, and in human economics (Wing 1935, Huntington 1945; see also J. Cycle Res. 1952 on, and other publications of the Foundation for the Study of Cycles), but the biological significance of these hidden periodicities remains to be demonstrated.

According to an extensive analysis made by Siivonen (1948) of data extending back through one hundred years, the short-term cycle averages 3⅓ years, with two 3-year and one 4-year cycle coming each decade. He believes that the 9–10 year cycle (average 10 years) results from each third short cycle having a greater amplitude than the other two, and that the long-term cycle is therefore only a modification of the more basic short-term cycle. Although there is doubt about the fundamental nature of this relation, it is true that the 3–4 year cycle is better expressed in the far North and the 9–10 year cycle in more southerly latitudes. The 3–4 year cycle may change to a 9–10 year cycle, correlated with latitude, even in the same species (red fox, marten). South of latitudes 45°–50°N in North America and about 60°N in Europe, variations in population size appear progressively less extreme and cyclic, more irregular or random in character. Thus the numbers of four species of gallinaceous birds during peak years divided by their counterpart numbers during low years changes from 3.8 in Lapland, to 2.4 in northern Finland, to 2.0 in central Finland, to 1.7 in southern Finland (Siivonen 1954). Cycles may be distinct and definite in the far North because only a few species are involved and the environment is relatively monotonous and severe; in more southerly latitudes, population fluctuation becomes more irregular and uncertain because of the interaction of many species and a more moderate environment.

Are cycles real?

To designate fluctuations as cyclic implies considerable regularity for them. In mathematical usage, a *cycle* is a recurring variation of regular timing or phasing and of constant amplitude. Fluctuations are considered *periodic* if the phase is constant but the amplitude varies. What ecologists call cycles are really *oscillations* because both phase and amplitude are inconstant. Justification for calling the fluctuations cyclic, rather than random, lies in the demonstration that the variability that is evident, especially in phase, is less than is to be expected by chance and that reasonably accurate predictions can be made of the course of future variations in population size (Davis 1957, MacLulich 1957). However, there has been considerable controversy concerning the true significance of cycles (Cole 1954, Hickey 1954).

The short-term cycle is commonly 3, 4, or 5 years long, although it may be as short as 2 years, or as long as 6 years (Elton 1942). The snowshoe rabbit cycle varies between 8 and 11 years; the lynx cycle, between 8 and 12 years (MacLulich 1937). The coefficient of variation, standard deviation divided by the mean, for different species having the short cycle varies from 30 to 50 per cent, and is of the same order of magnitude for the longer cycle (Cole 1951). It is of interest that by drawing numbered cards from a well shuffled deck or rolling dice (Palmgren 1949, Hutchinson and Deevey 1949) or plotting random numbers (Cole 1951) short and long cycles may be obtained of about the same relative lengths and variation coefficients as animal population cycles.

In comparing the frequency of peaks in populations and in random numbers it has been a common practice to designate any number as a peak which is higher than both the preceding and following numbers, regardless of the amount of difference between them. This, however, is not justified with natural populations of animals, since minor variations may be due to sampling errors or to secondary factors modifying a major trend. According to criteria used in this text, a peak would not be considered real unless the size of the population at that time is at least two or three times its size during the preceding and following depression. When only such conspicuous peaks are considered, oscillations in random numbers are lengthened and some of their correspondence to natural cycles is lost (Cole 1954). Extreme fluctuations between peaks and lows in population cycles are ordinarily of much greater amplitude than occur in mathematical models (Pitelka 1957). Of course, the criteria by which a particular peak is to be evaluated depend on the accuracy to which the population size was measured. These peaks should be determined in as objective a manner as possible. Before oscillations in the size of natural populations are considered cyclic, they should first be tested statistically for randomness. Only after that is done is it profitable to look for periodic or automatic mechanisms that may be involved.

The reality of cycles may be further tested by the amount of synchrony that they exhibit. If it is shown that peaks and troughs in the oscillations of different species in a local area are not correlated in time, and oscillations of populations in different regions occur independently of each other, one should take warning that a variety of factors may be involved that fluctuate in their action at different times, in different places, and on different species, in essentially a random manner. If such synchrony is determined, then some master factor or set of factors must be affecting all populations alike, although it is still necessary to determine whether the action of the master factor on the population is cyclic in its timing and effect, or whether it is being exerted in an irregular manner. We need to examine the extent to which population oscillations are synchronized.

Synchrony

With the 9–10 year cycle, local areas may show peak populations that are out of phase with other local areas by one, two, or three years. But when large regions are considered, the peak is manifested over three or four years in the course of which most local areas reach maximum populations while the following trough in the regional cycle may spread over five or six years when very few, if any, local areas have large populations (Butler 1953). A similar relation probably holds between local and regional fluctuations with the 3–4 year cycle. Synchrony is sometimes evident in local populations that are isolated by a hundred or more miles from other populations of the species (Brooks 1955).

Some variation in cyclic tempo occurs in different parts of the world, although generally they are close to being in phase. Local areas out of phase with the main cycle commonly come back into phase by the time the next peak is reached. The main cycle of grouse and ptarmigan over most of Canada and in northern United States has shown peaks in 1896, 1905, 1914, 1923, 1932–33, 1941–42, and 1950–51. In the maritime provinces of Canada—Newfoundland, New Brunswick, Nova Scotia, and Prince Edward Island—the cycle is advanced 3 years ahead of the main cycle; in Alaska, the cycle lags by 3 years. In Britain, the grouse and ptarmigan cycle has a mean length of 5–6 years, but in Finland and Scandinavia it is only 3–4 years, although some of the same species are involved. In North America the grouse cycle is nearly synchronous with the cycle of the snowshoe rabbit, while in Scandinavia it coincides with the cycle of lemmings (G.R. Williams 1954).

The lemming cycle in Canada is similar to that in Norway (Elton 1927). Recent peaks in the 3–4 year cycle for small rodents in Finland, Norway, and

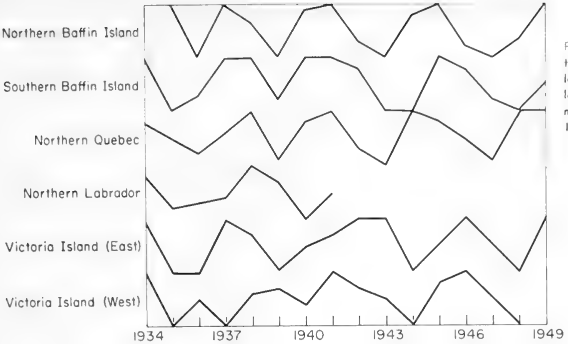


FIG. 17-4 **Relation between peaks and lows of lemming cycle at different localities in eastern and northern Canada (Chitty 1950).**

eastern North America have occurred in 1923, 1926, 1930, 1934, 1938, 1941–42, 1945–46, 1948–49, and 1953, with deviations of one or more years for particular regions (Siivonen 1954). A peak occurred in Alaska in 1956.

The predator cycle is dependent on the cycle of the herbivorous mammal or bird prey species. The correspondence in the cycles of predator and prey is usually close, although that of the predator sometimes lags a year behind that of its prey (Chitty 1950, Butler 1953). The snowy owl emigrates in large numbers from Canada into the United States within a year after the decline in the lemming population (Shelford 1945). In those parts of Greenland where the fox population lives largely on lemmings, the 3–4 year fox cycle is very pronounced, but this is not true for the coastal areas where the fox depends on a variety of food other than lemmings (Braestrup 1941).

Intrinsic causes

According to early mathematical theories of Lotka and Volterra (D'Ancona 1954) and of Nicholson and Bailey (1935), a population consisting of a single prey species and a singe predator or parasitoid species occurring together in a limited area, with all external factors constant, automatically displays periodic oscillations or cycles in the numbers of both species. As the predator population increases, it will consume a progressively larger number of prey until the prey population begins to decrease. As the number of prey diminishes, there will be less food for the predator, and they will thus decline. After a time the number of predators will be so reduced that the high reproductive rate of the remaining prey will more than compensate for the loss from predation, and the numbers of the prey species will again increase. This will be followed shortly by an increase

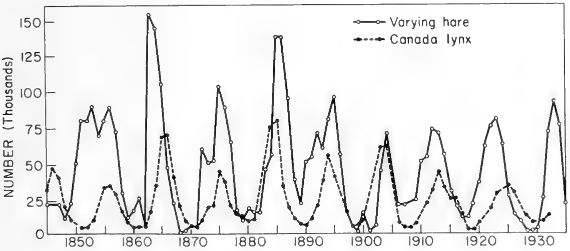


FIG. 17-5 **Population cycles of the snowshoe rabbit and one of its chief predators, the Canada lynx, in northern Canada (data adjusted for years 1912 to 1920), based on number of pelts handled by the Hudson Bay Company (from MacLulich 1937).**

in numbers of the predator. The cycle would thus continue indefinitely. According to the differential equations, the predator will never be able completely to destroy the prey, nor will the predator species ever completely disappear by reason of starvation.

There is considerable controversy concerning this theory (Andrewartha and Birch 1954). Gause (1934, 1935) conducted a test in a classic series of experiments with protozoan cultures. An experimental food chain was established: boiled oatmeal⟶bacteria⟶*Paramecium caudatum*⟶*Didinium nasutum.* When five *Paramecium* were introduced one day and three *Didinium* two days later, the population of *Paramecium* was exterminated by the predator. The predator, left without food, disappeared soon after. In another experiment,cover sediment was introduced into the microcosm, in which the *Paramecium* could hide, thus to escape the attacks of *Didinium.* The same number of each species was introduced at the same time. The number of predators increased, and they devoured many of the prey. However, the remaining prey escaped into the cover, and the predators died of starvation. When this happened, the prey, now unchecked, increased in an unlimited manner. When, on the other hand, a microcosm was prepared in which there was no refuge, and one *Paramecium* and one *Didinium* were introduced on every third day, a series of oscillations resulted. It is suggested that continual cycling of prey and predator populations could be maintained only with immigration of individuals from the outside. In other experiments, interrelated cycles of *Paramecium* and the yeast on which it fed were established (Gause 1935).

In experimental greenhouse plots of strawberries, populations of an herbivorous mite, *Tarsonemus pallidus,* and its predator, another mite, *Typhlodromus,* fluctuated regularly in relation to each other. At low populations, the prey species was relatively secure in the cover offered by hairs, spines, and leaf crevices, thus avoiding annihilation. The predator species survived because it utilized honeydew and other nourishment as substitute food until the prey species again increased in numbers (Huffaker and Kennett 1956).

Reciprocal fluctuations in the density of the azuki bean weevil and its larval parasitoid, a braconid wasp, were sustained experimentally under constant conditions for 112 successive generations. Apparently the prey was able to survive in the low of the cycle because of the difficulty the parasitoid experienced in finding the surviving individuals; the parasitoid, however, never became extinct (Utida 1957).

These examples indicate that oscillations in the populations of predators and prey can be sustained for relatively long periods of time if such factors as cover, buffer food, or immigration are introduced into the experiment. This background of experimental studies is useful in the analysis of possible causes of the more or less regular oscillations in animal numbers that are observed under natural conditions.

In an area near Point Barrow in northern Alaska, Siberian lemmings were scarce from 1949 to 1951, increased in 1952, and were near or at a peak in 1953. Associated with this cyclic rise in the lemming population was a marked increase in the number of predators. There was no breeding in 1951 of pomarine jaegers, snowy owls, and short-eared owls; very few were even seen. In 1953, however, breeding pairs were recorded in densities respectively of about 18, 0.3, and 3–4 per 250 hectares (per square mile). Least weasels and Arctic and red foxes increased from scarce or no record to common. Because of this heavy predation, the lemming population was reduced by mid-July of 1953 to $\frac{1}{10}$ or less of what it had been when the snow cover melted in early June (Pitelka *et al.* 1955).

Cyclic changes between 1929 and 1940 in the collared lemming at Churchill, Manitoba, were accompanied by marked fluctuations in breeding populations of snowy and short-eared owls and of the rough-legged hawk (Shelford 1943). This rapid build-up of predator populations must be attributed to their ability to shift from one region to another according to availability of local prey. The lemming becomes more vulnerable to predation when large populations consume the vegetative cover. Influxes of predators sufficient to exert a controlling role in outbreaks of mice (Banfield 1947), ruffed grouse, and snowshoe rabbit (Morse 1939), and bobwhite (Jackson 1947) have been reported for regions as far south as Toronto, Minnesota, and northwest Texas.

The collared lemming breeds in the winter, at least to some extent, as well as during the summer (Sutton and Hamilton 1932), as does, apparently, the Siberian lemming (Pitelka *et al.* 1955). When lemmings are exposed to heavy predation during the summer, it is likely that the main population growth comes between August and the following June, during which time they are protected by a snow cover. When snow is inadequate, heavy predation doubtless continues throughout the year. With the lack of snow insulation, considerable mortality may also result from effects of low temperature (Shelford 1943). There is no evidence, however, that snow cover occurs in cyclic harmony with the lemming populations, necessary were snow the critical factor producing the lemming cycle.

A number of general theories of possible intrinsic cycle causes (Dymond 1947, Grange 1949, Lack 1954a) have been found inadequate. Particular cycles have been explained for several species, such as for *Daphnia* under experimental conditions (Slobodkin 1954), sockeye salmon in the Fraser River

(Dymond 1947), and black crappies in the Illinois River (Thompson 1941), but these explanations have limited application.

A persistent theory of the general cause of cycles hypothesizes that animal populations build up to a peak, at which time an epidemic disease occurs so reducing numbers that the disease can no longer spread. The cycle then starts over again. Epizootics observed in cyclic species are those caused by the blood-sucking stomach worm *Obeliscoides cuniculi* in the snowshoe rabbit; the blood protozoan *Leucocytozoon bonasae* in the ruffed grouse; protozoan infection of the brain caused by *Toxoplasma* in rodents; and so forth. However, these diseases have been encountered in some cyclic declines but not in others and offer no explanation of the regular recurrence of the cycles. *Toxoplasma*, for instance, was reported in three early population declines of rodents, but was not demonstrably present in more recent declines (Elton 1942).

It is generally agreed that the basic cycle is that of the herbivores: rodents, grouse, snowshoe rabbit, and the like. With a rise in number of herbivores, predator populations may eventually increase sufficiently by reproduction and immigration to reduce the herbivores, but the predator population cycle depends fundamentally upon the herbivore cycle. The herbivore cycle may in turn be dependent on interrelations with its plant food supply. This suggests the following explanation.

Northern plants are often unable, in the short season available, to make a luxuriant vegetative growth and produce seed every year. During lemming peaks, the animals deplete their usual food plants and are forced to turn to emergency species which are not self-sustaining. A period of two or more years may be required, following an irruption in the lemming population, for full recovery of the vegetation both quantitatively and qualitatively. The relation between herbivores and plants is very similar to that between predator and prey. The difficulty with this hypothesis is the lack of evidence that lemming mortality during population declines is actually a result of starvation. Species depending on seeds for food would be similarly affected by the interval between abundant seed crops (Lack 1954a, Thompson 1955a, Watson 1956, Lauckhart 1957).

Variations in mineral salts within plants may be involved in the cycles of herbivorous species. Variations in climate may affect the bacterial flora of the soil and consequently the availability of calcium to plants. In Bavaria, it has been possible to correlate the gradual decrease in calcium content of hay with the development of "licking disease" in cattle. Other elements, although needed only in minute quantities in animal metabolism, sometimes lead, if absent, to an upset in the acid-base balance of the body and the development of acidosis and ketosis or other effects (Braestrup 1940, 1942).

Inadequate nutrition, either quantitatively or qualitatively, is well known to affect the rate of reproduction in animals (Hammond 1955). The size of egg clutches and the vigor of the hatched young in grouse and other tetraonids in Finland seem to depend on whether the females are able to get new green vegetation for food in the critical period just before the start of egg-laying. That this vegetation become available requires that temperature be sufficient to melt the snow cover and to initiate plant growth early in the year (Siivonen 1957).

Changes in reproductive vigor and health may also depend on the vitamin content of the food consumed (Mason 1939) and on the extent of the animal's exposure to solar radiation. The vitamin content of animal food is known to vary quantitatively from time to time (Lehmann 1953).

It is obvious that at times of high population densities animals are subject to increased stresses of various sorts in their search for food and cover and escaping predators. They may have to go longer distances to find the essentials for existence and to fight with other animals for possession of them. All of this puts an extra drain on their energy resources at the same time that they may be compelled to subsist on inferior food or tolerate nutritional deficiencies of one sort or another. The body adapts physiologically to these stresses under the stimulus of increased hormone secretion from the adrenal and pituitary glands, but when the stresses for existence and reproduction become too great, death results. It has been postulated that the die-off at the end of a cycle is due directly to such an exhaustion of the adrenopituitary system rather than to such external factors as lack of food, disease, or predators (Christian 1950). "Shock disease" is a manifestation of this stress syndrome. It has been repeatedly observed in Minnesota during the decline of the snowshoe rabbit cycle. Symptoms of the exhaustion phase of the stress syndrome have also been observed in wild populations of European meadow voles (Frank 1953). The continuous decline of populations for three to five years may be due to constitutional defects resulting from the stress of overcrowding being transmitted to following generations (Chitty 1952), but direct evidence for this is meager.

The difficulty in finding a satisfactory explanation of cycles as they occur under natural conditions is that they may be only one manifestation of an underlying, more fundamental, cycle in physiological vigor which is not easily detected. Changes in population size are not always correlated with changes in physiological vigor, since extremes in weather may at times produce catastrophes even in healthy and vigorous populations. But changes in physiological vigor

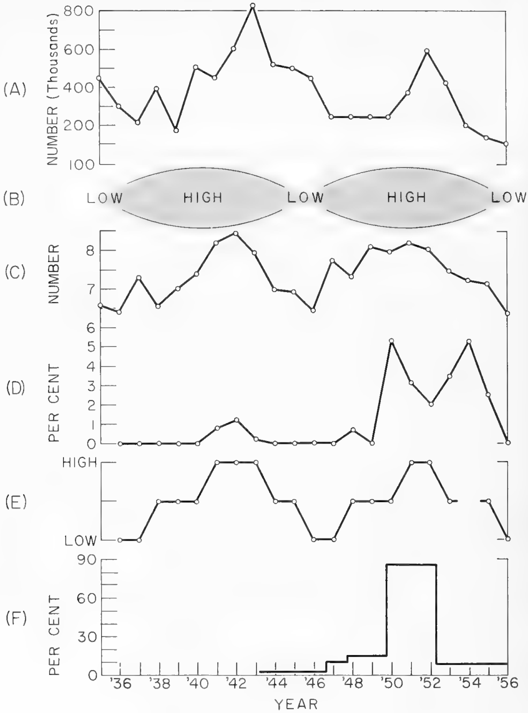


FIG. 17-6 **Changes in population and reproductive and physiological vigor of muskrats in Iowa, correlated with the 9–10 year grouse-rabbit cycle (peak years 1941–1942, 1950–1951) elsewhere over North America (Errington 1957). (A) autumn populations; (B) grouse-rabbit cycle; (C) size of litters; (D) young breeding in year of their birth; (E) tolerance of crowding; (F) resistance to disease.**

become evident with variations of fecundity and success in raising young, in susceptibility to disease, and in individual behavior (Errington 1945, 1954, 1957). When chinch bugs were cultured experimentally in the laboratory, starting each year with new individuals collected out-of-doors, there were marked differences during the nine-year period of study both in number of generations raised per year and in number of young per generation. The rating of reproductive vigor rose from 1.4 in 1917 to 31.2 in 1919, dropped to 1.4 in 1921, and rose again to 270 in 1925. These differences from year to year were apparently not related to the density of population, and could not be otherwise explained (Shelford and Flint 1943). Changes in reproductivity and behavior of muskrats in Iowa did not correlate closely with variations in population size of the species, but did coincide in a general way with the grouse-rabbit cycle in other parts of North America.

Cycles in the environment

We have considered so far only factors *intrinsic* to populations; *extrinsic* factors (Hutchinson and Deevey 1949) may play a contributing role. Certainly the amount of synchrony within a species evident over extensive areas and between different species or events that are otherwise clearly unrelated (Dewey 1960) is greater than can be explained by chance alone and suggests that some climatic or extraordinary factor may be effective, either directly or in controlling the time schedule at which the intrinsic factors function.

There have been various attempts to show cycles in the weather. Bruckner (1890) examined records since 1700 of temperature, precipitation, and other factors and suggested a cycle of around 35 years. Scarcities of ducks reported in the 1820's, 1860's, 1890's, and 1930's appear correlated with drought and may possibly represent the intervals of the Bruckner cycle (Rowan 1954).

Weather is affected by variations in solar radiation (Abbott 1931, Clayton 1943). Sunspots, chromospheric eruptions, solar coronal disturbances, and ionospheric and geomagnetic disturbances are indices of solar activity, but not direct measurements of it. The agent presumably effecting changes in the atmosphere and in living organisms may be short-wavelength ultraviolet radiations or emitted charged particles. Emissions from the sun are constantly undergoing great fluctuations, with maximum intensities for short periods being a hundred or a thousand times the minimum intensities.

Sunspots are the only expression of solar activity that has been measured over a long period of time (Willett 1953). The intervals between peaks in the mean daily number of sunspots per year fluctuate from 7 to 17 years, average 11.2 years. A correlation between number of sunspots and temperature, rainfall, and cloudiness is sometimes indicated but needs more complete substantiation before it can be fully accepted (Thomson 1936). For instance, an analysis of records spanning 109 years for the period May through October in southern Wisconsin indicates lower temperatures, greater precipitation, and less sunshine in years when sunspots were increasing or at a maximum than when they were decreasing or at a minimum (Morris 1947). A similar correlation between summer rainfall and the sunspot cycle has been demonstrated for the Toronto, Canada, area (Clayton 1943).

The sunspot cycle is as variable in length as are the cycles of grouse and snowshoe rabbit, and there have been repeated attempts to correlate these cycles (MacLagan 1940, Huntington 1945). It is doubtful, however, if such a correlation is real. Since 1750, the sunspot cycle has coincided with the snowshoe rabbit and lynx cycles part of the time, but goes out of phase until one becomes the inverse of the other. If solar radiation is responsible for population cycles, it is clear that the number of sunspots is not a reliable index for judging the intensity of radiation.

Since the growth of trees and the width of the annual rings they form is largely dependent on rainfall, one may conjecture the weather record back 3,000 years by measuring the width of annual rings in the giant sequoias. This analysis of tree rings indicates the possibility of a variety of weather cycles, some important ones being in the neighborhood of 9–10 years (Douglass 1928). Weather cycles of 3–4 years are difficult to demonstrate, but an analysis of changes in barometric pressure and other characteristics of the annual atmospheric circulation over the British Isles indicates that they may exist (Goldie 1936). Cycles or outbreaks resulting from climatic factors are not necessarily absolutely synchronous over large areas. There is a limit to the size of the area over which a change in weather produces a single common effect. Outbreaks of spruce budworm progressed eastward in Canada between 1945 and 1949. These outbreaks were probably less a result of spontaneous dispersal of the moth, although this was a contributing factor, than of the progressive eastward circulation of favorable polar air masses (Greenbank 1957).

Solar radiation may affect animals and plants in other ways than through the weather. The atmosphere above the earth's surface is divisible into the troposphere, which extends to a height of 3–4 km (5–6 miles); the stratosphere, which rises to about 30 km (50 miles); and the ionosphere, which extends beyond. The concentration of oxygen diminishes with height above the earth, and becomes very low in the stratosphere. However, at heights of about 10 to 20 km (15 to 30 miles), there is a thin but concentrated layer of ozone (O_3). Oxygen and ozone are responsible for absorbing most of the ultraviolet radiation (below 3200 Å) emanating from the sun before it reaches the earth's surface. Atmospheric gases, especially carbon dioxide and water vapor, absorb most of the infrared wavelengths (over 20,000 Å) (Shaw 1953). A little ozone in the atmosphere at the earth's surface is stimulating to animals, but a high amount is harmful. There is some experimental evidence that ionization of the air, i.e., the conversion of neutral gas molecules into electrically charged ions, may affect the health and the vigor of animals. The height of the ionosphere and ozone layers above the earth is controlled by the intensity of solar radiation, and it is possible that cyclic variations in the height of these layers may affect organisms in ways that are little understood at the present time (Reiser 1937, Huntington 1941).

Fluctuations in solar ultraviolet radiation vary the extent of ionization of air and the rate of ozone formation. The ozone layer serves as a protective blanket which prevents ultraviolet rays from destroying all life on the earth. In small doses, ultraviolet is anti-rachitic, germicidal, and erythemal; in some species ultraviolet also affects skin pigmentation (Luckiesh 1946). Animals obtain vitamin D either as a product of direct radiation of the skin or in the food that they consume. Wavelengths other than ultraviolet are important, of course, to photosynthesis and the trophic cycle, and for heat.

Continuous ultraviolet radiation of the sun has been measured only haphazardly in the past, and in only a few localities, but the data available indicate only a general relation to the sunspot cycle. Variations in monthly averages of ultraviolet intensity and sunspot numbers may show an inverse rather than a direct relation for a year at a time (Pettit 1932), and variations in yearly averages do not closely correspond (Thomson 1936).

In order to establish any correlation between ultraviolet and variations in the size of animal populations, it is necessary first to determine what stage in the yearly cycle of the animal's activities is sensitive to its effect and then to use quantitative data on ultraviolet intensity for only those critical periods. Likewise, other factors, such as rainfall, may mask the effect at certain intensities. Such analyses are complicated, but a few such studies indicate that medium intensities of ultraviolet radiation combined with optimum conditions of rainfall or weather correlate with highest populations of chinch bugs, bobwhite quail, prairie chickens, pheasants, cottontail rabbits, pronghorns, and the amount of butterfat in cow's milk (Shelford 1951a, 1952, 1954a).

Solar radition is not received in equal intensities in all parts of the world. Its intensity varies because of inclination of the earth's axis relative to the sun, differences in terrain, amount of cloudiness, and so forth. Solar radiation likewise does not have an identical effect on all species because of differences in their sensitivity to it and because critical periods in their life cycles come at different times of the year.

The lack of agreement among scientists as to the cause of oscillations in population size is evident from the number of explanations that are offered. It is clear that much more information on animal populations under both experimental and natural conditions is required to obtain full understanding of the dynamic forces involved.

SUMMARY

Populations may increase or decrease in size progressively through a period of time; they may suddenly irrupt when conditions become favorable, or decline precipitately with unfavorable weather, or they may vary cyclically. The most apparent cyclic phenomena are the 3–4 year rodent cycle and the 9–10 year grouse-rabbit cycle. Populations of several predators display correlated patterns. Cycles are most clearly developed in the far North.

Many theories have been advanced as to the immediate cause of population cycles; coactions between prey and predator, disease, depletion of food supplies, and changes in nutrient value of foods, physiological stress, and physiological vigor, but a complete and satisfactory explanation is not yet at hand. There is enough synchrony in the timing of cycles over the world as to suggest that variations in weather or solar radiation may be involved.

18

Niche Segregation

The *ecological niche* is a particular combination of physical factors (microhabitat) and biotic relations (role) required by a species for the normal course of its life activities.

The term and concept was first developed by Joseph Grinnell (1917, 1924, 1928) of California. He considered the ecological niche the ultimate distributional or spatial unit occupied by just one species, or subspecies, to which that species is held by structural and instinctive limitations such as climatic factors, kind and amount of food, suitable nesting-sites, and cover. He recognized the close relation between animal distribution and cover, and he spoke of animals generally and birds in particular as having *preference* for a particular niche, *choosing* surroundings consistent with their needs. At about the same time, the Englishman Charles Elton (1927) independently defined the niche in more functional terms as an animal's *place in the biotic environment, its relation to food and enemies.* The present-day concept of the niche is an elaboration of these basic ideas, with emphasis on the relation of the organism to both the physical and biotic factors of its environment. The restriction of a species to a particular niche depends on its structural adaptations, physiological adjustments, and developed behavior patterns.

In many respects, the species in its niche is the only finite unit of animal distribution; at least the relationship is the one most subject to objective and concrete definition. The concept of niche in the hierarchy of ecological distributional units is more or less equivalent to the concept of species in the hierarchy of taxonomic units. When we begin to group niches into the higher units of habitat, biocies, biociation, biome, and realm we become as increasingly vague and arbitrary as we are when classifying species into genera, families, orders, classes, and phyla.

CHARACTERISTICS OF THE NICHE

Microhabitat

The physical features of substratum, space, and microclimate are basic determinants of whether a particular niche can be occupied by a given species. The basic differences in marine, fresh-water, and terrestrial habitats restricting the distribution of communities is immediately obvious. The features differentiating microhabitats are less apparent, but assume major significance when particular occupants of it, rather than the community as such, are under investigation (Prosser 1955).

The intimate relation between niche segregation, substratum, and microclimate is well shown in the distribution of four species of ants in a pine forest of

Scotland (Brian 1952). On decaying stumps, the number of nests of *Formica fusca, Myrmica scabrinodis, M. rubra,* and *Leptothorax acervorum* were found to be in the ratio of 23:20:12:7, but on the ground away from stumps, the ratio was 1:13:18:1. The apparent restriction of *F. fusca* and *L. acervorum* to stumps is probably attributable to the fact that they are not mound-builders; rather, they commonly make galleries in wood. *L. acervorum* makes its galleries in wood that is too hard for the other species to work; galleries so small that the larger species are excluded. A difference between species in point of position occupied on the same stump was also observed. *F. fusca* tended to occupy the warmer southerly sites but often extended over the entire stump. *M. scabrinodis* was widely distributed, but there was a tendency to concentration on the east side of the stumps. *M. rubra* occurred principally in the cooler, moister north and west sectors. Away from the stumps, *M. scabrinodis* was especially characteristic of small knolls resulting from the decay of stumps no longer favored by *M. fusca,* while *M. rubra* extended into cooler moister soils. *F. fusca* was the most aggressive and socially dominant species, unchallenged in its occupancy of the best sites. *M. rubra* tended to occupy the second-best sites, leaving them only when they became temporarily unsuitable. *M. scabrinodis* often came into the vacated sites and when once established could not be dislodged.

In earlier chapters, we have described how the characteristics of the soil, which the females first test with their ovipositors, determine where grasshoppers and tiger beetles will lay their eggs. Of 18 types of rodents studied in Utah, 4 were found only in rocky situations, 2 only in gravelly soils, and 2 only in sandy soils; the other 10 were less limited by the type of soil (Hardy 1945). In aquatic habitats, species segregate according to whether the bottom is rock, sand, or mud. The swift current limits the inhabitants of streams to species possessing clinging structures and proper orienting behavior.

Congeneric species of ectoparasitic mites and fleas on small mammals commonly are distributed between several different host species. When they occur on the same host, they are segregated by species on different parts of the body, a given species is present only when the host occurs in a particular type of vegetation, or they occur at different seasons (Jameson and Brennan 1957).

The importance of microclimate in niche segregation of species is shown by a study made in Danish bogs (Nørgaard 1951). The low humidities and high temperatures obtaining at mid-day on the surface of the peat mat restrict one species of spider to the stalk region of the sphagnum. Another species of spider tolerates these conditions, so the two species divide the habitat between them.

Microclimate is often a major factor in determining whether a species can maintain itself against competition in a particular microhabitat. This has been shown experimentally. When equal numbers of two related species of beetles are introduced into the same flour container and placed at a particular combination of temperature and relative humidity, one species becomes established, the other is eliminated. The particular species favored in the various microclimates are as follows (Park 1954):

34°C–70 % R.H.	*Tribolium castaneum*
34°C–30 % R.H.	*Tribolium confusum*
29°C–70 % R.H.	*Tribolium castaneum*
29°C–30 % R.H.	*Tribolium confusum*
24°C–70 % R.H.	*Tribolium confusum*
24°C–30 % R.H.	*Tribolium confusum*

Similar reversal of dominance has been found to take place at high and low temperatures with different species of grain beetles (Birch 1953), *Drosophila* flies both in Europe (Timoféeff-Ressovsky 1933) and in North America (Moore 1952), two insect parasitoids using the same host (DeBach and Sisojevic 1960), and turbellarian flatworms (Beauchamp and Ullyott 1932). Usually the species favored by a given micro-climate has a higher rate of population growth at that particular temperature or humidity.

There is a positive correlation between high oxygen tensions required by trout for saturating their blood hemoglobin and the oxygen-rich waters that they select. The restriction of these fish to cold waters is correlated with the fact that a rise in temperature decreases the oxygen-loading capacity of the hemoglobin. Catfish and carp, common to warm waters of low oxygen high carbon dioxide content, have hemoglobin that loads and unloads at low oxygen tensions and is less sensitive to changes in carbon dioxide tension and temperature (Prosser *et al.* 1950).

Arctic mammal species differ in thickness and density of fur, which insulate against loss of body heat, and this determines whether they can sleep above ground and be active during the winter or whether they must confine themselves to nests and runways below the snow level (Scholander *et al.* 1950).

In central Illinois, the short-tailed shrew is largely subterranean in habit and occurs in moist habitats; the woodland white-footed mouse is nocturnal and inhabits the forest floor; the prairie vole is restricted to grassland and the most arid of the habitats of the three species. There is a connection between the amount of water available in the habitats and the level of water exchanges in the animal. At 19°C, for instance, the rate of water absorption and loss in the shrew is twice that of the mouse. The rate of total water turnover in the vole is about the same as in the mouse, but water loss through the lungs and skin is much lower, indicating acclimatization to a drier habitat (Chew 1951).

Diurnation and aspection

When two or more species are competing for the same resources of a single habitat, this competition is reduced or eliminated if one species makes use of these resources at a different time of day, or in a different season, than the other.

The white crappie and black crappie are very similar in habits, food requirements, and local distribution, except that the white crappie is more often found in small rivers and creeks than the black crappie, which prefers hard-bottom lakes. Both species feed most extensively at dusk; there is a smaller feeding activity peak at dawn. Both species feed to some extent during the night. However, the white crappie feeds considerably more during the daylight period than does its more aggressive black cousin, and this slight difference in timing may be sufficient to permit it to occur in the same areas as the black crappie (Childers and Shoemaker 1953).

During a winter in England, when birds were coming to banding traps for food, it was noted that the European robin did so most frequently just after sunrise and just before sunset, the European blackbird just before and after midday, while the blue tit had peaks of feeding between the feeding times of the other two species (Lees 1948).

The females of the butterfly *Colias eurytheme* may be either orange or white; all males are orange. There is partial separation of the two color phases in that the white females are relatively more active in the early morning and the yellow females later in the day (Hovanitz 1948).

The two grasshoppers *Arphia sulphurea* and *A. xanthoptera* occupy similar niches except that *A. sulphurea* overwinters in the nymph stage, reaching maturity from April to late July, while *A. xanthoptera* overwinters in the egg stage and hence requires a longer time to mature in the spring. The adults of the latter species occur from late July to early November (Blatchley 1920).

Three kinds of sockeye salmon occur in Cultus Lake, British Columbia (Ricker 1938): (1) the normal anadromous stock, whose offspring may either migrate out to sea or remain as (2) residuals, and (3) the land-locked salmon, which remain continuously in the lake. The anadromous and residual populations differ in breeding coloration, but both spawn from October to December. The land-locked forms, which closely resemble anadromous sockeye in breeding coloration, spawn only in August and September.

The tern *Sterna virgata* nests on the Kerguelen Islands in October and November; *S. vittata* uses the same nesting area in January and February. The niche of each species differs somewhat further in that *S. virgata* feeds to some extent in inland waters, but *S. vittata* is strictly marine (Murphy 1938).

Tropical species of dragonflies and damselflies which have recently extended their range northward confine their main periods of flight to the warmest months and to the middle of the day. Native species that are better adapted to colder climates are active in early spring and autumn and in the twilight hours of the day (Kennedy 1927). Times of emergence of stream insects are also correlated with their ancestral places of origin and the extent of their acclimatization to temperature.

Shelter and vegetation

Animals require shelter or *cover* as a protection against unfavorable weather and enemies. Caves, overhanging ledges, deep valleys or canyons, or burrows in the ground may serve as shelter for terrestrial animals. The darkness of night is a protection against diurnal predators; daylight is a protection against nocturnal ones.

Vegetation is an important source of shelter for animals. Some animals cannot tolerate too much solar insolation, hence seek shade. In arid habitats, jack rabbits shift the location of their forms on the ground at different times of the day to stay in the shade of bushes, and it is a common sight in prairie or desert regions to see horned larks, meadowlarks, or other birds lined up in the narrow shadow cast by telephone poles or fence posts. Burrows of all sorts, whether in the ground or in trees, give the animal good insulation against both winter cold and summer heat. The foliage of trees, shrubs, and even grasses and vines reduces the amount of heat radiated from the bodies of animals, especially warm-blooded ones, on cool clear nights, and vegetation in general serves as a windbreak. Birds keep to the lee side of exposed patches of woods during cold windy weather.

By staying under cover, prey animals may escape notice of passing predators, or if detected, may more easily avoid capture. Dense vegetation, thorny thickets, burrows, and other situations impenetrable to predators are sometimes called *escape cover*. We also speak of *nesting cover, winter cover,* and *roosting cover,* depending on the particular purpose which the cover serves. Animals are often protectively colored to conceal themselves better from enemies in particular kinds of cover.

When the beetles *Tribolium confusum* and *Oryzaephilus surinamensis* are introduced experimentally into a flour medium, *Tribolium* is ordinarily successful, *Oryzaephilus* is eliminated. But when the flour medium contains pieces of glass tubing of such bore as will exclude *Tribolium* but let the larvae of *Oryzaephilus* enter and pupate, both species survive (Crombie 1946).

Most vertebrates and some invertebrates, especially insects and spiders, build nests, usually of plant material. The type of nest it builds is grossly characteristic of a species and dependent on inherited behavior patterns, yet individual nests are uniquely modified to fit into particular situations. Nests protect eggs and young against weather, and are usually well concealed from enemies.

Bird species are commonly found at different heights or in particular strata of the vegetation associated with the characteristic location of their nests (Beecher 1942), where they seek refuge from enemies (Dunlavy 1935), where they do their feeding (Hartley 1953), or the location of their song-posts (Kendeigh 1947). Birds nesting in the tree-tops often feed outside the forest (Colquhoun and Morley 1943). Bird feet are as variously adapted to foraging in different strata or in different habitats as bills are variously adapted to procuring different kinds of food. It is often obvious, from the arrangement of toes, length of the legs, and other characteristics, whether a bird scratches the ground for its food, gets its food in the air, wades in marsh, is a swimmer and diver, a percher, or a tree-trunk climber. However, the minor adaptations of legs, bill, and wings in closely related species that enable them to occupy different niches within the same general type of vegetation are more difficult to detect (Dilger 1956). Segregation to a niche may involve, in addition to obvious external characters, many adaptations throughout the body in skeleton, musculature, and other organs (Burt 1930, Richardson 1942). Many types of animals other than birds, for instance mosquitoes, are segregated by strata to where they most commonly occur (Snow 1955).

Warblers are numerous in the evergreen-deciduous forest ecotone of eastern North America because they nest and feed in so many diverse niches (Kendeigh 1945):

Blackburnian warbler—top level of evergreen trees
Black-throated green warbler—middle level of evergreen trees
Magnolia warbler—low level of evergreen trees
Redstart—secondary deciduous growth
Black and white warbler—tree trunks
Black-throated blue warbler—shaded shrubs
Chestnut-sided warbler—sunlit shrubs
Canada warbler—wet shaded ground
Yellowthroat—wet sunlit ground
Ovenbird—dry shaded ground
Nashville warbler—dry sunlit ground
Louisiana waterthrush—stream margin
Northern waterthrush—bog forest

Mammalian adaptations to different strata have already been discussed. When given a choice between a grassy habitat and a tree-trunk habitat, the short-tailed forms of *Peromyscus* mice selected the grassy habitat; the long-tailed forms, the tree-trunk habitat (Harris 1952). It has been demonstrated that the long tails of some species and subspecies give them a greater proficiency in climbing than their shorter-tailed relatives exhibit (Horner 1954). In the arid country of southern California the giant kangaroo rat is predominant in flat country covered with brush; on brushy slopes and rolling hilltops the Fresno kangaroo rat replaces the giant kangaroo rat; the Heermann's kangaroo rat is forced to live on the open plains since it cannot compete successfully with the other two species on brush-covered land (Hawbecker 1951).

Considerable evidence was presented in Chapters 7, 8, and 9 to show how animal distribution correlates *locally* with types of vegetation, and more will be presented in Section IV with respect to *geographic* distribution. Except for a few herbivorous and parasitic species, animals do not respond to the taxonomic composition of vegetation when they seek cover or food, but rather to life-form of plants; or they respond to the micro-climatic conditions established by the vegetation.

In northern Europe, the kinglet *Regulus regulus* occurs with the chickadee *Parus atricapillus* in spruce and pine forests, but is mostly absent from the birch forests which the chickadee frequents. The kinglet is unable to feed extensively at tips of the pendulous birch twigs because, unlike the chickadee, it is less able to hold itself in an inverted position, because of poor development of certain muscles in the leg (Palmgren 1932).

The ovenbird is absent from coniferous forests unless a few deciduous trees are also present, since the bird requires broad leaves for construction of its oven-shaped ground nest. The red-eyed vireo feeds on insects taken from the leaves and the smaller stiff twigs of deciduous trees. It is mostly absent from coniferous forests where the needle-shaped leaves are attached on all sides of flexible twigs and the bird finds difficulty in obtaining a footing (Kendeigh 1945). When birds of different species were given a choice between the branches of coniferous trees and those of deciduous trees, there was evident a direct correlation between length of foot-span, i.e., the distance from the tip of the middle front toe to the tip of the hind toe, and the frequency of perching on the evergreen branches. Birds with small foot-spans greatly preferred the branches of deciduous trees (Palmgren 1936).

Three species of garter snakes are found together in Michigan, but *Thamnophis butleri* is restricted to grasses and sedges near water, *T. sauritus* prefers bushy areas near water and is a frequent climber, while *T. sirtalis* occupies a variety of habitats regardless of proximity to water (Carpenter 1952).

The evidence indicates that if the type of cover required by a species is missing, that species will not occur even if all other conditions are favorable. This is of particular concern to the wildlife manager. He must learn to control succession, either by accelerating or retarding it, to give species of game the cover that they need (Leopold 1933, Elton 1939).

Food and predators

Since most organisms select their food from that most easily available to them, it is usually more important in characterizing their niches to indicate the type of food consumed and the stratum or exact microhabitat from which it is obtained than merely to give a list of species that are taken. Thus, freshwater fishes are best classified as mud-eaters, plant-eaters, plankton-eaters, mollusk-eaters, insect-eaters, fish-eaters, detritus-eaters, or omnivora (Forbes 1914). In a similar manner birds have been categorized into aerial-soaring, or perching insect-eaters; those which feed on foliage insects, seeds, or nectar; timber-searchers or drillers; feeders on ground insects, or seeds, and predators (Salt 1957).

The accurate description of feeding niches requires careful attention to details. Two or more species may feed together in the same community but be segregated from each other because they search for their food from different plant species, from different parts of the same plant, or they take different foods from the same parts of the same plants. Furthermore, species may overlap broadly in their feeding habits during most of the year but be clearly segregated during periods when food is scarce (Gibb 1954, Betts 1955).

The difference in type of vegetation inhabited by each of the three species of Michigan garter snakes mentioned a moment ago correlates with differences in kinds of food each consumes: *Thamnophis butleri* feeds almost entirely on earthworms and leeches; *T. sauritus,* on amphibians, fish, and caterpillars; and *T. sirtalis,* on both earthworms and amphibians, as well as a few mammals, birds, fish, caterpillars, and leeches (Carpenter 1952). Several species of *Drosophila* flies may occur in a single region, especially in the tropics, but each species feeds preferentially on a different species of yeast (Dobzhansky *et al.* 1956, Cunha *et al.* 1957). The spider-wasps *Anophus semirufus* and *A. apiculatus* have many very similar behavior patterns, but they avoid competition at a critical point. *A. apiculatus* hunts for its food in the sandy areas where both species nest, while *A. semirufus* moves to woods or shrubby areas to feed and feeds on a different group of organisms at that (Evans 1953).

Differences of food habits between related species often correlate with differences in size. Thus the large-billed parrot crossbill of Europe feeds on pine cones, the smaller-billed red crossbill on spruce cones, and the still smaller-billed white-winged crossbill on larch cones (Lack 1944). Two species of fish having very similar requirements occur in the same type of habitat in British Columbia, but *Cottus rhotheus* has a larger mouth than *C. asper,* and feeds on larger kinds of food (Northcote 1954). Size differences even occur commonly between related species of copepods that live together in the same body of water (Hutchinson 1951). Male and female differences of size, structural adaptations, and habits may occasion distinctive preferences in kinds of food taken and feeding location which make it possible for the two sexes to live together more comfortably within a small area than were their requirements absolutely identical (Rand 1952).

For describing the position a species occupies in the food chains of a community, it is necessary to indicate not only the kinds of food eaten but also what species prey on it and the manner in which they do so. Some parasitoids are quite specific as to the kinds of animals in which they deposit their eggs. If a parasitoid that is specific to a prey species is present in a niche, the simple presence of that parasitoid may determine the success with which the prey species will compete for and fully occupy the niche.

BEHAVIOR ADJUSTMENTS

Somehow an animal must get into a hospitable niche out of the multitude of niches available to it. Doubtless, some animals accomplish this passively by the instrument of random dispersal of spores, eggs, or larval stages, some of which by chance reach favorable locations, there to mature and survive. But higher animals have more complex nervous systems, greater intelligence, and their sense organs are more highly evolved. They are equipped to search actively for and recognize niches hospitable to them either by sight, smell, contact, or other means. For instance, the intricate migratory behavior of birds and other animals is such that they seek out nearly constant climatic environments throughout the year.

The apparent ease and speed with which a new generation of individuals discriminates a hospitable

TABLE 18-1 Percentage evaluation of sign stimuli for recognition of niches in different species of pipits (*Anthus*) (Svärdson 1949).

Species	*A. trivialis*	*A. pratensis*	*A. campestris*	*A. spinoletta*
Habitat	Forest-edge	Dry meadows	Sandy areas	Mountains, rocky shores
Light and open country	30%	40%	40%	35%
High outlooks	37	14	20	26
Green color	20	20	5	5
No vegetation on ground	5	5	30	15
Water nearby	2	15	1	15
Conspecific males nearby	4	4	2	2
Other external stimuli	2	2	2	2
Totals	100%	100%	100%	100%

niche means that they must in some way recognize the merits of that niche by definite characteristics of it that may be in the nature of sign stimuli (Table 18.1). Such characteristics are usually prominent, though they need not necessarily be the most essential features of the niche (Lack 1937).

Probably most animals exercise a deliberate, although not necessarily conscious, evaluation process in choosing one niche from those available. This has been tested experimentally by exposing the animals to gradients of environmental factors, either in the laboratory or field (Harris 1952); a variety of apparatus and procedures is available for such tests (Shelford 1929). Usually there is a coincidence of the species' experimentally ascertained preferendum and its natural preferendum. For instance *Elipsocus melachlani* and *E. westwoodi,* both psocid insects, occur abundantly on larch trees, but *E. melachlani* frequents those dead branches heavily encrusted with lichens, and *E. westwoodi* frequents living branches covered with the alga *Pleurococcus.* Laboratory experiments showed clearly that when each species was given a choice, each selected its customary habitat. Furthermore, the feeding of *E. westwoodi* was restricted almost entirely to the alga, although *E. melachlani* would feed on both the alga and on lichens (Broadhead and Thornton 1955).

For certain species, niche preference can be attributed to appropriate behavioral patterns alone. Isopod species occur in water and on land but only in places where the humidity is high. What success the group has achieved on land appears to be the result of their avoidance of the rigors of ordinary terrestrial conditions by means of behavior mechanisms that retain them in these moist cryptozoic niches, rather than to the development of any special morphological or physiological adaptations (Edney 1954).

A stereotyped behavior pattern appears to make the magnolia warbler build a nest supported in the interlocking leaves or twigs of a conifer rather than in the vertical fork of a tree or shrub, as the redstart regularly does. The black-throated green warbler originally had a nest-building behavior similar to that of the magnolia warbler, but in some regions it has taken to building in forks, a behavior which has expanded its range into both deciduous and coniferous forests. Why is the American robin restricted to localities where it can get mud to put into its nest? Others members of the family Turdidae do not use mud in their nests. There is, on the other hand, an advantage for barn and cliff swallows to use mud in constructing their nests because it enables them to use locations on the vertical sides of cliffs or buildings free of competition from other species. There appears to be no physical reason why a barn or cliff swallow could not build its nest in crevices or holes like other swallows, why a bank or rough-winged swallow could not build a mud nest like the barn or cliff swallow, or why a robin could not build like other thrushes. Such niche segregations are apparently consequences of restrictions imposed by behavior patterns alone, although one can never be sure but that each species has some hidden adaptation that keeps its characteristic kind of nest the best nest for it, and its preferred niche the best niche for it.

It is possible that certain species of birds are confined to coniferous forests because they are of northern origin and coniferous forest was the original community available to them; similarly, the broad-leaved deciduous forest is conjectured to have been the original community inhabited by species of southern ancestry. Presumably each group evolved heritable, instinctive behavior patterns which continue to drive it back to the ancestral community in which it belongs, so to speak, even though other types of communities have become available (Lack and Venables 1939).

Where two species with similar niche requirements come into competition, one species must possess better adaptation to it if it gains full possession of the niche to the exclusion of the other species (Lack 1944). Preadaptation or possession of suitable adaptations also appears a necessary prerequisite for a species to invade a new niche or habitat and successfully displace another species already occupying it, as frequently occurs (Simpson 1953a). The search for such microadaptations as might give one species an advantage over another in a competition for a particular niche is a real challenge to ecological research.

INHERITANCE

The fact that all individuals of a species behave almost identically in many of their activities indicates that these behavior patterns or instincts are in some form passed on or inherited from one generation to the next. Behavior that is learned after birth is much more variable between individuals. Behavior patterns are rooted in the structural arrangements of neurons and synapses. Once a stimulus is received a definite action results. Predisposition for a species' behavior patterns could well be inherited genetically through chromosomes and genes like any other structural or functional characteristic. These inherited behavior patterns are doubtless subject to evolutionary development as much as are structural and functional adaptations; indeed, the one may have developed synchronously with the others (Kendeigh 1952, Spieth 1952).

The often large and elaborate nests built by termites are really manifestations of behavior patterns inherent in the species. The nests of higher termites are built specifically by the sterile workers; plainly, whatever is involved in the capacity the workers have to build a certain type of nest must be transmitted genetically, through the sexual forms only. Adaptive modifications in nest structure occur and phylogenetic sequences in nest structure that correlate with phylogenetic sequences in morphological characters can be demonstrated (Emerson 1938).

The two toads *Bufo americanus* and *B. woodhousei* differ in rate of embryonic development and embryonic temperature tolerance but interbreed freely. Embryos of hybrids show an intermediate rate of development (Volpe 1952). The call of a naturally occurring hybrid toad (*Bufo americanus* x *B. woodhousei*) was found to be intermediate between the calls of the two parent species (Blair 1956).

Three sibling species of the cricket *Nemobius fasciatus* differ slightly in structure and color but are scarcely distinguishable except by the songs of the males. Although they do not interbreed under natural conditions, they were induced to do so under experimental conditions. The song of the F_1 males was intermediate between those of its parents, indicating genetic influence (Fulton 1933).

The spinning behavior of the flour moth has been shown to be inherited on a Mendelian genetic basis; it is dependent on light and food factors. At least two genes are involved; in the F_1 generation the non-spinning behavior is almost, but not quite, dominant; in the F_2 generation there is segregation of spinning individuals (Caspari 1951).

The segregation of the prairie deer mouse and woodland white-footed mouse into different niches is very definite (Table 2.1), as is also the segregation of related species occurring in chaparral (McCabe and Blanchard 1950). The same segregation to different habitats holds even between prairie (*bairdii*) and woodland (*gracilis*) subspecies of the same species (*Peromyscus maniculatus*). It is of interest that laboratory-reared individuals not previously conditioned to their natural habitats were given a choice under experimental conditions, *bairdii* selected grass habitat; *gracilis*, a tree-trunk habitat. This suggests genetic inheritance of habitat preference. In hybrids between the two subspecies, choice of the grass habitat was dominant over choice of the tree-trunk habitat (Harris 1952).

There may be transmission of behavior patterns to succeeding generations by tradition rather than by genetic mechanisms; i.e., training of young, young imitating parents, conditioning or imprinting. It has been demonstrated that some parasitoid wasps lay their eggs only in the same kind of larvae as they themselves became conditioned to during their early growth and feeding. Young birds and other animals become imprinted to their own parents, to their own species, and perhaps to their proper niche, at critical stages in their development (Baldwin 1896, Cushing 1941, 1944, Thorpe 1945).

It is very probable that the manner in which niche segregation is passed on to succeeding generations is not the same in all species. We may believe, however, that most behavior of animals has a genetic basis, but may become highly modified through practice, imitation, and experience.

INTERSPECIFIC COMPETITION

Segregating effect

Charles Darwin stated in *The Origin of Species* the case for interspecific competition as an instrument segregating species into different niches as follows (Crombie 1947):

1. The reproductive capacity of organisms is greater than the carrying capacity of the environment.
2. The range of an organism's tolerance of physical conditions and choice of food is limited.
3. The failure of an organism to survive, or be born at all, may be a result of the direct action of unfavorable habitat, predators, parasites, or competitors.

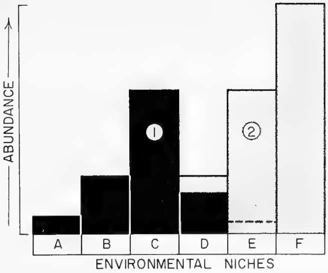


FIG. 18-1 **Species 1 finds optimal conditions in niche C, and reaches greatest abundance in that niche. It is also able to utilize niches B and D, but with less efficiency, and niches A and E only very poorly. Species 2 cannot utilize niches A, B, and C at all, finds D only partially suitable, but E and especially F very favorable. Species 1 and 2 overlap in niche D, but species 2 prevents any occupancy of niche E by species 1. The absence of competition in niche A makes it open to a species evolving adaptations to it (from Mayr 1949).**

4. When competition occurs, it is severest between organisms with the most similar requirements.
5. In general, the closer the taxonomic relationship between them, the more similarity there is in needs and habits of species.
6. When new forms appear in a given locality, either by evolvement there or by invasion after evolutionary divergence elsewhere, they will either eliminate or be eliminated by their nearest relatives if they compete with them, unless
7. Each form becomes adapted to a different niche, in which case competition between them will cease, and they may occur in proximity.

Evidence that interspecific competition is the most critical factor confining a species to this or that niche is available with the expansion of the species beyond the usual limits of its niche when this competition is removed. This expansion is often evident in geographic differences in the niche characteristics of a species. In Scotland, the mountain hare occurs at high elevations, the common hare at lower ones. In Ireland, which was isolated as an island before the common hare could reach it, the mountain hare occurs at both high and low elevations and is differentiated into distinct subspecies (Huxley 1943). In the Canary Islands, the chaffinch *Fringilla teydea* breeds only in pine forests. The closely related *F. coelebs* usually breeds in broad-leaved forests above and below the pine, but not in the pine forests. On certain islands, *F. teydea* is missing, and on those islands *F. coelebs* occurs in the pine as well as in the broad-leaved forests (Lack 1944). Other examples of a similar sort are given, for birds, by Moreau (1948).

Success in competition between species of turbellarian flatworms depends on temperature and water current, but when the competing species is absent, the remaining species disperses far into the microhabitat usually occupied by its competitor (Beauchamp and Ullyott 1932).

Under natural conditions in habitats favorable to it, the male Anna's hummingbird is usually successful in maintaining a high population and forcing the male Allen's hummingbird into less favorable peripheral territories. The success of the Anna's hummingbird in competition with the Allen's hummingbird is attributable to its establishment of defended territories earlier in the season, by reason of which it is more familiar with the terrain and alert to intrusions. It sings persistently to warn off competing males, and the larger size and flashier coloration of the Anna's hummingbird give it authority (Pitelka 1951). In other habitats, however, the male Allen's hummingbird may consistently displace the Anna's hummingbird (Legg and Pitelka 1956).

The general effect of interspecific competition is restriction of a population more closely within its optimum niche. Intraspecific competition exerts pressure impelling individuals to disperse into less favorable situations. The relative pressure exerted by these two forces determines whether at any particular time the species is contracting or expanding its range (Svärdson 1949).

Interspecific competition is reduced or eliminated altogether when the combined requirements of all species are less than the supply of materials available. Land snails, insects, aquatic clams, and copepods sometimes occur together in a considerable profusion of species but with little evidence of competition between them (Boycott 1934, Fryer 1957, Ross 1957). Voles, during upswings in population, may become superabundant for periods of two or three years. During such periods several species of hawks and owls may feed in the same field without competing because there are more than enough voles to supply all. During downswings in the rodent population, however, competition does occur, and some or all the predator species are forced to turn to other prey (Lack 1946).

Parasites or predators may keep the populations of competing species below the level which available food resources of the habitat can sustain so that competition is reduced or disappears. For instance, when two species of weevil are placed together in a limited amount of food, one species is eliminated by the other in about five generations. However, when a wasp equally parasitic on the larvae of both species is introduced into the mixed culture, the populations of both species decline markedly below their normal levels in single pure cultures, and they both continue to exist together indefinitely (Utida 1953).

Closely related insect species may differ in their adaptations to climatic factors. As the weather differs between different localities during different months or from one year to another, two or more species may reach high abundance at different times, correlated with prevailing weather conditions, in what otherwise appears to be the same ecological niche (Ross 1957).

Niches of different species may overlap during most of the year but be clearly defined during critical stages in the life cycle. Plethodontid salamanders wander around freely most of the time, but during the reproductive period they are sharply segregated. In the North Carolina mountains, *Desmognathus quadramaculatus* is predominant in clear rocky streams, *D. phoca* lays its eggs in muddy streams on the under surface of rocks or logs, while *D. fuscus carolinensis,* which also occurs in muddy streams, deposits its eggs in the moss and mud on the upper surfaces of logs (Noble 1927).

A microhabitat may be occupied simultaneously by two or more species if their combined populations do not exceed the carrying capacity of the microhabitat. This may occur when the populations of the species involved are limited by conditions in some other part of their niches. Thus the niches of house wren, bluebird, black-capped chickadee, tufted titmouse, white-breasted nuthatch, and tree swallow overlap because they all nest in small cavities in trees or boxes. Usually the number of nesting sites is ample to the demand, so that there is no competition for them. The population of each species is restricted by factors other than available nest sites, perhaps by food supply, unfavorable climate, parasites, or predators. The wren feeds mostly on the ground under bushes, the bluebird in open fields, the chickadee on the smaller tree branches, the tufted titmouse on the larger branches and on the ground, the white-breasted nuthatch on the trunk of trees, and the tree swallow in the air. Competition occurs between them only when one or more species temporarily increases in abundance so that there are not enough nest-sites to go around.

When competitive species occupy the same microhabitat, they sometimes set up mutually exclusive territorial relations, based on responses to similarity of body form and behavior (Simmons 1951) or call notes (Dilger 1956, Lanyon 1957). This divides the space and reduces competition.

Because of parasites, unfavorable weather, predators, or other causes, species do not continuously saturate their habitats. It is only when they do that competition becomes clearly evident. Competition in the house wren takes various forms including destruction of eggs and young and even killing of adults. In a 19 year study of a 6-hectare (15-acre) plot, such drastic competitive acts, both intra- and interspecific, occurred only when the number of male birds was more than 10. When the number of breeding house wrens was reduced to 10 or less, in consequence of heavy over-winter mortalities, no such competition occurred (Kendeigh 1941b).

The niche relationships and the amount of competition between species sometimes varies geographically. The vertical range of the salamander *Plethodon glutinosus* in the southern Appalachians is sharply defined from those of three different subspecies (*jordani, shermani, metcalfi*) of *Plethodon jordani,* but completely overlaps the ranges of two other subspecies (*clemsonae, melaventris*) (Hairston 1951).

During a spruce budworm insect outbreak in the coniferous forests of northern Ontario, three species of warblers—bay-breasted, Tennessee, and Cape May—greatly increased in numbers, partly because of their aggressiveness and partly because they were more accustomed to feeding on this type of food. Other warblers were held in check and one species, the magnolia warbler, actually decreased in numbers because of competition with the three favored species. Competition between birds for song posts and territorial space was considerable with nearly a third of all conflicts observed occurring between individuals of different species (Kendeigh 1947). It is probable that niche segregation of species becomes established at times of stress or crises like this, and after the behavior pattern once becomes fixed in the species, only sporadic attacks of one species on another are thereafter sufficient to check random variations away from the standard pattern. At times other than those of stress, direct conflict between species is not often observed so that its importance in segregating species to particular niches is occasionally not fully appreciated (Lack 1944, Udvardy 1951, Andrewartha and Birch 1954).

Gause's rule

The evidence presented in this chapter demonstrates the important concept that has come to be known as Gause's Rule or, more recently, the "competitive exclusion principle" (Hardin 1960) : *an ecological niche cannot be simultaneously and completely occupied by stabilized populations of more than one species.* In other words, two or more species with closely similar niche requirements cannot exist indefinitely in the same area. Two species with expanding populations attempting to occupy the same niche will sooner or later come into competition for possession

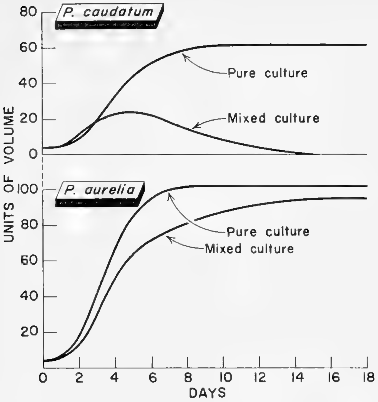


FIG. 18-2 **Growth of populations of *Paramecium caudatum* and *P. aurelia*, cultivated separately and in mixed populations (from Gause 1934).**

of it. Rarely, if ever, will they be equally adapted, and ordinarily the one with the better adaptations or greater aggressiveness will win out and occupy the niche to its full carrying capacity. The basic idea of this rule was understood from observations of natural distribution long before it was verified experimentally (Grinnell 1904, Jordan 1905).

In experimental cultures, *Paramecium caudatum* and *P. aurelia* maintain separate populations at a high level, but when the two species are mixed, they quickly come into competition. As long as the food supply is ample, both species increase in biomass, but as the food supply approaches exhaustion, *P. aurelia* persists and *P. caudatum* declines until it finally disappears. An analysis of the relative adaptation of the two species shows that *P. aurelia* is capable of faster population growth and is more resistant to the accumulating waste products than is *P. caudatum* (Gause 1934). Similarly, *Daphnia pulicaria* in mixed cultures causes the extinction of *D. magna* when oxygen and food become limited (Frank 1957), and *Tetrahymena pyriformis* persists while *Chilomonas paramecium* disappears in mixed cultures of these protozoans (Mucibabic 1957).

When two species of flour beetles with similar requirements for food, space, and other conditions are cultured together in the same volume of flour, one species always becomes extinct and the surviving species then establishes a stabilized population. In cultures free of parasites, *Tribolium castaneum* is the successful species, but in cultures containing the sporozoan parasite *Adelina tribolii*, *T. castaneum* becomes extinct and *T. confusum* persists, since it is less susceptible to the parasite (Park 1948). Parasites or predators may then influence the success of competition between species by affecting one more than the other (Crombie 1947).

It appears that when two species with similar niche requirements meet in competition under natural conditions, one of three things will happen (Lack 1944):

1. One of the two species will be so much better adapted that it will spread rapidly through the range of the other and exterminate it.
2. One species will be better adapted to a portion of the range, in which it will eliminate the other species, but the other species will be better adapted to the remainder of the range and will occupy it exclusively. Thus the two species will occupy adjacent geographic regions with perhaps a zone of overlapping occupancy.
3. Each species will be better adapted to a different portion of the niche, to which it will become restricted; with this separation, each species will then spread through the range of the other.

Advantages of niche segregation

Probably the major advantage animals gain by occupying different niches is escape from continuous intense competition. It is also true that the niche occupied is favorable to the species physically in furnishing suitable substratum and micro-climate, although many species have the ability to live elsewhere were competition not involved. Automatic segregation of a species into its niche through inherited behavior patterns avoids the great expenditure of energy and loss of time that would be required if this segregation had to be worked out anew each year or each generation. Segregation into niches avoids confusion of activities between organisms in the community and permits a more orderly and efficient life-cycle on the part of each species. Furthermore, the segregation of each species into different niches permits the occupancy of the area by a larger number of species, since they will better divide the available resources between them. Similarly the more distinct the niche of a species is, the more it can avoid conflict with its neighbors and lead a life that is orderly, productive, and efficient. Competition is thus a potent factor in giving ecological structure to the community.

TAXONOMIC COMPOSITION OF COMMUNITIES

Predominance

It is characteristic of the taxonomic structure of communities that a few species furnish the greatest bulk of the population entirely out of proportion to the rest of the species. Thus in stream riffles, two species make up 85 per cent of the total riffles populations and another two species constitute a similar percentage of the mud bottom pool populations (Table 5-1). In the littoral zone of Lake Erie, one species furnishes 85 per cent of the population on cobble and gravel bottoms, and another species makes up 68 per cent of the population on mud bottoms (Table 6-2). In populations of 79 species of birds nesting on a large tract including advanced stages of succession, 5 per cent of the species (4 species) included 37 per cent of the individuals, 10 per cent (8 species) for 56, and 50 per cent (40 species) for 96 per cent (Evans 1950). The abundant species are ordinarily of small size, herbivorous in their food habits, and at the bottom of the food chains and pyramids.

Variety of species

When a barren area is first colonized, a variety of species may invade and become temporarily established because competition is negligible. As the populations increase in size and individuals are crowded together, competition for the limited resources sets in, and the less well adapted species are eliminated (Yount 1956).

In general, all over the world, established communities in extreme or impoverished habitats consist of fewer species than do communities in fertile and more favorable habitats. The tropical rain forest is noteworthy for the great variety of species that it possesses, while arctic areas have, comparatively, greatly reduced faunas. Pioneer communities newly established on bare areas regularly consist of fewer species than later seral and climax ones (Tables 7-4, 8-3). The reason for this is that infertile pioneer communities and those in extreme habitats can support little variety in the way of niches, while communities in rich habitats are able to develop a great diversification of them.

When an area occupied by a community is broken up into a large number of small, different microhabitats and niches, few of them can be very extensive, hence their average population is generally less than that of species in extreme habitats where the variety of niches is smaller. Tropical and climax communities characteristically have a rich variety of species, but relatively low populations of most species. In pioneer and extreme habitats, to which relatively few species are adapted to survive, the species present may become enormously abundant. In spite of occasional exceptions, there tends to be an inverse relation in the composition of communities between the number of species and the average number of individuals per species.

Segregation of related species

Closely related species usually have somewhat similar adaptations and niche requirements; this may affect their distribution in communities in relation to each other.

In a study of 55 animal and 27 plant communities from a wide variety of habitats (Elton 1946), it was found that 86 per cent of the genera of insects and other animals and 84 per cent of the genera of plants were represented by a single species. The average number of species per genus of animal and plant in each community was 1.38 and 1.22 respectively, compared with an average of 4.23 species per genus for 11 large insect groups that occur in the British Isles as a whole. This means that while closely related species may occur in the same regional fauna, related species are more apt to be segregated into adjacent communities or habitats than into the same one. This conclusion has been disputed on a mathematical basis because of the small size of the communities and the small number of species involved (Williams 1947) but is supported by other studies (Lack 1944, Bagenal 1951).

It is true that in larger habitats or more diversified communities the larger number of niches ordinarily present should permit related species to occur. Yet, where related species could occur in large tropical communities of Africa, bird species belonging to the same genus occurred together in the same community in only 26 per cent of the communities, and if the weaver finches Ploceidae are excluded, only 16 per cent of possible overlap in habitat distribution is realized. This segregation of related species into different communities applied to an equal extent with species belonging to the same family (Moreau 1948). There are some genera of birds and other animals, however, in which a large variety of related species may be found together; notably, certain wood warblers *Dendroica,* buntings *Emberiza,* white-eyes *Zosterops,* whistlers *Pachycephala,* weavers *Ploceus,* hawks *Accipiter,* and the insects *Drosophila, Anopheles, Aedes* (Mayr 1947). Certain habitats, such as Lake Baikal in Africa, are unusual in possessing a great variety of closely related aquatic species (Brooks 1951).

The tendency for related species to be segregated into different communities or regions is an old concept and may be stated: *given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort* (Jordan 1905). The principles and reasons underlying this law require an understanding of speciation, which will be taken up in the next chapter.

Ecological equivalents

Communities in general are of fundamentally similar organization, and the facts we have already considered about food chains, trophic levels, and pyramids of numbers and biomass attest this. Consequently, a coniferous forest has many niches similar to those available in a deciduous forest, a grassland has some niches that are much the same as forest niches, a pond has some of the same niches as do lakes. The niches in a forest, a grassland, or a pond on one continent are very much the same as those to be found in similar communities on other continents. Communities could well be analyzed, compared, and evaluated in respect to the niches of which they are composed rather than the species they contain. Species are taxonomic units, niches are ecological units. Similar niches in different communities or in different regions are commonly occupied by species possessing similar but not necessarily identical habits, adaptations, and adjustments (Table 8-3). Such species are called *ecological equivalents* (Friedmann 1946, Dirks-Edmunds 1947). Equivalent species are not necessarily closely related taxonomically.

The explanation of why a particular species has come to occupy a particular niche in a particular part of the world requires a knowledge of where it originated, how it dispersed, and how it evolved its present adjustments and characteristics. When populations invade new regions and environments and become geographically isolated, they commonly differentiate into new species. Each species thus becomes the product or visible expression of a particular combination of environmental factors, interactions, and locality, and as such the species is the practical taxonomic unit with which the ecologist must deal. The process of speciation is thus of great ecological interest since it is an adaptive process that leads to the filling in of empty niches and to the most efficient and complete utilization of the environment (Mayr 1949).

SUMMARY

The ecological niche is a particular combination of microhabitat and biotic relations required for the existence of a species. The niche of a species is defined by the features of the substratum and microclimate to which that species is peculiarly adjusted, the time of day and season of year when it is mainly active, the type of shelter or cover it requires, the manner in which it uses vegetation in its reproductive performance, the type of food it consumes, and the predators that prey on it.

Animals, particularly higher types, have more or less stereotyped behavior patterns associated with their restriction to particular niches. These behavior patterns may be genetically inherited and subject to evolutionary development, or they may be transmitted to succeeding generations through training or conditioning (imprinting) of the young.

Segregation of species into different niches is doubtless the result of interspecific competition. According to Gause's rule, an ecological niche cannot be simultaneously and completely occupied by stabilized populations of more than one species. Occupancy of different niches reduces interspecific competition, furnishes the species with microhabitats to which they are especially adjusted, reduces confusion and disturbance, and permits a greater variety of species to occur in the same region.

Communities commonly have a predominance of a few species composing the bulk of the populations. Communities in extreme or impoverished habitats have fewer species than those in fertile or favorable ones. Closely related species tend to be segregated into different but adjacent regions separated by barriers.

Since communities in various parts of the world are fundamentally similar in organization and structure, species occupying similar niches in them make similar adjustments. Although not necessarily related taxonomically, these species are ecological equivalents. Understanding how a particular species has come to occupy a particular niche in a particular part of the world requires a knowledge of speciation, which will be considered in the following chapter.

19

Ecological Processes and Community Dynamics:

Speciation

Speciation is the process of evolutionary differentiation between populations, which may result in one older species becoming split into two or more new ones. Speciation usually entails divergence of the new species into different niches. An understanding of the basic principles of speciation is therefore a prerequisite to an understanding of animal distribution.

TAXONOMY

As the term is used by taxonomists, a *population* is a local aggregation of individuals that differs slightly, but characteristically, from other local aggregations of the same species.

Geneticists define a population as a reproductive community sharing a common, characteristic gene pool. Every local population is different from every other one; but they are not easily distinguishable from one another, and therefore are given no formal nomenclature. What a population includes may vary from the entirety of a species to but a few individuals, according as the rate and extent to which individuals interdisperse between localities to make a common gene pool.

Among bisexual forms, a *species* is a group of populations capable of successfully interbreeding, reproductively isolated under natural conditions from other such populations. Species are usually morphologically distinct, but the distinguishing characteristics are sometimes barely discernible. Hybridization may occasionally occur between clearly defined species under captive or unnatural conditions, but does not occur with any significant frequency under natural conditions.

Fossils found separated in different geological strata, or living populations separated in space, are considered capable of successful interbreeding, and therefore to be of the same species, if essentially similar structures, functions, and behaviors can be adduced for them. It is unfortunate that species cannot presently be recognized by entirely objective means, but even if this were readily possible there would be difficulties, inasmuch as populations may be at various stages in the differentiation of complete reproductive isolation. Species are distinguished by the familiar bionomial nomenclature standardized by international rules (Mayr *et al.* 1953).

A *subspecies* is a geographically defined group of populations which differs in color, size, or some other taxonomic characteristic from other populations within the same species but nonetheless interbreeds with them freely, regularly, and successfully where their ranges come into contact. Subspecies are commonly distinguished by a trinomial nomenclature, although the desirability of this has been questioned

(Wilson and Brown 1953; *Syst. Zool.* 3, 1954: 97–126, 133). The taxonomic differences between subspecies are usually less pronounced than those between even closely related species, but they are genetically fostered differences nonetheless (Sumner 1924, Huxley 1943). Race and variety are terms sometimes used as synonyms for subspecies, or for populations even less well defined than a subspecies. It is difficult to determine whether populations that differ phenotypically are subspecies or species when their ranges do not verge, for in the absence of opportunity for them to commingle, it remains uncertain whether interbreeding would or could occur. The assignment of taxonomic rank under these circumstances is dependent upon considerable subjective inference. Boundaries between adjacent subspecies are frequently arbitrary in that they fit differences between the populations for some characters but not others. Differences between subspecies or populations are often correlated with differences in topography, soil, climate, or vegetation, and, at least in some instances, appear to be adaptive to these differences in the environment.

If a subspecies becomes isolated by a barrier so that it is prevented from interbreeding with the rest of the species, variations in taxonomic characters may accumulate and the population evolve so distinctively as to pass beyond the rank of subspecies into that of species. However, not all or even most subspecies change into species, a process which depends on effective, permanent reproductive separation and on the forces of natural selection. *Speciation,* more precisely, is the process of differentiation between populations of the same species in consequence of reproductive isolation (Simpson 1953).

Populations that do not differ by clearly defined or conspicuous taxonomic characteristics, but nevertheless do not interbreed because of physiological or behavioral differences, are described as *sibling species.* Sibling species have been noted especially among Diptera (*Drosophila, Anopheles*), Hymenoptera (ants), Lepidoptera (especially moths), and Protozoa (*Paramecium*) (Mayr *et al.* 1953). It is apparent that the evolution of physiological and behavioral differences often precedes the differentiation of recognizable taxonomic distinctions (Krumbiegel 1932, Thorpe 1930).

Two species the distributional ranges of which do not overlap (i.e., there is geographic isolation between them) are said to be *allopatric.* Two species are said to be *sympatric* when their ranges overlap, even though they may locally be ecologically segregated into different habitats; for example, the situation in which one species of snail is limited to floodplain and another species to upland habitats, or one species of rodent confined to the foothills and a closely related species to a higher zone on mountains only a short distance away. Populations should be considered sympatric if they occur within the common dispersal ranges of their young, so that there is at least possible a continuous and appreciable interbreeding and flow of genes among them.

ISOLATION OF POPULATIONS

Sympatric species do not interbreed because one or more isolating mechanisms keep them separated. We will proceed to examine what isolating mechanisms are, and how geographic isolation permits them to arise.

Isolating mechanism

Isolating mechanisms that prevent sympatric species from freely interbreeding are largely or entirely biotic factors (Mayr 1942, Huxley 1943, Allee, Emerson, *et al.* 1949, Dobzhansky 1951, Patterson and Stone 1952). They are the following types:

Ecological: segregation of species into different habitats, communities, or niches by reason of structural adaptations, physiological adjustments, or behavior responses.
Ethological: difference in sign stimuli or behavior patterns required for successful species and sex recognition and for mating.
Mechanical: lack of physical conformity of sexual organs, chemical incompatibility of sperm and egg.
Genetic: hybrid sterility or decrease of fertility.

Ecological isolation was described and illustrated in the discussion of niches (Chapter 18).

Animals may fail to find breeding partners; i.e., they may remain *ethologically* isolated. Careful studies in all vertebrate groups and in such invertebrates as insects, spiders, crustaceans, and snails indicate that animals identify the sex of individuals of their kind only by actively recognizing special clues or sign stimuli (Tinbergen 1951). These clues may be special color markings, shape or outline, scent, song or call-notes, touch, behavior patterns, or some combination of these. Courtship leading to copulation is often complex and involves a number of steps, each step in the behavior serving as a releaser for the next (Fig. 2-7). If a step is not performed properly and in its sequence, the courtship performance ceases forthwith, and there is no sexual consummation. Different species may be effectively isolated from interbreeding simply because the sexes of one possess different sign stimuli than the sexes of the other, and the sexes of one kind characteristically pursue patterns of pairing behavior that are not stimulating to the sexes of the other.

Ethological isolating mechanisms (Spieth 1958), effective under natural conditions, often lose efficacy when those conditions are disturbed; by so much they are difficult to work with experimentally. Where their home ranges overlap, two species of mice, *Peromyscus leucopus* and *P. gossypinus*, frequently occur in the same habitat. Yet, very few hybrids have ever been found. When brought into the laboratory, however, the two species not only hybridize freely, but produce fertile offspring. It appears that ethological factors keep them separated under natural conditions (Dice 1940).

Two closely related budworm species, *Choristoneura fumiferana* found on balsam fir, and *C. pinus* found on jack pine, are isolated ecologically on different host trees, and because the first species completes its mating season before adults of the second species appear on the wing. Ethological isolation occurs when occasionally their mating periods overlap. Females will mate only with males of their own species, even though males of both species attempt to mate indiscriminately (Smith 1954).

Species related but of different sizes may be unable to fit their copulatory organs together, because of structural incompatibilities. Such hindrance to interbreeding is a *mechanical* isolation. Failure of male toads to clasp females of larger or smaller species results in reproductive isolation between species of *Microhyla* (Blair 1955). Polygyrid snails of the genus *Stenotrema* have definite behavior patterns prerequisite to copulation. A careful study of several species in this genus (Webb 1947) showed that differences in these behavior patterns are sufficient to keep some species separated, but that in other instances it is differences in the structure of the copulatory organs that apparently prevents interbreeding.

Genetic isolation occurs when there is inability to produce offspring because of incompatibility of spermatozoa and eggs, abnormalities of growth, or the offspring are sterile. Sperm of the sea urchin *Strongylocentrotus franciscanus* sufficient to give 73 to 100 per cent fertilization of eggs of the same species produced only 0 to 1.5 per cent fertilization of *S. purpuratus* eggs. Eggs of one species may sometimes be successfully fertilized by sperm of another, but all sorts of disturbances may occur in the zygote, such as chromosome elimination during cleavage, arrest of gastrulation or organ formation, and death of embryos in advanced stages. A well-known example of a usually sterile hybrid is the mule, the result of a cross between a male ass and a female horse.

Genetic and mechanical isolation usually furnish more certain reproductive separation between species than do ecological or ethological isolation. The latter two forms probably represent early steps in the process of speciation; the former two, the culmination of speciation.

Geographic isolation

Physiographic barriers such as land masses, mountain ranges, and bodies of water can effect complete or nearly complete isolation of populations. Population segments of a species may become geographically isolated when reproductive individuals cross a barrier by chance. For instance, individuals may be blown by storms or carried by rafts to outlying islands. A barrier may arise subsequent to the dispersal of a species, such as when species disperse into a new area by way of land bridges which later disappear.

When barriers are only partially effective so that gene flow between adjacent populations is hindered but not stopped, and natural selection goes on independently in each area, some differentiation of the populations may occur but not above the level of subspecies. Species that are widely dispersed over a continent often display several local centers where differentiation is occurring. Individuals dispersing outward from these centers, however, meet and interbreed so that intergradation of characters occurs, and there is gene flow from one end of the species' range to the other. The rate of gene flow is directly proportional to the rate at which individuals disperse from birthplaces, in the face of any intervening barriers. This is true even of birds and insects. Less than 5 per cent of young pied flycatchers surviving to one year of age return to their places of birth in order to nest; the other 95 per cent disperse widely. Only 4 subspecies have differentiated in this species, since there is widespread promiscuous interbreeding between individuals. On the other hand, 63 per cent of young song sparrows surviving to sexual maturity return to nest in the vicinity of their birthplaces; only 37 per cent disperse elsewhere. This results in a limited flow of genes from one locality to another and is correlated with the development of 28 subspecies (Diver 1939, Marshall 1948, Haartman 1949).

When the rate of gene flow is slow, mere *distance*, even over territory unbroken by physiographic barriers, may permit populations to vary enough for subspeciation, or potentially even full speciation, to occur. In the range from Maine to Florida, populations of leopard frogs readily interbreed with adjacent populations. But when individuals from Maine are brought together with individuals from Florida, the two cannot interbreed successfully (Moore 1946). There is a progressive change from North to South in several characteristics of the leopard frog, and it is of interest that if populations intermediate in the

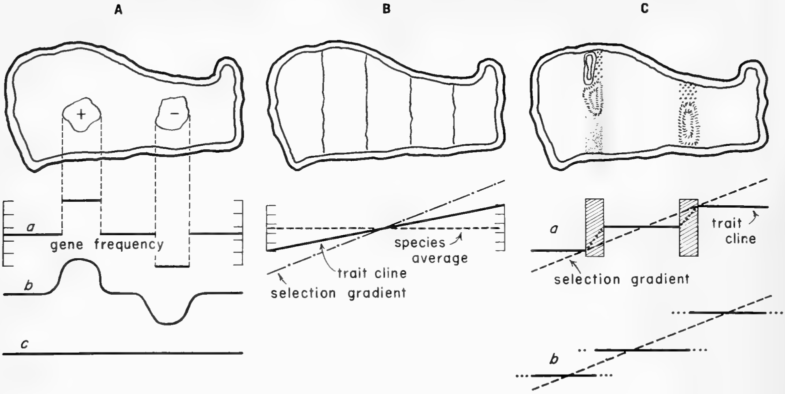


FIG. 19-1 **(A) local plus and minus variations in any characteristic of a species occupying a uniform habitat eventually disappear because of gene flow throughout the population (panmixia). (B) when the habitat characteristics of a geographic range occupied by a species gradually change from one extreme to another, a selection gradient is established that partially counteracts the tendency toward panmixia, producing a *cline* in the characteristics of the species. (C) when partial barriers to otherwise free gene flow occur in an environment or selection gradient, a stepped cline (a) produces distinct races or subspecies. If the barriers become complete, the isolation of populations may result in divergent evolution and complete speciation so that later, after the barriers disappear (b), biological isolating mechanisms prevent the populations from interbreeding (after Womble 1951).**

range should be eliminated, the populations at each of the two extremes of the range would be considered separate species. As it is, however, at least some gene flow takes place throughout the range, and all populations must be considered as belonging in the same species.

Only through geographic isolation can populations differentiate into distinct species. There is no established case in which any change in habitat, behavior, structure, or genetics acting singly or in combination has, in the absence of geographic isolation, been sufficient to prevent at least some significant gene exchange with the rest of the species, with resultant preservation of the species. With one apparent exception, biotic factors apparently cannot by themselves bring full differentiation of new species. The exception is the simultaneous development of polyploidy in certain individuals, which renders them sterile with normal members of the species, although not with each other. Polyploidy rather commonly gives complete genetic isolation in plants, but it is rare in animals.

In the presence of geographic isolation, genetic variations and natural selection may bring the affected population to a different course of evolution than in the parental species, especially if adaptation to a new environment is also involved. Biotic isolating mechanisms may develop in the process. If the geographic barrier formerly separating the population should disappear, and the hitherto isolated population again comes into contact with the rest of the species, interbreeding will not then occur. This is the process of speciation, the details of which we will now examine more carefully.

VARIATIONS IN POPULATION CHARACTERISTICS

Observable differences in structure, function, and behavior between individuals belonging to the same species are common. Actually, no two individuals, except perhaps identical twins, have exactly similar characteristics. Early Mendelian geneticists believed that speciation occurred as the instantaneous result of major mutations (macro-evolution) (Bateson 1894, Goldschmidt 1940). Modern geneticists are nearly unanimous in the view that it is the gradual accumulation of many small variations over many generations (micro-evolution) which eventually gives a population reproductive isolation and, consequently, species identity.

Non-heritable variations

Not all variations of organisms are of direct significance in speciation. Non-heritable changes in body structures, functions, and behavior are common. If muscles are used continually and intensively, they become thicker and stronger; if one kidney is removed, the other becomes hypertrophied; skin subjected to frequent rubbing or pressure thickens and becomes horny; and so on through a lengthy catalog. Animals progressively exposed to ever more severe temperatures or lower oxygen concentrations will tolerate extreme conditions, which, had they been suddenly presented, would have been fatal. Insect larvae transferred to a new type of food often become so conditioned to it that they produce a strain that prefers that food to other more usual food of the species. Chimney swifts in wilderness North America nested in hollow trees, but with settlement of the country and the construction of chimnied buildings during the last two centuries, the species has changed its behavior almost completely, accepting chimneys as a satisfactory nest-site location.

Many phenotypic adaptations persist generation to generation, either as similar responses made by each generation to constant environmental conditions; as the result of imitation of parents, conditioning of young, or imprinting (Cushing 1941, 1944, Thorpe 1945); or because the particular genes responsible for these characteristics have been sorted out (canalized) from the general gene pool of the species (Waddington 1957). One would expect a change in behavior or function, arisen in consequence of exposure to the new conditions, usually to presage the evolutional development of a new structure, for natural selection cannot bring about the structural adaptation or perfection of an organ unless the organ is already being used for the new purpose (Prosser 1957). According to the so-called *Baldwin effect,* a mutation which affects established behavioral or functional adjustments is more likely to become permanently fixed in the germplasm than if the population were not already so adjusted phenotypically (Baldwin 1896, 1902, Simpson 1953a).

Polymorphism

When individuals of a population can be grouped into several color phases, distinct body sizes, or other character variations, the population is said to display *polymorphism.* Polymorphism of a character arises in a species when heterozygotes persist in an environment in the face of natural selection and homozygotes are reduced or eliminated. For instance, individuals with certain characteristics may be better adapted to environmental conditions during the spring, while individuals with other characteristics are superior in summer or autumn. This results in a mixture of types in the population more or less segregated by seasons. Likewise populations may vary in characteristics as adaptations to local habitat conditions. An increase or decrease in the frequency of a given characteristic appears a result of variations in the selective pressure of the environment, permitting individuals with certain characteristics or gene combinations to survive at one time or place; other individuals, at other times and in other places. In an environment that presents the same set of selective pressures year after year, there commonly occurs a stability in the ratios of the different forms in which a character is manifested (Ford 1940, Dobzhansky 1951, 1956, 1958, Sheppard 1958).

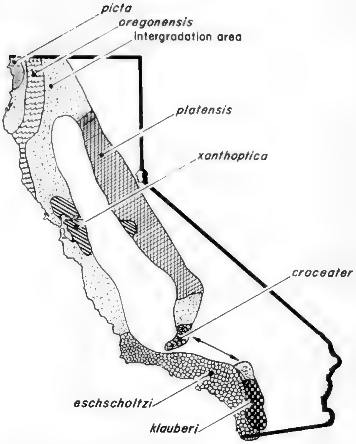


FIG. 19-2 Speciation through distance in the salamander species *Ensatina eschscholtzii* in California. The coastal subspecies *picta* may represent the ancestral type and demarcate the center of dispersal from which clinal lines became dispersed southward in the coastal and interior mountains separated by a barrier. Recently, the subspecies *xanthoptica* crossed this barrier. Interbreeding occurs between adjacent subspecies, but partial reproductive isolation obtains between *xanthoptica* and *platensis,* and complete isolation similar to that of species obtains between *eschscholtzii* and *klauberi* (Stebbins 1949).

Most species differ not by single genes but by hundreds certainly, possibly by thousands, of genes. When *panmixia* (free interbreeding) obtains in a

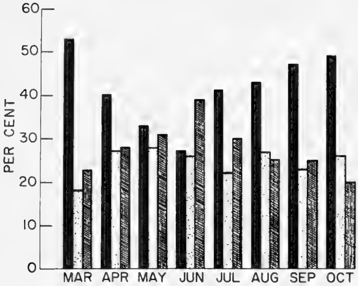


FIG. 19-3 Seasonal changes in relative frequency of the third chromosome with the standard (black), arrowhead (stippled), and Chiricahua (cross-hatched) gene arrangements in a natural population of *Drosophila pseudoobscura* (Dobzhansky 1951).

species, these genes may be arranged in all sorts of combinations to form an almost infinite mixture of character modifications (Caspari 1951). Heterozygotes are, therefore, much more flexible in adaptively responding to the environment than are homozygotes. The more characters for which an individual is heterozygous, the more adaptable its offspring are likely to be. Adaptive polymorphic populations are more efficient in exploiting the environment than are genetically uniform ones. Conversely, species that are widespread geographically through many habitats are genetically more diversified than are those restricted to few or specialized habitats. There are limits, however, beyond which a character cannot change. The continual tendency for characters to fluctuate around a mean or intermediate condition gives a population *genetic homeostasis* (Lerner 1954).

Genetic drift

Although certain characters may result from the action of a single gene or pair of genes, many, perhaps most, characters within a species are polygenic; i.e., they are affected by a multiplicity of genes. The exact form in which a character is expressed depends on the particular combination of genes which the individual or population possesses (Waddington 1957).

If a fertilized female, a single pair of animals, or at most a few hundred individuals become separated from the rest of the species, there will be represented in them a considerable decrease in the number of genes available to the main body of the species, since no individual or small group of individuals can possess all the genes that occur within the species' pool. Inbreeding within small isolated populations may thus bring into prominence traits which are expressed only irregularly and inconspicuously within the species as a whole. Establishment thus of restricted genotypes in small population by loss of genes or accidental changes in frequencies at which certain genes occur is called *genetic drift*, or the *Sewall Wright effect* (Wright 1931). Character variations formed in this manner often appear to be non-adaptive, and there is controversy as to whether such characters are important in species formation.

The possibility that genetic drift is a significant factor in speciation under some conditions is shown, however, by ground finches of the Galapagos Islands (Lack 1945), species of which differ chiefly in the size and shape of the bill. Species belonging to the same genus consume the same kind of food. Differences in bill characteristics apparently developed as small populations became isolated on different islands within the Galapagos group, even though the islands were similar in climate, vegetation, and habitats generally. The particular bill characteristics that the various species possess apparently resulted from a chance combination of genes that became segregated on each island. With inbreeding, these bill characteristics became genetically fixed. It is of interest that the peculiar bill characteristics came later to have a secondary significance in furnishing sign stimuli in courtship and in territorial defense. This has given ethological isolation to some species and prevented interbreeding where species, thitherto dispersed and isolated, have come again into contact.

Similar fixation of special characteristics may occur in species subject to catastrophic or cyclic reductions in abundance. The genotypes of the few survivors will determine the genetic makeup of the entire new population that develops in the area (Elton 1930, Timoféeff-Ressovsky 1940). For example, the arctic fox is a cyclic northern species possessing a white and a so-called blue color phase. Over most of the fox's range, the blue phase is much less common than the white, but on certain islands only the blue phase occurs. It is possible that at some time in the past, at the bottom of a population cycle, only homozygous blue foxes survived; reproduction of these animals and their offspring rendered the entire new population blue. This does not mean, however, that blue color is necessarily non-adaptive or that it may not be genetically linked with a character that is adaptive.

Mutations

Mutations may be the result of chemical changes in the individual gene or to chromosomal

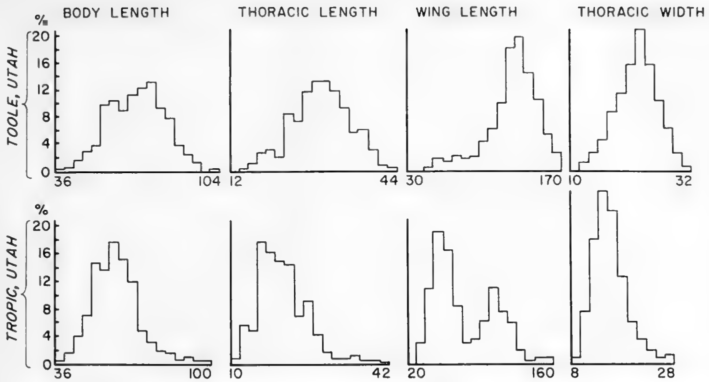


FIG. 19-4 **Variations in body and wing measurements between two local populations of the gall wasp. Abscissas are in micrometer scale units; ordinates, in percentages of the population in each measurement class (after Kinsey 1942).**

aberrations, the latter in the form of changes in the number of chromosomes (haploidy, polyploidy) or of arrangement of genes on the chromosomes (deletion, duplication, translocation, inversion) (Dobzhansky 1951). The rate at which any one gene mutates varies greatly from one kind of gene to another, but the average rate is of the order once in every 100,000 or 1,000,000 individuals. Between 0.4 and 10 per cent of the individuals in each generation may possess mutated genes. Natural populations may therefore be well supplied with small mutations of differing potential values to the organism (Schmalhausen 1949). Mutations of different sorts apparently occur haphazardly and are not influenced by environmental conditions; only accidentally do they give special advantages to an organism. Adaptations of a species to a particular habitat or niche is effected through natural selection of the favorable mutations out of the many that occur.

The size of the population and the rate at which a particular gene mutates affect the odds that a mutation of that gene will become established in a population. In a stabilized population, two offspring must survive and mature to replace the parents on their death. If in one parent gene A mutates to the nonlethal gene A', the odds are 1:1 that genotype AA' will appear in one of their two offspring and that the mutant gene will be transmitted to the following generation. If both offspring are heterozygous, the odds for continuation of gene A′ into the next generation are increased to 3:1. On the other hand, if the parent carrying the mutant gene fails to reproduce or if all the offspring die, the mutation is lost. The odds that a single mutation will persist through 127 generations is estimated to be only 1:67 (Fisher 1930).

If the mutant gene A′ is a dominant, the character is immediately expressed in the phenotype; if it is recessive, the character will not appear in the phenotype until two heterozygous individuals mate to give rise to the homozygous recessive $A'A'$. In a small population, inbreeding between heterozygous individuals will quickly produce both homozygous dominant and homozygous recessive genotypes, as well as the heterozygous line, and provide a variety of phenotypes upon which natural selection may work. In a large population, mating between heterozygous individuals will be less frequent because these individuals will constitute a lower proportion of the total population. However, if the gene mutates repeatedly in different individuals, the high mutation rate will greatly increase the number of individuals carrying the gene and increase the chances that the mutant character will become expressed in the population.

Hybridization

The critical test of whether or not speciation has occurred comes when a barrier between two geographically isolated populations breaks down, so that the formerly isolated populations again come into contact. If speciation is complete, they will not interbreed; if it is not, hybridization will occur. The detection of hybridization between two populations may be difficult, for *introgression* commonly occurs; that is, the hybrids backcross with either or both parental populations, and the backcrosses resemble the parental populations very closely. The result of introgression is the gradual intrusion or transfer of the characters of each population into the other, so that all distinction between them disappears (Anderson 1949).

If two populations differing in habitat requirements interbreed, the first generation hybrids will often show best adjustment to an intermediate environment. A second generation, if it occurs, will then consist of individuals of both ancestral and hybrid types, each of which requires its own peculiar habitat for optimum development. If there is a paucity or absence of intermediate habitats, the intermediate forms will be selected *against*, and die out. If the hybrids are sterile or have a lower reproductive capacity than the parental populations, they also will be selected against. Any ecological, ethological, or genetic divergence between the two populations that reduces the gamete wastage in hybrids will be selected for, with consequent *reinforcement* of the isolating mechanism. It happens often, therefore, that niche segregation or differences in behavior between closely related species will become decidedly more pronounced in the overlap zone of their ranges than elsewhere. The result, of course, is continued divergence of the two populations until interbreeding between them ceases, and they form distinct species (Brown and Wilson 1956).

On the other hand, there are circumstances in which fertile hybrids are not selected against. If the area in which the hybrids are formed offers a variety of habitats, some of which are different than the habitats occupied by the parent population, the hybrids may find themselves fully as well adapted to them, and by so much be fully as well adapted to that area as are their parents. Under these circumstances the hybrids will survive, introgression will occur, and the formerly isolated parental populations will fuse into one. Introgression between populations has been observed and recorded in areas where man by removing forests or producing other disturbances in the environment has destroyed barriers that maintained a sharp ecological isolation of populations; the phenomenon doubtless occurred repeatedly in the geological past with changes in physiography, climate, and vegetation (Anderson 1948, Blair 1951, Sibley 1954, Hubbs and Strawn 1956).

A third possibility exists. Where hybrids obtain some advantage or show better adaptations than their parents, they will be selected *for*, and may eventually replace both parental populations. This appears to be taking place with *Colias* butterflies in northern Canada at the present time (Hovanitz 1949).

Asexual and self-fertilizing forms

Asexual and self-fertilizing organisms include half or more of the Protozoa and many invertebrates and plants. These organisms offer problems of species recognition and evolution that are in many respects different than those in bisexual forms. Each individual is reproductively isolated from every other individual, giving rise to offspring that are genetically alike by fission, budding, sporulation, or self-fertilization. Mutations, however, arise, and if favorable, may transform a strain or clone as the result of natural selection. Local clones may differ therefore in phenotypic and genotypic characters in the same manner as bisexual populations, even though there is no opportunity for variation to occur through assortment and recombination of the genes. Clones that are genetically distinct are in the nature of sibling species. Such clones, however, are for convenience considered as belonging to one and the same taxonomic species, if they show similar morphological characters that are readily distinguishable (Meglitsch 1954, Boyden 1954, Sonneborn 1957).

NATURAL SELECTION

Natural selection is a continual force exerted on each successive generation. Before natural selection can take place, however, there must be phenotypic *variations* between individuals, from which selection can be made. In order for these selected variations to have significance in speciation, they must be genetically fixed and *heritable*.

In most species, many more offspring are produced than can possibly survive. Because of this *overproduction*, there is competition between the offspring for the necessities of life, which, together with the strife between predator and prey and between organisms and their physical environment, creates a *struggle for existence*.

There is differential survival in this struggle for existence because some individuals have structural, functional, or behavioral variations that give them advantages over individuals lacking those variations. The superior genotypes will make a relatively larger contribution to the gene pool of the next generation. The result of *differential survival* and *differential reproduction* is popularly known as the *survival of the fittest*.

The accumulation of favorable variations in a population brings the species generally to a better *adaptation* to the physical conditions of the habitat, avoidance of predation, more efficient physiological functioning, and new behavior patterns. *Natural selection* favors those variations that are adaptive, and thereby fosters the continued existence and improved reproduction of the species. If the population undergoing these changes is geographically isolated so that the favored changes do not spread throughout the species, then differentiation of characters leading to speciation occurs. The actual mechanics of natural selection are disputed, although understanding of the general processes involved is steadily increasing.

When the ratio of one character to another changes from 1.00:1.00 to 1.01:1.00 in each generation, the character is being selected for; more individuals with the character are surviving than are individuals without it. With a selective advantage of 1 in 100, a dominant character will become established in 99 per cent of a population in about 1200 generations (Huxley 1943). This rate is considered rapid evolution. A selection pressure of even 1 in 1000 represents fairly rapid change, but when selection is decreased to 1 in 1,000,000 or more, evolution is relatively slow. A good mathematical analysis of selection pressures is given by Li (1955).

The action of natural selection is evident in the following examples. Scale insects, flies, and other insect pests are commonly controlled by hydrocyanic gas or DDT sprays. However, after many applications, surviving populations display immunity. Apparently, normal populations are mixtures of resistant and non-resistant genotypes. In the absence of the fumigant, there is no selection between the two genotypes, but with continuous fumigation, the resistant types survive and reproduce until they become predominant in the population (Dobzhansky 1951). Natural selection presumably functions in much the same manner to make the color of local populations of small mammals and snails match the color of the soil or vegetation as protection against predators (Dice and Blossom 1937, Blair 1951a, Sheppard 1954); to correlate the pigmentation of butterflies with local differences in temperature, moisture, and solar radiation (Hovanitz 1941); to bring parallel variants in many kinds of fish when in the same kind of environment (Hubbs 1940); and generally to establish the many other adjustments and adaptations of organisms to their particular niches.

Natural selection is relatively less effective in small populations than in large ones. Small populations may be locally restricted, come into conflict with few competing species, and experience only a favorable habitat. Because of the low selection pressure, chance combination of genes (genetic drift) may produce characters of little or no adaptive value that yet have a good chance to persist while really adaptive characters may be lost. In the Hawaiian and Society Islands, there is a great variation in the characteristics of snails that variously occur on the different islands and locally in different isolated valleys or regions on the same island (Gulick 1905, Crampton 1932). This is apparently a result of the fixation of random variations in small populations not subjected to any considerable selective pressure. In populations that are increasing rapidly in size, in the upswing of cycles, say, there is little selection, and non-adaptive variations may persist as well as adaptive ones. As populations come to saturate habited niches and disperse into new or less favorable habitats, competition, predation, and parasitation increases, and individuals become exposed to evermore severe physical and climatic conditions. Natural selection then functions, and characteristics that are adaptively advantageous will tend to persist while those less favorable or even harmful are eliminated.

Mutations upon which natural selection works are often recessive. They do not become fully expressed in the phenotype except when the individual is homozygous for the character. Nevertheless they are important, and in stabilized populations tend to persist indefinitely in constant proportion to the dominant alleles (Hardy-Weinberg law). A recessive character will become more prominent in a population if that particular gene continues to mutate toward the recessive, or if the homozygous recessive phenotype has adaptations that give it selective advantages. In this latter case, natural selection may ultimately result in complete suppression of the dominant allele so that the hitherto recessive allele becomes permanently fixed in the population as the only gene for the character.

Since emergent species usually entrain adaptations to new environments, it would appear that those characteristics by which we distinguish species and higher taxonomic categories generally are such as serve some useful purpose to the organisms either structurally, functionally, or in point of behavior. It is often very difficult to determine a useful function for all distinctive characteristics of a species, yet one can seldom be positive that a seemingly minor character does not serve, say, as a releaser for some critically necessary behavior or is not vitally important in other unsuspected ways. However, not all characters that distinguish species or higher taxonomic categories are necessarily adaptive (Robson and Richards 1936, Simpson 1953). Some characters originally adaptive may have lost their usefulness, although they persist in the organism. With natural selection no longer acting on them, they usually retrogress and may eventually disappear as have skin pigmentation and eyes in many cave animals, for instance. Other characters may even have a slightly unfavorable

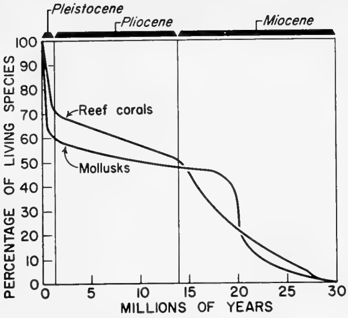


FIG. 19-5 **Age and time of origin of present-day species of reef corals and mollusks as shown by their percentage of occurrence in fossil faunas of the East Indies (after Umbgrove 1946).**

value, but be closely linked genetically with selectively preferred favorable characters and thus continue in the organism.

Before a population can occupy a new region or even expand its niche it must show at least some *preadaptation* for it (Allee, Emerson, *et al.* 1949, Simpson 1953). Preadaptation may take the form of a wide range of tolerance that can encompass the conditions of the new habitat as well as the old; or it may take the form of a new use for a structure, different from its original function (Bock 1959). The European rabbit certainly showed a good deal of preadaptation to the Australian environment; it became a local pest within three years of the introduction of 24 individuals in 1859. We have earlier described why preadaptation must have been necessary for the origin of parasitism. Preadaptation permits individuals to exist in new habitats or to perform new functions, but subsequent perfection of an adaptive trait depends on the accumulation and selection of additional favorable genetic variations over many subsequent generations.

ADAPTIVE RADIATION

When a species bypasses or surmounts a dispersal barrier, it may penetrate an area having a variety of niches novel to the species. A plastic species may quickly differentiate adaptively into a number of new species, each becoming established in an unoccupied niche or, if sufficiently aggressive, displacing an original but less adaptive occupant. Such *adaptive radiation* is known to have occurred in the case of ancient marsupials, which crossed from Asia to Australia and differentiated into the variety of species now found there.

The invasion and occupancy of the Hawaiian Islands by snails, insects, and birds is of special interest. There are some 3722 insect species endemic to the islands. All of these species appear to be derived from some 250 ancestral forms that arrived in 14 separate invasions since Pliocene time (Zimmerman 1948).

The ancestral prototype of the honeycreeper birds reached the Hawaiian Islands sometime within the last five million years (Baldwin 1953). Different populations became isolated on different islands, as a result of which there arose the so-called red and black nectar-eating species that are grouped in the subfamily Drepaniinae. As the nectar-feeding niches became fully occupied, a population diverged in its behavior, feeding more heavily on insects than on nectar. The new niche allowed redispersion of the population through the various islands, and there ensued a second burst of speciation yielding the so-called green insect-eating forms belonging to the subfamily Psittirostrinae. Additional speciation produced short- and long-billed species of insect-eaters. Somewhere in the lineage of the latter group, the birds acquired seed- and fruit-eating habits, and the long bill also became a thick bill. Rapid evolution in this family still appears to be in process.

RATE OF EVOLUTION

There is evidence that, under natural conditions, variations in local populations may sometimes be manifested within a surprisingly few generations (Huxley 1943). Melanistic forms of butterflies now occur in industrial areas of England where vegetation has become coated with dark-colored debris, although 100 years ago such butterflies and the industrial soot as well were virtually absent (Kettlewell 1956). House mice isolated on a sandy island have become within 100 years a distinctly paler population than the one on the adjacent mainland (Jameson 1898).

The period of time required for evolution from one taxonomic level to another varies enormously between different kinds of organisms. It has been estimated that the rate of change in characteristics of several lineages of mammals since Pleistocene time, when it can be measured quantitatively, for instance in the length or breadth of the skull, is of the order of 0.2 per cent per 1000 years (Kurten 1958). Apparently, subspecies commonly require 10,000 years to become well defined, and may continue to evolve for 500,000 years before rising to the species level. The evolution of a fully defined species usually requires at least 50,000 years and frequently a very much longer time. Some living mammal species are 1,000,000 years old, and some lower vertebrate and invertebrate species have persisted relatively unchanged for 30 million years (Simpson 1949, 1953).

The rate of change, divergence, or evolution of populations into new species depends partly on the rate at which new mutations are occurring in the species' gene pool, and partly on the rate and extent to which the environment is changing. In a long-continued uniform environment, a species becomes stabilized in a favorable relationship with the habitat and community. The various ecological niches are effectively occupied, and little evolution occurs. New mutations can add little to perfected adaptation. If the habitat changes, however, established adaptations may no longer be appropriate, and variations hitherto rejected might now prove beneficial. A mutation selected for in one or more species may initiate a chain of events that alters the internal balance of the whole community, with resultant rapid evolution (Olson 1952). For instance, there has been considerable differentiation of animals into subspecies during and since the Pleistocene glaciation, but probably most of our present-day species originated in pre-Pleistocene time.

SUMMARY

Speciation is the process of evolutionary differentiation often leading to species formation, a process usually also involving separation or divergence of populations into different ecological niches. Sympatric species do not interbreed because of ecological, ethological, mechanical, or genetic isolating mechanisms.

Geographic isolation of two populations of the same parental species appears prerequisite to complete speciation. As long as a significant amount of gene flow occurs between populations, they diverge no further than subspecies.

Populations may show different characteristics as nonheritable variations, heritable polymorphism, genetic drift, mutations, and hybridization.

With natural selection, those individuals possessing adaptive variations obtain a greater chance for survival and reproduction, and consequently contribute more to the gene pool of the population. This leads to a change in the characteristics of the population and possible speciation. Exposure to new habitats or niches may thus bring adaptive radiation into a variety of new species.

20

Distributional Units

Through the study of geographical ecology we attempt to understand how organisms are distributed over the world, and what forces brought about this distribution. Most organisms are of restricted distribution—only a few groups of animals, notably cyprinid fish, frogs of the genus *Rana,* colubrid snakes, passerine birds, rodents, and man, can be called even nearly cosmopolitan. In order to understand existing distributions, we must consider the histories of species, where they originated, how they got where they are now, and why they are not found in other parts of the world. This takes us into climatology, zoogeography, and palaeontology. In this section we will be dealing with the broader problems of the composition, characterics, and origin of geographic units in the distribution of organisms, rather than with the local units of communities and habitats discussed in Section II. These distributional units, like communities, are distinctive groups of organisms spatially distinct from other groups, but they do not always show functional integration as do communities and are sometimes characterized by genera, families, and orders rather than species. We will begin our discussion with zoological *realms,* areas defined largely by the past and present relations of the larger land masses to each other. Then we will proceed to a consideration of how the physiographic peculiarities of those land masses affect the origin and dispersal of organisms. Finally, we will consider the major ecological units, biomes, determined by climate and vegetation.

ZOOLOGICAL REALMS AND REGIONS

Geographic faunal divisions are characterized by the distinctiveness and uniformity of the taxonomic groups represented. They are relatively self-contained units isolated from other similar units so that there is no free and easy intermingling of species. There have been many attempts during the last hundred or more years to divide the world into such units (Kendeigh 1954). Probably the best system was that devised by Sclater (1858), modified by Huxley (1868), and extended by Wallace (1876). Although present-day students of special animal groups are inclined to modify the system further to fit best the distributions of those organisms with which each particularly deals, it commonly takes the form demonstrated in Fig. 20-1.

The regional divisions approximately coincide with continents. That the continental land masses should serve as the basis for the first major subdivision of the fauna of the world is to be expected, since they are mostly separated from each other by large bodies of water that serve as effective barriers. However, different continents have become isolated

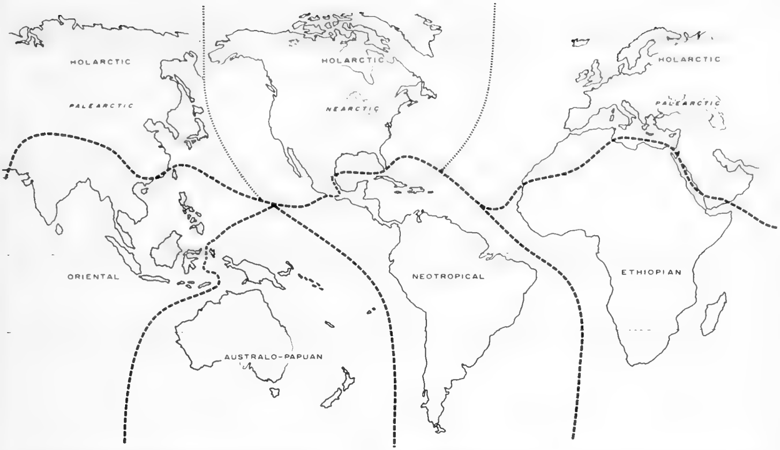


FIG. 20-1 **Zoological regions of the world. Adapted from Map No. 201 HA, Goode Base Map Series; copyright by the University of Chicago.**

Zoological realms	*Regions*	*General location*
Notogaea	Australo-Papuan	Australia, New Guinea (Papua), New Zealand, and neighboring islands
Neogaea	Neotropical	South and Central America, West Indies
Arctogaea (Megagaea)	Ethiopian	Africa, Madagascar
	Oriental	Tropical Asia, with associated continental islands
	Holarctic	Eurasia and North America

from each other at different times in the geological past and hence are not entirely equivalent in point of faunal distinctiveness. Australia has been separated from Eurasia for a very long time. Australia lacks a rich fauna, but that which it has is very distinctive, in recognition of which it and neighboring islands are delineated as the Notogaeic (meaning *Southland*) realm. South America has for long been far distant from Eurasia, where evolution of modern orders and families has proceeded most rapidly, and was long isolated from North America. Its fauna is unique, and it has therefore been given the name of Neogaeic (meaning *new land*) realm. The Ethiopian, Oriental, and Holarctic regions do not individually have such marked distinctiveness from each other as do the Australian and the Neotropical regions. Hence they are grouped into the Arctogaeic (meaning *Northland*) realm. We must now look at the characteristics of these realms and regions in more detail (Newbigin 1950, Beaufort 1951, Darlington 1957).

Australo-Papuan region

The Notogaeic realm and Australo-Papuan region may be subdivided into the Australo-Papuan, New Zealand, and Oceanic Islands sub-regions. (Some students raise these sub-regions to the rank of regions because there are in fact important differences between them.) Included in the Australo-Papuan sub-region are Australia, Tasmania, New Guinea and the nearby Aru Islands, the Bismarck Archipelago, and the Solomon Islands. These areas, except for the Bismarck Archipelago and the Solomon Islands which lie close and to the east, were united by dry land bridges in times past, for they are situated on the same continental shelf. New Zealand and the Oceanic Islands of the South Pacific are distant; the latter, at least, were always isolated. The fauna of the Polynesian Islands is certainly derived from New Guinea. It is a matter of controversy whether an actual land connection ever existed between Australia and the Oriental Region or whether there was only a series of stepping-stone islands by which dispersal took place. The Celebes, the Moluccas, and the Lesser Sunda Islands lie intermediate between the Oriental and Australian Regions and derive their fauna from both directions.

The Australo-Papuan region is marked by the absence of most groups of placental mammals, although some have been introduced. The original mammalian fauna consisted chiefly of monotremes, a diversity of marsupials, murid rats and mice, and bats. Well represented among birds are parrots and parakeets, cockatoos, lories, honey-eaters, birds of paradise, pigeons, megapodes, and kingfishers. Noteworthy is the presence of the emu (Australia), cassowary (New Guinea and adjacent islands), lyrebird, scrub-bird, and kiwi (New Zealand), and the absence of woodpeckers. Reptiles are well represented in the region, including *Sphenodon,* in New Zealand. Salamanders and true frogs are absent or scarce, but tree frogs occur in a great variety of species. The fresh-water fish fauna is scant, but includes the dipnoan lungfish *Epiceratodus.* Among the invertebrates, relict crayfishes of the family Parastacidae and a variety of land snails are of interest. Except some bats, there are no native mammals in New Zealand. The bird fauna is poor, with several flightless forms. In general, as one proceeds eastward and northward away from Australia and New Guinea the variety of animal life found on the isolated islands progressively decreases, but because of the isolation of the islands, many peculiar endemic forms are found.

Neotropical region

The Neotropical region making up the Neogaeic realm includes all of South America and the West Indies, and extends through Central America to include the southern lowland part of Mexico.

The fauna of this region includes a large number of endemic forms. Among the edentates, the sloths, armadillos, and anteaters are largely peculiar, although one species of armadillo extends north to Texas and east to Florida. There is a variety of marsupials present that doubtlessly entered South America from the north, although only one living marsupial occurs at present in the United States. The hystricoid rodents include the tree-porcupines, guinea pigs, agoutis, chinchillas, and others, of which only the porcupine has spread into North America. Prehensile-tailed monkeys and marmosets are characteristic, and tapirs occur here as well as in the Oriental region. Insectivores are largely absent.

The avifauna is rich and includes the tinamous, hoatzin, trumpeters, sun-bitterns, cariamas, seedsnipe, rhea, puffbirds, toucans, hummingbirds, and several unique families of passerines. Altogether, the Neotropical region has about 2500 species of breeding birds; Ethiopian region, 1750; Palaearctic sub-region, 1110; Nearctic sub-region, 750; Australia and Tasmania together, 650.

Reptiles are well represented, and among amphibians the tree frogs Hylidae reach their greatest diversification of species. Toads are present, but only a few true frogs and a few salamanders among the tailed forms. Among fishes, the catfishes, characins, and the eels are well represented, and one of the three remaining genera of lungfishes, *Lepidosiren,* occurs. Minnows are absent.

Islands in the West Indies have a reduced fauna, species of which appear to be variously derived from Central and North America. Of mammals, only rodents, bats, and the peculiar insectivore *Solenodon* are found. Fossil evidence, however, indicates a richer mammalian fauna in the past, which apparently arrived by an over-water route, perhaps on rafts (Simpson 1956). Except in Trinidad, the freshwater fish that occur in the West Indies are also tolerant of salt water.

The occurrence of many related forms in South America, Australia, and Africa, and the absence or poor representation of those forms, even as fossils, in North America and Eurasia has made the explanation of how they became distributed difficult. Land bridges across the South Atlantic and South Pacific have been postulated, but the idea is not generally accepted at the present time. The continental drift theory attempted to explain the distributions. An intervening connection at least of South America, Australia, and New Zealand at some time in the geological past with a large continent, Antarctica, in the south polar regions has been suggested (Glenny 1954). There is some evidence that Antarctica at one time had a warmer climate, but its secrets are now largely buried under many meters of snow and ice and must await development of new exploratory tools.

Ethiopian region

All the rest of the world, outside of the Notogaeic and Neogaeic realms, belongs to the Arctogaeic realm. Especially characteristic of this realm are the presence of ungulates, insectivores, catarrhine monkeys, and ganoid and cyprinoid fishes. Arctogaea is divided into three main regions. In the Ethiopian region is included all of Africa south of the northwest corner; and, since the Red Sea is of relatively recent origin and is not an important barrier, the southern part of Arabia. In the northeastern quarter of the realm the fauna reflects a mingling with the fauna of the Oriental region. Madagascar and other islands of the Mascarene group are sometimes considered a region distinct from continental Africa because they have a number of peculiar forms (Rand 1936).

At the levels of order and family, there are some similarities between the forest and savanna faunas of the Ethiopian and Oriental regions; at genus and species levels, however, differences are conspicuous. The similarities at higher levels are explained by geological history. During the Miocene and Pliocene, Africa, Arabia, and India shared a rather uniform, moist climate. Continuous land bridges supporting a rich uniform vegetation connected the three areas, and animals moved freely between them. An ocean barrier then developed between Africa and Arabia on the west and India on the east, and drying of the climate in northern Africa and Arabia interposed arid grassland and desert between the forests of central Africa and India. Separation of the forest fauna into two isolated populations has permitted evolution of distinct species and genera in those families and orders that the two regions share in common (Moreau 1952).

The Ethiopian region is remarkable in having neither deer nor bears. Except for the guinea-fowl, there are few gallinaceous species, so common in the Oriental region. It has several endemic bird families, however, including the Musophagidae and Coliidae; Africa also has the ostrich. Hornbills occur both in Africa and the Oriental region. Peculiar to Africa, but extending north into Palestine and Syria, are the mammalian hyracoid coneys. Africa is noted especially for giraffes, antelopes, zebras, elephants, and other ungulates that wander around in large herds. The presence of the large hippopotamus and rhinoceros should be mentioned and also the number of cats (lion, leopard) and dogs (jackals, foxes, hunting dogs, and others). The tiger of the Orient is absent. Edentates include the aardvark and scaly anteaters. Among the primates are found lemurs, baboons and macaques, the chimpanzee, and the gorilla. Rodents and insectivores are well represented. It appears that most of the mammals, except for the elephants, coneys, and aardvarks, had a Holarctic origin and entered the Ethiopian region from the North. Reptiles are well represented in Africa; the chameleons are highly varied in Madagascar. Salamanders and the tree frogs are absent from the amphibian fauna.

The fish fauna in the Ethiopian region contains a great proliferation at the species level. Several relict species, such as the lungfish *Protopterus*, occur; and several families of primitive teleosts are endemic. Otherwise there is considerable relationship between the fish fauna of the Ethiopian and Oriental regions.

The Madagascar or Malagasy sub-region has been isolated from Africa certainly since the Eocene and possibly since early Mesozoic. Most modern families of mammals have evolved since early Tertiary and would have had to enter Madagascar by the sweepstakes route, it is no wonder then that such groups as ungulates, rodents, carnivores, and monkeys are so poorly represented, at best, in this sub-region. On the other hand, peculiar insectivores (Centetidae), carnivores, rodents, and primates (especially lemurs) occur here, the derivatives of primitive stock which is poorly represented if not extinct on the continent. A similar situation obtains among groups other than mammals. The avifauna include several families, genera, and species peculiar to the sub-region. Bird groups show affinities both with continental Africa and the Oriental region; and it is possible that some forms may have been driven hither by heavy winds. In general, the avifauna differs more from the Ethiopian region than the latter does from the Oriental region (Rand 1936). Madagascar has no poisonous snakes, but there is a good representation of other reptiles. It is of special interest that Madagascar, the Comoro Islands, Bourbon, Mauritius, Rodriguez, Aldabra, Admiralty Islands, and Seychelles in the Indian Ocean all support peculiar species or subspecies of large land tortoises. The only other place in the world where large tortoises occur is on the Galapagos Islands off the west coast of South America, but these are not related, being independently derived from small forms. There are no strictly limited fresh-water fish on Madagascar, although fresh-water forms also tolerant of salt-water occur. Parastacid crayfishes are found in Madagascar, South America, and in the Australian region, but nowhere else.

Oriental region

The Oriental region includes tropical Asia, conspicuously demarked from the Palaearctic to the North by the Himalayas. To the West it gradually gives off into the Ethiopian region. An inexact boundary line (for our purposes, we may adopt Weber's line here) separates it from the Australo-Papuan region to the Southeast. Java, Sumatra, Borneo, and the Philippines belong to the Oriental region and, according to Gressitt (1956) so properly do many of the outlying Pacific islands. The Indian peninsula is an old land mass separated from continental Asia during the Eocene by the Tethys Sea, which intruded eastward from the Mediterranean through much of southern Asia before the uplift of the Himalayas. India may have been connected with Africa at various times in the past, most recently during the Miocene and Pliocene as discussed earlier.

Tree-shrews; the gibbon, orangutan, and tarsier; fresh-water tortoises (Platysternidae); and the slender-nosed fish-eating gavials are exclusive to the

Oriental region. Other interesting forms characteristic of this region, although not exclusive to it, include two kinds of loris; the pangolins, an elephant, a tapir; two rhinoceroses, several species of deer and antelopes, wild pigs, many rodents, a porcupine; the tiger among several other cats; bears, several kinds of monkey; and, among birds, many pheasants, the bee-eaters, rollers, broadbills, bulbuls, and sunbirds. Many kinds of poisonous snakes occur, and lizards are well represented. True frogs and toads occur; tree frogs and salamanders do not. The most primitive spadefoot toads, Pelobatidae, occur here, other forms being found in Europe and North America. The Apoda also occur throughout the Oriental region; elsewhere, only in the Neotropical and Ethiopian regions. A varied fish fauna exists.

There is a marked difference between the fauna of northern and southern India; probably a consequence of the extensive volcanic eruptions that occurred in early Tertiary which devastated extensive areas in central India, the so-called Deccan traps, and formed an effective East-West barrier that persists even at present to some extent. Southern India and Ceylon have a fauna related generically to that of Siam, Indo-China, the Malay peninsula, the East Indies, and the Philippines. The extensive Tertiary intrusion of the sea between southern India and Ceylon and the eastern portion of the region, has permitted the extensive evolution of distinct species in the areas. The various islands of the East Indies that fall within this region have received their fauna during the various times they were connected by dry land with each other and with the mainland.

Holarctic region

The broad Bering land bridge connected North America and Asia through much of the Tertiary, and there was considerable movement of animals back and forth between the two continents. There is similarity at least in the genera of many animals in the northern portions of the two continents, and many species are found in both areas. Salamanders are largely limited to the Holarctic; edentates and primates, other than man, are mostly lacking. The horse and camel evolved first in North America and then spread to Eurasia and Africa but became extinct in North America. The horse was reintroduced into North America within historic time by the white man.

As one progresses southward on the two continents below the Arctic tundra and coniferous forest, the fauna changes (Udvardy 1958) enough to separate the Palaearctic and Nearctic sub-regions. The chief differences distinguishing the two are at the level of species and genera and a few families. Differences are more pronounced among birds and reptiles than with mammals. Antelopes, sheep, goats, and certain other groups are in greater variety of species in the Palaearctic; water moles of the subfamily Desmaninae are unique to the sub-region. On the other hand, the Nearctic has several families of birds, such as the vultures, turkeys, mockingbirds, vireos, and wood warblers that have not spread into Asia and Europe. Rattlesnakes, salamanders (Ambystomidae), suckers, and catfishes common to the Nearctic are either absent in the Palaearctic or poorly represented.

FAUNISTIC SYSTEMS

When populations become isolated geographically, they tend first to differentiate into subspecies differing in superficial characteristics, then into new species that would not interbreed even if the isolation were lost, and finally into genera and units of still higher rank. There is a general relation between the size of the area and the extent to which taxonomic differentiation proceeds. Continental masses isolated from one another are usually prerequisite to the development of orders and families, and the analysis of geographic distribution of animals at these taxonomic levels is recognized in the realms, regions, and sub-regions already discussed. Each of these major geographic areas is subdivided into units of lesser size, wherein genera, species, and subspecies become differentiated. There has been considerable study of different methods of recognizing, evaluating, and classifying these lesser units in the distribution of animals which has resulted in different *faunistic systems*. The more important of these systems need now to be analyzed, especially in reference to the Nearctic sub-region.

Faunal areas

The first attempt to subdivide North America into geographic units of biological significance was made by Schouw in 1823, for plants. His work stimulated zoologists to undertake a number of similar efforts (Kendeigh 1954). J. A. Allen (1892) developed one of the best and most realistic of the faunistic systems. The northern hemisphere was divided into circumpolar arctic and north temperate realms and an American tropical realm separate from tropical realms in the eastern hemisphere. The north temperate realm he divided into North American and Europaeo-Asiatic regions, and into cold and warm temperate sub-regions. There is considerable merit in this system: in the Holarctic, a close similarity of the North American and Eurasian faunas obtains in

FIG. 20-2 **Biotic provinces of North America (Blair 1950, Dice 1943, Miller 1951, Smith 1949).**

the tundra (arctic realm) and coniferous forests (cold temperate sub-region), but greater and greater intercontinental divergences become apparent as examination progresses southward (Udvardy 1958). Allen considered humidity to become more important than temperature southward in North America, because it determined the prevalent type of vegetation with which animal distribution was correlated. So he separated the warm, temperate sub-region into an eastern humid province that was heavily forested and a western arid province containing grassland and desert. These provinces were characterized by the presence or absence of prominent generic types of animals. Allen's minutest subdivision was the faunal area, characterized by a combination of species not found elsewhere.

Life-zones

The life-zone system was developed between 1890 and 1910 by C. Hart Merriam (Kendeigh 1954). Merriam postulated that animal life in North America had dispersed during past geological time from two great centers; one in the far North, the *boreal,* and the other in the Southwest, the *sonoran.* Boreal animals dispersed southward along the higher elevations in the mountains, thence over the continent generally as they became acclimatized to the progressively higher temperatures of lower altitudes and more southerly latitudes. Sonoran forms dispersed northward through the lowlands as they became acclimatized to cold. Believing, contrary to Allen, that temperature was more important than moisture and types of vegetation in controlling the distribution of animals, Merriam extended the faunal areas indicated as Alleghanian, Carolinian, and Louisianian on Allen's map westward as belts to the Pacific and re-designated them the Transition, Upper Austral, and Lower Austral life-zones. The boundaries of the life-zones coincided closely with isotherms. Each life-zone supposedly contained boreal and sonoran organisms in a characteristic and definitely proportioned mixture. Each of these three life-zones he then divided, at about the 100° meridian, into eastern humid and western arid faunal areas to indicate the secondary role played by moisture and vegetation.

Flaws in this system have become apparent in recent years. For one thing, the life-zone, as a transcontinental belt, is not a unit that can be recognized everywhere by a characteristic and uniform faunal composition. The Lower Austral zone in Georgia or Florida, for instance, is composed of animal and plant species almost totally different from the composition obtaining in the same zone in Arizona. This has led to the realization that while temperature is of undoubted importance in controlling animal distribution, differences in type of vegetation, in moisture and terrain, as well as in geological history of community groups are factors usually equally as important as temperature, sometimes more so, in determining what species will be present. Furthermore, while the past history of some genera and species can be traced directly to boreal and sonoran distributional centers, it is clear that many species and especially subspecies evolved in various smaller centers (biotic provinces) elsewhere over the continent. Finally, evaluation of local, especially mountainous, areas in terms of biotic communities has tended to confuse the life-zone system with the biome system.

Biotic provinces

A concept of biotic provinces first began to attract attention about 1911, and the provinces were defined and mapped by Dice in 1943 and again in 1952a. A biotic province is a *continuous geographic area* that possesses a fauna distinguishable, at the species and subspecies levels, from the fauna of adjacent areas, at least to a certain degree. The boundaries of biotic provinces are more likely to coincide with physiographic barriers than with types of vegetation. Unlike faunal areas, life-zones, and biomes, biotic provinces never occur in discontinuous geographic fragments since they are intended to show regional areas of differentiation.

A biotic province which includes a mountain may have several types of vegetation or life-belts, each serving as a center of differentiation for its characteristic fauna when compared with similar life-belts in other provinces. The biotic province system is being used at the present time by some mammalogists, ornithologists, and herpetologists in the study of particular taxonomic groups, but there has been no general synthesis of these studies and of plant groups to render the provinces truly "biotic" in nature.

Faunal groups or elements

In all the systems described, faunal distribution has been analyzed in terms of geographic areas, and the chief criterion for determining the limits of an area has been that of distinctiveness between the fauna of different areas. Recently, largely from the impetus of herpetofaunal studies by Dunn (1931); avifaunal studies by Stegmann (1938), Mayr (1946), and Miller (1951); of Simpson's studies of mammalian fauna (1947); and the plant studies of Wulff (1943) and Cain (1947), a different analytical approach to faunal and floral problems has developed. By this more recent approach, those species with similar centers of origin, dispersal routes, geological histories, and habitat preferences are the elements of a fauna or flora which are analyzed. The objectives are to learn the place where and time at which these groups of species originated, how the groups came to occupy a particular part of the world, became adapted to live in new environments, and how they evolved into the present-day living species. A type of vegetation, life-zone, or biotic province may contain species from several different faunal elements that have come to live together. Thus in the bird composition of California one can recognize boreal,

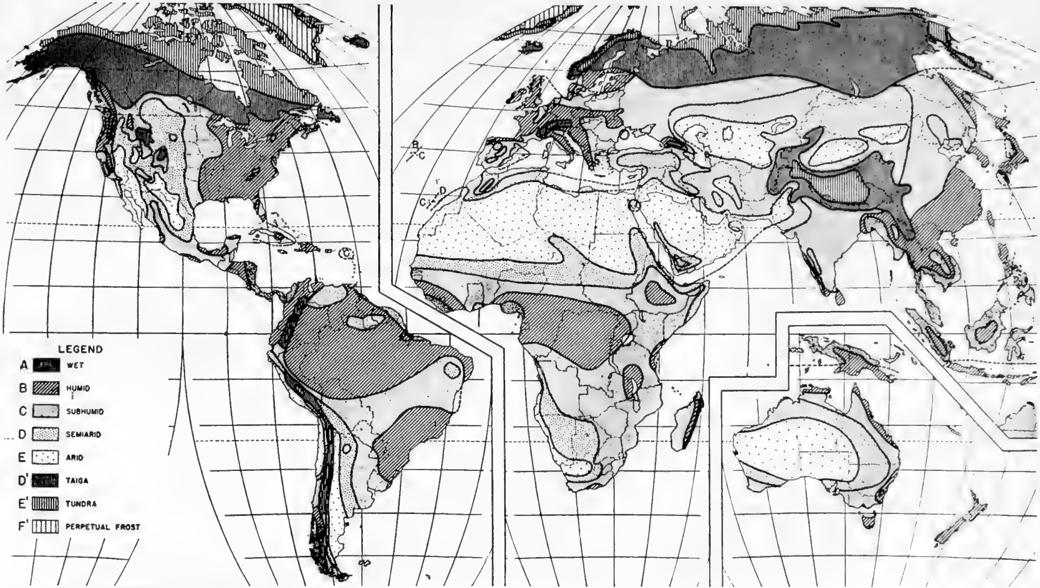


FIG. 20-3 Distribution of principal climates of the world (Blumenstock and Thornthwaite 1941).

Great Basin, Sonoran, and authochthonous elements (Miller 1951) (see also Table 10-1).

THE ECOLOGICAL SYSTEM

A still different approach for the study of animal distribution is the ecological one, involving the biome concept (Clements and Shelford 1939). The other systems described are zoogeographical in their attention to centers of origin, dispersal routes, and evolution. The ecological system emphasizes environmental relations and community dynamics. This does not mean that zoogeographers do not consider the relations of climate and terrain in controlling dispersal and evolution, nor that ecologists are not concerned with the geological history of the forms with which they deal, but the viewpoints and objectives are different.

Basic to the understanding of the ecological system is the recognition of communities composed of characteristic combinations of animal and plant species, of successional relations between communities, and that succession in all local habitats eventually ends in a climax community pattern, the most important ecological characteristic of a geographic area (Cain 1939, Whittaker 1953). The development of an understanding of these ideas has been a major concern of this book, especially Chapters 5 to 9.

The major unit in the ecological system is the biome. A *biome* is a biotic community, characterized by distinctiveness in life-forms of the important climax species. On land, the most important climax species are usually plant dominants that occur in distinctive vegetation and landscape types; in the ocean, the important organisms that define biomes are usually the predominant animals, which are sometimes also dominants.

Seral communities are developmental stages. They are as much a part of the biome as developmental instars are a part of a species of insect. The animal and plant constituents of seral stages are, however, more widely distributed than are species belonging to climax communities, since the habitats in which they belong are more nearly alike in different parts of the world than are the habitats that contain the climax. Seral species are not generally useful, therefore, to defining the limits of biomes. The majority of animal constituents of the climax community, however, are characteristic only of the climax vegetation or habitat and therefore of restricted distribution.

The principal biomes of the world, insofar as they have been identified, are the following:

Terrestrial	*Marine*
Temperate deciduous forest	Oceanic plankton and nekton
Coniferous forest	Balanoid-gastropod—thallophyte
Woodland	Pelecypod-annelid
Chaparral	Coral reef
Tundra	
Grassland	
Desert	
Tropical savanna	
Tropical forest	

The vegetational portion of the biome is sometimes called the *plant formation* (Weaver and Clements 1938). A *plant association* is a subdivision of a biome or formation, distinguished by uniformity in the species composition of the climax plant dominants. The *associes* is the equivalent seral plant community, regardless of whether it belongs to the same or a different type of vegetation than the climax. The important point to remember here is that the biome is distinguished by the life-forms of the climax dominants, but subdivisions of the biome are recognized principally by taxonomic composition.

The type of climax in a terrestrial area is determined mainly by the conditions of climate, although secondary correlation also occurs with major soil groups. Were climate the only factor involved and the terrain uniform, the climax community would be monotonous in its composition and structure, except as one community graded into another with change in climate. Where the composition and character of the prevailing vegetation varies more or less permanently with changes in physiography, soil, or fire factors, we may speak of physiographic, edaphic, or fire *subclimaxes* or faciations.

This is in agreement with the *monoclimax* viewpoint; that is, that there is only one true climax in an area, determined by the prevailing climate. An opposing concept is that of *polyclimaxes*. Proponents of the latter viewpoint give nearly equal significance to climate, soil, topography, and other factors, and believe that each major variation in composition or structure of the mature vegetation should be considered as equally important. Hence, several climaxes, or at least a complex community pattern that varies in structure and species composition from one site to another, may be claimed for an area (Whittaker 1957). The controversy is largely one of emphasis and semantics.

A *biociation* is a subdivision of a biome distinguished by uniformity and distinctiveness in the species composition of the climax community, particularly of the animal predominants. The *biocies* is the

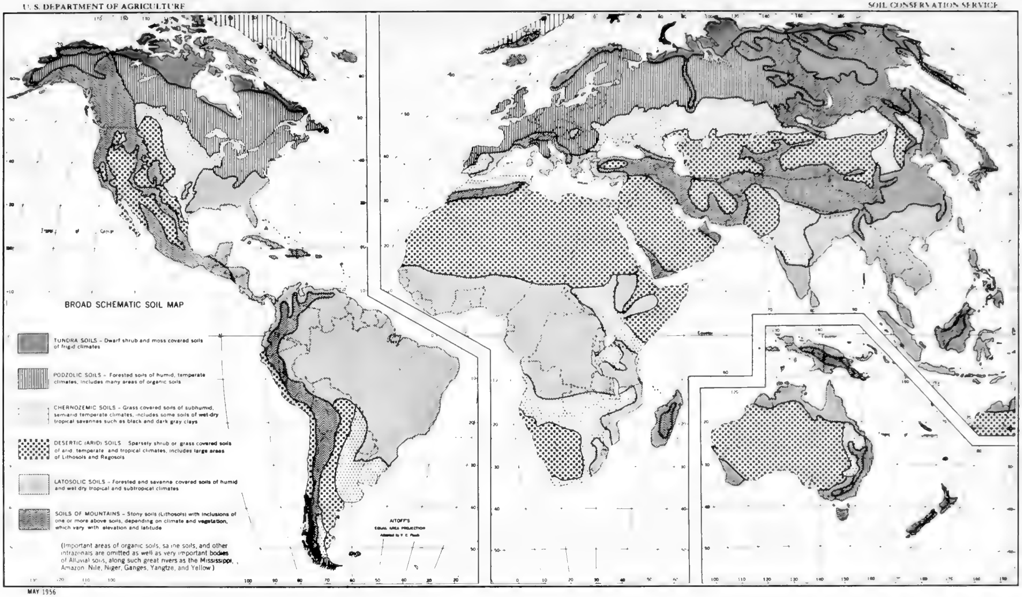


FIG. 20-4 Distribution of the principal soil groups of the world (Simonson 1957).

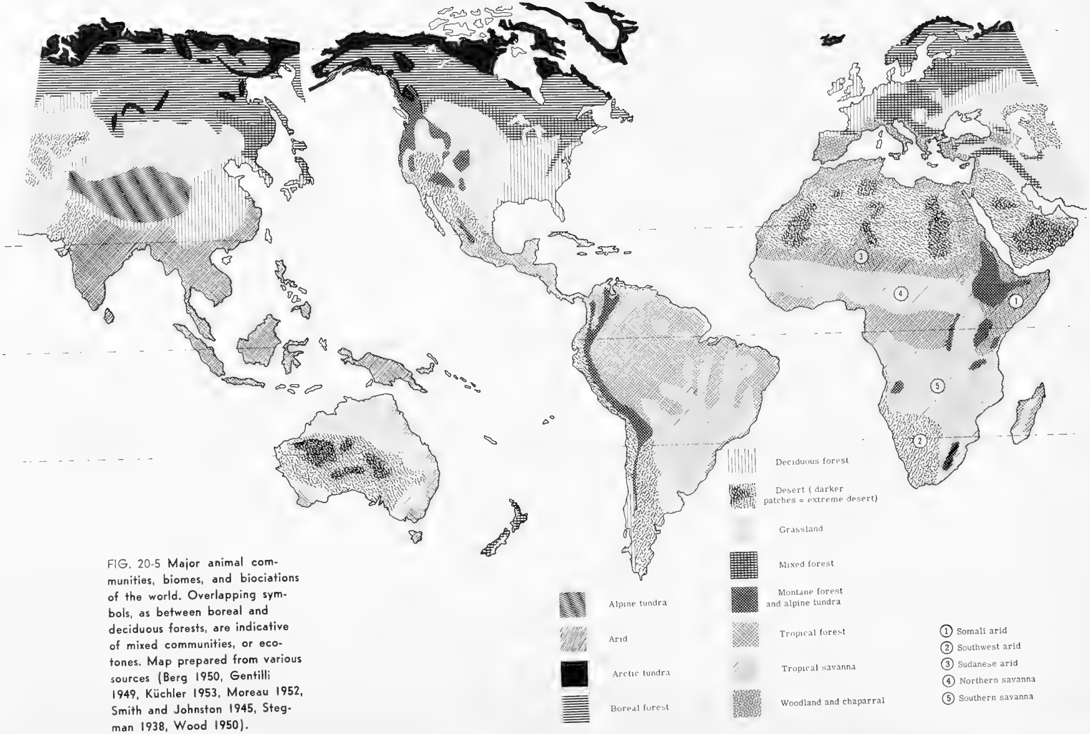


FIG. 20-5 Major animal communities, biomes, and biociations of the world. Overlapping symbols, as between boreal and deciduous forests, are indicative of mixed communities, or ecotones. Map prepared from various sources (Berg 1950, Gentilli 1949, Küchler 1953, Moreau 1952, Smith and Johnston 1945, Stegman 1938, Wood 1950).

equivalent seral community. With the biome, we recognize the primary importance of the life-form of the principal climax organisms for establishing the major units into which the geographical distribution of organisms are naturally divided. The biociation concept does not regard differences in the species composition of plant dominants, such as are recognized in the plant associations, as establishing the fundamental subdivisions of the biome for animals. So long as they are of the same life-form, variations in the plant species composition produce only minor differences in dominance, insufficient, for the most part, to induce striking changes in the species composition of the rest of the community. The relation between biocies, associes, and changes in vegetation that occur with succession (Fig. 8-4) obtain also between biociations, associations, and changes in vegetation that occur geographically. Actually, the animal ecologist has no absolute need to identify the species composition of the plant dominants if he can describe the vegetation accurately in other ways (Dansereau 1951). If one wishes not to define plant communities on the basis of the taxonomic composition of the dominants alone, the concept of biociations may be equally useful for the analysis of distribution of plant species. The so-called natural areas of Cain (1947) are a step in this direction.

A biociation may originally derive its species components from several faunal elements (Table 10-1), but once the community constitutes a unit, it may thereafter serve as an element itself, and a geographic area may be described in terms of the biociations and biocies it contains. Biociations differ from biotic provinces in that the latter are geographic areas, rather than communities, and in mountainous areas may contain several life-belts or different types of community. Furthermore, biotic provinces may be characterized in part by the presence of particular subspecies. Subspecies are not used in defining biociations.

The faunal system of Allen bears some resemblance to the biome system. Allen's barren-ground fauna is equivalent to tundra; the cold temperate subregion together with the Pacific Coast district equates with coniferous forest; the warm temperate subregion with deciduous forest; the Great Plains district with semi-arid grassland; the Great Basin district with arid grassland and sagebrush; and the Sonoran sub-province with desert. The different faunas within these major divisions may correspond to biociations. Although the terminology is different and the refinement of details is greater, the system of biomes and biociations is manifestly built upon the basic foundation laid by a long line of zoogeographers (Kendeigh 1948, 1954).

It is clear, then, that two sets of factors control local and geographic distribution of organisms. The first set is ecological, including the physical factors of nature of the substratum and climate for terrestrial organisms and the composition of the water for aquatic forms; the biotic factors, especially of food, cover, reproductive requirements, competition, and predators; and the psychological factors of behavior adjustments, inherited mores, and specific niche requirements. On the other hand, zoogeographic factors include the considerations of place of origin; dispersal pathways, rates, and barriers; and evolutional acquisition of new structural, functional, or behavioral adjustments that permit invasion of new areas, surmounting of old barriers, or incorporation into new communities. The present-day distribution of animals and plants into different community units is the result of all these forces at work, both at the present time and for untold generations in the past.

SUMMARY

There are three zoological realms and five zoological regions into which the world is divided. Free dispersal between regions is prevented by the major barriers of oceans, mountain ranges, and deserts; each region is thus characterized by distinct orders and families of organisms.

Within each region secondary barriers separate divisions of lesser rank characterized by genera, species, and subspecies. Of the Nearctic region of North America, such differentiation has prompted the recognition of faunal areas, life-zones, and biotic provinces.

In contrast to the analysis of fauna in terms of geographic units is analysis in terms of the elements that it possesses. A faunal element is a group of species coming from the same center of origin and having similar geological histories.

Zoogeography is the study of animal distribution in terms of centers of origin, dispersal routes, and evolution. The ecological system emphasizes environmental relations and community dynamics.

The principal unit in the ecological system is the biome. A biome is a major biotic community characterized by distinctiveness in the life-forms of the important climax species. Seral communities are developmental stages of the biome. The biome is divided into plant associations, distinguished by uniformity in the species composition of the climax plant dominants, and into biociations, identified by uniformity and distinctiveness in the species composition of the climax community, particularly of the animal predominants. Some nine terrestrial and four marine biomes are recognized, to the study of which we now proceed.

21

Paleo-ecology

Now that we have adopted the biome system as the point of departure for analysis of animal distribution, it is essential to learn something about the geological history of these community units: how they were first formed, when they first became well defined, how they dispersed over the world, and why they came to occupy their present locations. When we know the origin and geological history of vegetational communities on land, we will be better able to understand the origin, differentiation, and present-day distribution of the animal species that are components of these communities (Epling 1944). A review of geological succession generally will be helpful, although we will be mostly concerned with tracing the origin and historical development of the biomes during the Tertiary Era alone (see Table 3-1).

PHYSIOGRAPHIC CHANGES

At the beginning of the Tertiary, some 60–70 million years ago, the interior of the North American continent was still widely inundated by the epicontinental seas of the Cretaceous period. As these seas gradually receded, the continent acquired its modern topographic appearance. The Mississippi embayment area is an extension of the coastal plain that continues around the Gulf of Mexico and northward along the Atlantic coast. This coastal plain emerged progressively throughout the Tertiary Era. Its general character is much the same now as it has always been— tidal salt marshes and estuaries intermingled with shallow lagoons bounded by off-shore bars.

The Appalachian Mountain System first appeared near the end of the Paleozoic era and had become eroded to a peneplain by the beginning of the Tertiary. A new uplift then occurred, and erosion again followed. In the Miocene, only the Schooley peneplain, a nearly level surface only slightly above sea level, remained. However, monadnocks, hills of resistant rock rising some hundreds of meters, were left projecting out of the Schooley peneplain. Mount Monadnock, the White Mountains, Great Smokies, Cumberland Mountains, among others, are such formations. The Schooley peneplain subsequently underwent a series of archings and uplifts until it reached some 1200 m (4000 ft) above sea level along the central axis to give the region its present-day character. In New England, Pleistocene glaciation covered these mountains, rounded them off, scraped away the old soil, and left a poorer soil full of boulders.

The Ozark and Ouachita Mountains were also formed at the close of the Palaeozoic, underwent subsequent erosion, and experienced minor uplifts. Elsewhere in the central interior between the Appalachian Mountains and the Great Plains, peneplanation was the dominant force throughout the Mesozoic and Tertiary. Low coastal marshes extended around the Mississippi embayment, and marshes and swamps were frequent elsewhere. During the Pleistocene, glaciers moved tremendous quantities of soil and rock from Canada southward and from mountain ridges into valleys. The retreat of the ice front proceeded haltingly with alternating retreats and advances. When it was stationary but melting, the glacier formed concentric terminal moraines; when in active retreat, the glacier left a thick layer of till in its wake.

The Laramide orogeny, which occurred at the end of the Cretaceous period, formed a series of mountain ranges in the Rocky Mountain system, including the Big Horns, Wind River, Black Hills, Uintas, and the series of more or less parallel ridges in the Great Basin. Some of these mountains were high enough to support glaciers during the Paleocene. Rapid erosion filled the deep basins between the mountains with debris. By the Eocene, the mountains were much reduced, and by the Oligocene peneplanation was complete, although the surface was several hundred meters above sea level and monadnocks remained. This peneplain extended to the Pacific Ocean.

Beginning in the Miocene, increasing in intensity through the Pliocene into early Pleistocene, but decreasing since, mountain formation was extensive not only in the Rocky Mountains but also in the Appalachians, Ozarks and Ouachitas, Cascades, Sierra Nevada, and Coast Ranges. Volcanic action was extensive in the West, especially in Oregon and Washington. Highly fluid basalt welled out of long fissures in the earth's crust, filled valleys, altered drainage systems, and formed sheets up to 1500 m (5000 ft) thick over 80,000 sq km (200,000 sq mi). Mount Rainier, Mount Hood, and Lassen Peak were among these volcanoes. During early Tertiary, the Sierra Nevada and the Cascade Mountains were probably only low ranges which were peneplaned by the Miocene, but then both the Sierra and Cascades were uplifted by faulting and tilting so that the eastern edge of the block was 4000 m (13,000 ft) above sea level.

During early Tertiary, the area of the present Coast Ranges was in part an island archipelago, separated from the coast by a deep sea trough that is now the interior of California. Folding and faulting in the Coast Ranges began in the Miocene and were most active in the Pleistocene. Such activity is still going on as evidenced by the recent earthquakes. The Coast Ranges are the youngest mountains in North America.

CLIMATIC CHANGES

The climate 60–70 million years ago can only be deduced from sediment types and plant and animal fossils. After peneplanation of the western mountains there was little to obstruct the warm, moisture-laden, westerly Pacific winds sweeping across the continent. Rains were heavy, and fell frequently throughout the year. The Mississippi embayment helped to maintain a uniform oceanic climate. Tropical conditions extended as far north as the Dakotas and Vermont, and temperate conditions obtained nearly to the North Pole. With the elevation of the western mountains in the Miocene and Pliocene, especially the Sierra Nevada and Cascades, the westerly winds were forced to high elevations, cooled, and lost much of their moisture as precipitation on the windward western slopes during the winter; dry seasons prevailed during the summer. On the lee eastern mountain slopes, arid conditions developed because the winds, warmed as they descended the mountain, retained what moisture remained in them, thus producing a *rain-shadow*. Dry plains and desert thus developed in the Great Basin. More moisture precipitated as the winds crossed the Rocky Mountains. Mixing of the westerly winds with winds from the North and South, however, produced less aridity east of the Rockies than in the Great Basin, and east of the Great Plains the western mountain rain-shadows had no effect.

Concurrent with increasing aridity over the continent was cooling of the air. This began in middle or late Oligocene and brought a gradual southward shift of climatic belts which culminated in the very severe glaciation of the Pleistocene. The actual cause of the glaciation is obscure, but there is no doubt that the glaciation was accompanied by a drop in average temperature, and an increase in annual precipitation (Ewing and Donn 1956).

EARLY TERTIARY FLORAS

The geological record of Tertiary plants is good, particularly in the western United States. Volcanic ash, lake deposits, coastal swamps, and river basins preserved fossils well, more or less *in situ*. These fossils indicate that there were three principal floras, geofloras, or groups of plants that maintained identity together over wide ranges of space and time (Chaney 1947). It was from these floras and the faunas that they contained, that the modern vegetation types, biomes, plant associations, and biociations differentiated. Doubtless there was some latitudinal and altitudinal zonation in the early floras, but the development of present-day community units is the result of later; rigorous climatic zonation, and a more extensive physiographic diversification over the continent than prevailed in the early Tertiary. Instead of evolving new tolerance limits, species, with some exceptions, dispersed into those regions that continued favorable to them and became extinct in regions that became unfavorable. Species with similar ranges of tolerance thus came into association and, as interdependent coactions became established, into closely knit communities.

Neotropical-tertiary flora

This flora is known from several Paleocene, Eocene, and Oligocene deposits (Berry 1937). It was composed of tropical and subtropical plants now limited largely to southern Florida, Mexico, and the tropics. Its counterpart, the *Paleotropical-tertiary flora,* occurred in western Europe. Trees characteristically had broad, thick, evergreen leaves. The laurel familly, Lauraceae, was particularly well developed in North America, and some modern descendants are found in the temperate flora. The Neotropical-tertiary flora extended from the tropics as far North as at least 49° latitude in the West and 37° latitude in the East. With the drying and chilling of the continent that began in late Oligocene and Miocene, this flora retreated southward and eastward to the localities in which it is found today.

Arcto-tertiary flora

This flora completely encircled the North Pole, except for the Atlantic Ocean, with little variation in composition or character. Plants migrated freely across the Bering land bridge between North America, Asia, and Europe. Probably no land bridge existed directly between North America and Europe during the Tertiary (Lindroth 1957). On the Arctic islands and in northern Siberia, the flora reached North to within 8° latitude of the North Pole. How these species tolerated the long seasons of darkness is a problem; possibly, daily photoperiods, as well as temperature, were different then than now. An ecotone with the Neotropical-tertiary flora began at 57° latitude on the Pacific coast and 51° in southern British Columbia, Alberta, and Saskatchewan. In Asia, an ecotone began at 42° latitude in Manchuria; in central Europe, at 48°–50°.

Much of the present similarity between eastern North American and Eurasian floras and faunas may be traced to the continuous and extensive distribution of the Arcto-tertiary flora during the early Tertiary. Types that occur prominently in eastern North America and eastern Asia, for instance, are, among the plants, tuliptrees, magnolias, sweetgums, sassafrasses, witch-hazels, and partridge-berries; among the animals, paddlefish, alligators, fresh-water turtles, lizards (*Leiolopisma, Eumeces*), snakes (*Natrix, Opheodrys, Elaphe, Agkistrodon*), hellbender (Schmidt 1946); as well as various birds and mammals.

The chief differentiation of the Arcto-tertiary flora was latitudinal into *boreal* and *temperate units.* The boreal unit contained such trees and shrubs as the *Metasequoia,* baldcypress, pines, spruces, willows, birches, and hazels. The temperate unit included maples, alders, birches, hornbeams, chestnuts, dogwoods, hawthorns, beeches, ashes, walnuts, pines, sycamores, poplars, oaks, willows, baldcypress, basswoods, elms, and *Metasequoia.* Although there was some mixture, deciduous species predominated in the temperate unit; the boreal unit contained relatively more coniferous species. These same latitudinal relations obtain at the present time. The climate of the temperate unit was probably humid, with summer rainfall, and with moderate temperatures not regularly falling below freezing (Chaney 1948).

With the elevation of the western mountains in the Miocene and Pliocene and the drying and cooling of the climate, the Arcto-tertiary flora retreated from the far North, and the American portion lost its contact with Asia. In North America, the main movement of the temperate unit was to the South and East, but a secondary movement of broad-leaved evergreen and deciduous trees and shrubs proceeded southward along the moister mountain slopes, valleys, and Pacific coast. Beech, basswood, elm, and hornbeam disappeared from the West, probably because of the lack of summer rain there, but were prominent in the movement to the Southeast. *Metasequoia,* on the other hand, became limited to the Pacific coast in North America, and evolved into our present day redwood forests. Living *Metasequoia* are still to be found in central China. The boreal unit followed closely behind the temperate unit; and in the higher elevations of the mountains, it extended as far southward as the temperate. There were changes in the taxonomic composition of the Tertiary forest during this long period. Some genera were lost entirely, some new ones were added, others were changed by evolution; but all these changes were conservative, and the present-day mixed mesophytic forests of the Cumberland Mountains of eastern Tennessee have nearly the same composition and appearance as did the ancient forests. A related *Antarctic-tertiary flora,* derived from the Cretaceous flora and containing both conifers and deciduous trees, occurred in the Southern Hemisphere, but its history during the Tertiary was entirely independent of the Arcto-tertiary flora.

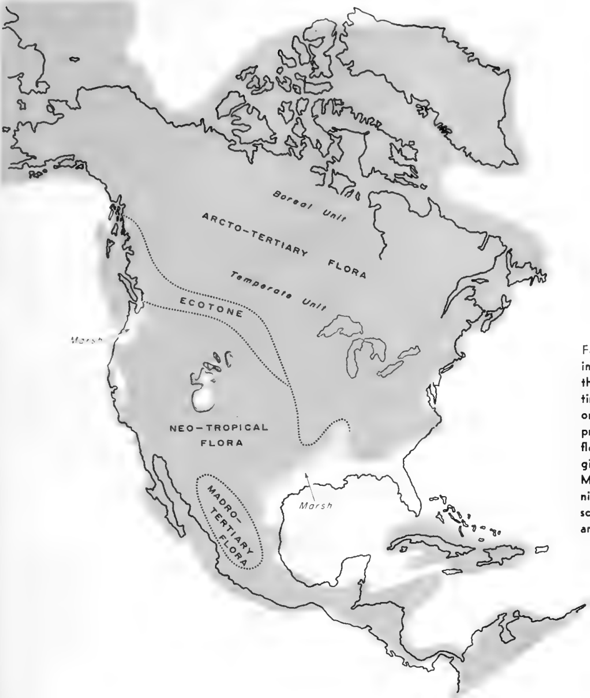


FIG. 21-1 North America during the early Eocene, showing the configuration of the continent (tinted area, superimposed on an outline of the continent at present) (Schuchert 1955), and floral units (from information given by Chaney 1947). The Madro-tertiary flora was beginning to differentiate in small scattered areas within the general area indicated (Axelrod 1958).

Madro-tertiary flora

The Madro-tertiary flora had its center of origin on the Mexican plateau in the region of the Sierra Madre, perhaps beginning in the Eocene in scattered dry sites on the lee sides or rain-shadows of high ridges and mountains. Its history previous to the Miocene is obscure. The flora contained a variety of small trees, shrubs, and probably some grasses, although the fossil record of grasses is poor. These species seem to have been derived principally from the Neotropical-tertiary flora in response to increasingly arid environments (Axelrod 1958). Minor elements of this flora extended into the Great Basin area, but its main movement northward occurred in the Miocene and Pliocene. During the latter epochs, the flora came to occupy large areas in southern California, the Great Basin, and the Great Plains, areas which were being vacated by the other two Tertiary floras because of the increasing aridity. Derived in large part from this flora are the present-day communities of woodland, chaparral, sagebrush, subtropical scrub (thorn forest), desert, and arid grassland. These communities are relatively young, as distinct entities; the North American desert biome, for instance, is probably not older than Upper Pliocene (Axelrod 1950).

THE PLEISTOCENE

Physical conditions

The Pleistocene was marked by a series of great climatic fluctuations throughout the world (Flint 1957). Thirty-two per cent of the land area of the world was buried under glacial ice; 10 per cent still remains ice-covered. In places, this ice reached a thickness of at least 1500 m (5000 ft), roughly the thickness of the ice sheets now on Greenland and Antarctica. Outwash from the glaciers carried sedimentation hundreds of kilometers beyond the farthest ice boundaries. Sea-level fell to 138 m (450 ft) below the present level as water became bound in glacial ice. This resulted in exposed coastal plains all around the world to an extent greater than at present (Russell 1957). There were widespread back and forth movements of animal and plant species as glaciers alternately advanced and retreated.

There is good reason to believe that North America was connected by a land bridge to Siberia over the Bering Sea and Strait at times of glacial advance, but not during interglacial periods (Hopkins 1959). The climate over this bridge was probably similar to that associated with tundra vegetation and not warm enough for forests to develop. According to one theory (Ewing and Donn 1956), the Arctic Ocean remained open water and largely free of ice during the time of the glacial advance and its eventual freezing over, thus cutting off the supply of moisture as precipitation, brought the glacier to a halt and then to retreat. A reconstruction of the appearance of North America at the time of the last (Wisconsin) glaciation is shown in Fig. 21-2. Possibly the Arctic Archipelago was not covered with ice (Antevs 1929). It is conjectured that the shores of the Artic Ocean may have had a reasonably mild climate during the advance of the glacier. Of the rest of the world, it is interesting to note that the British Isles were connected at this time to continental Europe (Antevs 1929); the Indo-Malayan Archipelago extended as dry land to include Sumatra, Borneo, and Java; and New Guinea was connected to Australia (Mayr 1944).

There were a number of successive thrusts of glacial ice, both in North America (Nebraskan, Kansan, Illinoisan, Wisconsin) and in Europe (Günz, Mindel, Riss, and Würm in the Alps; Pre-Elster, Elster, Saale, and Weichsel in the northern countries), that came at different times and extended different distances southward. Glacial and interglacial stages were probably synchronous in North America and Europe. During the interglacial periods the biota reoccupied the newly uncovered areas as the glacier melted back, only to be driven out as the glacier again advanced. It is possible that at the present time we are in an interglacial period, and in a few thousands of years the northern parts of the continent will again be covered with ice.

We are chiefly concerned with the last glaciation, which began perhaps 60,000 years ago and reached its maximum extension 18,000 or more years ago. In North America, the Wisconsin glaciation is divided into the Iowa, Tazewell, Cary, Mankato, Valders, and Cochrane substages. Each substage represents a separate glacial advance, one separated from its predecessor and successor by warm periods during which the glacial front retreated various distances. The first two glacial stages were the most extensive; the Mankato (at peak about 13,000 years ago) and the Valders (about 10,700 years ago) advances reached as far as the Great Lakes; the Cochrane glaciation (at peak about 7000 years ago) reached only slightly south of James Bay. Glaciation was extensive in northern Europe, but not in northern Asia, and occurred southward in the higher mountains.

It is estimated that, in northern Ohio, the ice advanced during certain stages of the Wisconsin glaciation at the rate of 100 m (350 ft) per year, and in southern Ohio at from 12 to 33 m (38 to 108 ft) per year (Goldthwait 1959). There is evidence that the advancing ice lowered the temperature sufficiently ahead of it—for a distance of 800 m (0.5 mile)—to decrease the annual growth of spruce and other coniferous trees but not to kill them until the glacier actually overrode and destroyed the forest (Burns 1958).

The drop in mean annual temperature over temperate North America is estimated to have been 5° to 10°C, but was probably greater at the edge of the glacier (Dillon 1956). Superficial oceanic water layers in the tropics dropped approximately 6°C (Emiliani 1955). The gradient from low to higher temperatures at the glacial front was probably steep. Storm tracks in North America during maximum glaciation extended from the west and southwest to the east and northeast; thus, warm winds were brought against the front of the glacier. There is controversy as to how far south of the glacier, the high pressure anticyclonic conditions developed by the great ice mass were felt (Hobbs 1926).

Precipitation appears to have been comparatively heavy during the glacial stages over much of the world. Accumulation of unmelting snow in the North, as the result of increased precipitation, built up the great glacial masses. Even in areas where continental glaciation did not occur (Africa and Australia, for instance), variations between pluvial and interpluvial periods probably coincided with the glacial and interglacial periods and produced far-ranging effects on the geographic dispersal of organisms

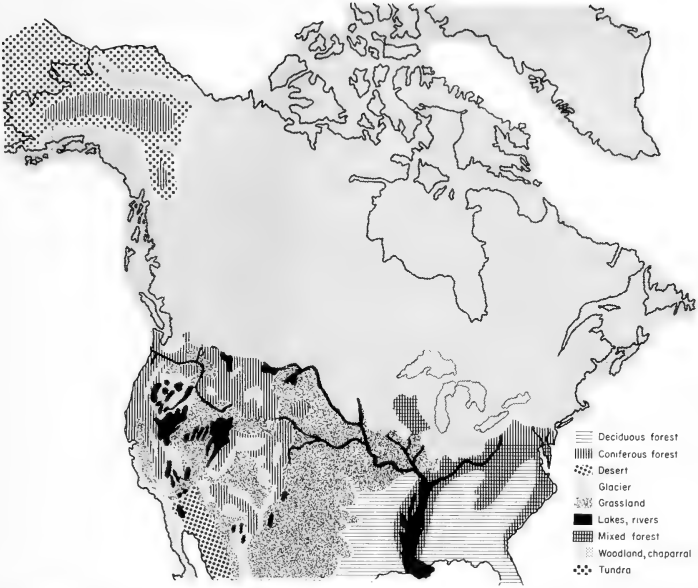


FIG. 21-2 **Conjectural map of vegetation in North America at the time of the maximum Wisconsin glaciation (from information given by Flint 1952, 1957, Meinzer 1922, Hobbs 1950, Braun 1950, Hansen 1947).**

(Moreau 1933). Lakes Bonneville and Lahontan, as well as many smaller ones, were formed in the Great Basin of North America during these pluvial periods (Meinzer 1922, Hubbs and Miller 1948).

There was considerable alteration of drainage patterns over the northern part of the continent. Old river valleys were filled or dammed by ice or moraines. New outlets were formed. Rivers previously separated became connected. The retreat of the glacier left vast level areas without drainage so that many lakes, swamps, and bogs remain in northern glaciated areas. In other places the large quantities of melt water cut new channels or widened old valleys, through which the surplus water was transported to the sea. Silt, sand, and gravel were spread out in outwash plains, from which winds picked up the finer material and deposited it elsewhere as loess in layers up to 2.5 or 3 meters thick (100 in.) over hundreds of square kilometers. The treatise of Thienemann (1950) is an extensive account of what happened to the fresh-water fauna.

Terrestrial biota and communities

Virtually all the fossil plants and mollusks during the Pleistocene are represented by living relatives (Baker 1920). Changes of ecological significance are, for the most part, in point of geographic distribution rather than organic evolution. But insects, especially beetles, which are well represented in the fossil record evolved rapidly into new forms. Many mammals became extinct. Large mammals present during early stages of the Pleistocene, but no longer occurring in North America, include camels, horses (one species later re-introduced), ground sloths, two genera of muskoxen, peccaries, a giant bison, a giant beaver-like animal, a stag-moose, several kinds of cats, mammoths, and the mastodon.

By the Pleistocene, there was doubtless a broad zone of coniferous forest across the northern part of the continent, and perhaps some tundra. Deciduous forest covered the eastern states; grassland occurred in the central part of the country; and coniferous forest was extensive in the western mountains and on the Pacific slope, much as at present.

Glaciation destroyed the coniferous forest over vast areas in the north, but there is considerable controversy as to the area south of the glacial boundary in which the deciduous forest was thus affected. Interpretation of the probable climate, of past and present distribution of plants and animals, and of the pollen record in bogs indicates that, in North America, the deciduous forest was not extensively displaced, but that it became mixed with coniferous species to varying distances south of the margin of the glacier (Epling 1944, Hansen 1947, Braun 1950, Thomas 1951).

Enormous amounts of cold water, melted from the glacier during the summer months and, perhaps, carrying chunks of ice, drained down the Delaware and Susquehanna Rivers in the East, the Ohio, Wabash, Illinois, Missouri, Platte, and Mississippi Rivers in the central part of the continent (Hobbs 1950), and the Snake and Columbia Rivers in the Northwest. Water filled these wide river valleys from the present bluffs on one side to the bluffs on the other, and doubtless extended the boreal microclimate for many kilometers (Wolfe 1951), perhaps permitting the establishment of coniferous trees and other northern species on their banks. The Atlantic coastal plain was exposed by the falling sea level. Cold glacial waters draining southward between the coast and the Gulf Stream probably created a microclimate of a type permitting northern species, including conifers, to invade the coastal plain as far south as Florida.

A tree line existed above 1200–1500 meters (4-5000 ft) on the higher Appalachian peaks. Coniferous forests that are now limited to the higher elevations of the Appalachian Mountains descended the mountain slopes perhaps as much as 600 meters (2000 ft) and covered large areas. In the mountains all over the world, the snow-line (Klute 1928) and biotic zones (Murray 1957) were at least 500 meters (1600 ft) and in some humid localities possibly as much as 1500 meters (5000 ft) lower than they presently are. The occurrence of pollen and the remains of spruce and fir in bogs and glacial deposits in Texas, Louisiana, Florida, North Carolina, and elsewhere on the coastal plain can probably be explained as the result of southward boreal forest intrusions that did not completely displace the deciduous forest. The ranges of many animal species also extended farther south during the height of glaciation than they do at the present time.

Loess was deposited extensively from Wisconsin to southwestern Indiana and west into Nebraska and Kansas (Flint 1957). This buff-colored, homogeneous, porous, calcareous, non-stratified deposit forms only in arid or semi-arid regions, and is indicative of grassland abutting directly on the glacial front. There is no evidence that extensive coniferous forest existed in front of the glacier during any of its advances in this area. The occurrence of snails in Pleistocene deposits in Kansas indicates that during Wisconsin time, for instance, open prairie occurred on the upland and deciduous woodland along streams much as they do at the present time (Frye and Leonard 1952). With the greater precipitation that was generally prevalent, some of what is now desert in the Great Basin and the Southwest was probably grassland then.

Evidence is scanty for the existence of tundra in North America south along the ice front during its advances, although tundra occurred in Alaska during the last Wisconsin stage. Tundra mammals, such as the muskox and woolly mammoth, are well represented as fossils along the old glacial margins, and a few fossils of these species have been found as far south as Texas, Mississippi, and Florida (Potzger 1951). These species, however, are believed to be derived from grassland forms, and it appears that the distinction between grassland and tundra faunas did not become sharply defined until late in the Pleistocene (Hibbard 1949).

In North America the coniferous forest survived glaciation in four separated refugia (Adams 1905, Halliday and Brown 1943). These refugia were in the region of the northern Appalachians, the northern Rockies, the Pacific slope of the Cascades, and Alaska (Hultén 1937). The Appalachian refugium during the Wisconsin epoch extended westward south of the Great Lakes, but was separated from the Rocky Mountain refugium by grassland. Except for the unglaciated pocket in southeastern Minnesota, southwestern Wisconsin, and northwestern Illinois, it appears that forests were absent along the ice front all the way from Illinois to the Rocky Mountains. The Rocky Mountain refugium was separated from the Pacific refugium by the Great Basin, the high peaks of the Cascades and Sierra, and by seasonal differences in precipitation. Probably this separation was only partially effective as a narrow belt of coniferous forest extended around the north border of the Great Basin. Coniferous forest in the Pacific refugium probably extended some hundreds of kilometers farther south than it does at the present time. The Alaskan refugium was probably connected by a land bridge across the Bering Sea with unglaciated areas in Asia. Fossil remains found in frozen muck and silt indicate the probable occurrence in Alaska during glacial periods of woolly mammoth, muskox, reindeer, and many other forms (Flint 1952).

Our description of how biotic communities were affected by the Pleistocene glaciation is not universally accepted. The southward extrusions of coniferous forest along the Mississippi River and the Atlantic coastal plains are conjectural. According to

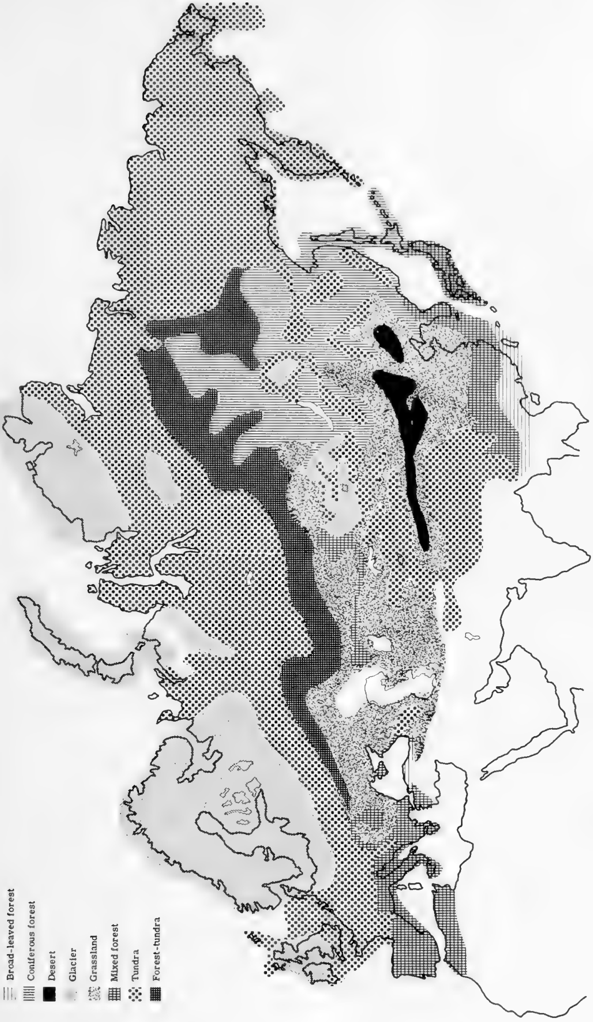


FIG. 21-3 Conjectural map of vegetation in Eurasia at the time of the maximum late Pleistocene glaciation (from information given by Frenzel and Troll 1952, Moreau 1955).

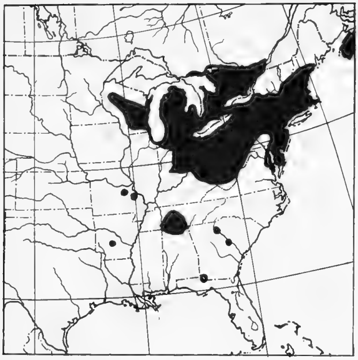


FIG. 21-4 The largest black area shows the present main range of the eastern four-toed salamander. The smaller spots in the southern states represent boreal relicts of a wide southern distribution during the height of the glacial advance. The isolated group in Nova Scotia may also represent a relict from a more northern dispersal of the species during the post-glacial climatic optimum (Smith 1957).

Deevey (1949) and Dorf (1960), the climate everywhere south of the glacial front was considerably refrigerated, deciduous forest was driven into refugia in Florida and Mexico, and tundra and coniferous forest prevailed everywhere in between. Griscom (1950) believes that continental refrigeration extended well into Mexico, causing extensive southward dispersal of northern birds and the elimination of the South American element previously present. Speciation supposedly occurred in populations of certain birds (Huntington 1952) and amphibians, reptiles, and mammals (Blair 1958) that became fragmented and isolated from each other in the Southeastern and Southwestern refugia. There is a likelihood, however, that these animals were segregated into southeastern and southwestern populations, not by effects of cold climate, but by the southward extension of grassland to the Gulf. It is probable that, during the Pleistocene period, there was either grassland or a tenuous savanna type of habitat in Texas that separated the forests of Mexico and those of the southeastern states (Martin and Harrell 1957). The broad cold waters of the Mississippi River may also have split and isolated eastern and western populations of some animal species at the times when melting of the glaciers was at its height.

In Europe and Asia, westerly winds were diverted south into the Mediterranean region, and high anticyclonic barometric pressures developing over the glacier brought dry, cold, northeasterly and easterly winds. Loess was deposited in a broad belt from western France east into the Balkans and northeast into Russia (Zeuner 1945). True tundra graded into loess and bush tundra and coniferous and deciduous forests are thought to have been forced into refugia in Spain, Italy, and the Balkans; there is some doubt, however, that the forests were displaced so far south (Hare 1953). The Mediterranean climate was, however, probably cooler and moister during the height of glaciation than it is at the present time (Zeuner 1945).

POST-PLEISTOCENE

Retreat of the glacier

The melting of the ice was quite rapid, perhaps 134 m (440 ft) per year in the Great Lakes region (Flint 1957). Melt water filled depressions to form vast pro-glacial lakes. Sea-level rose 1 m (3.5 ft) per century between 18,000 and 5000 B.C., but the sea apparently has risen very little since then (Russell 1957). The Great Lakes, in their early stages, had outlets down the Hudson and Mississippi Rivers and had different interconnections than at present. Still later, Lakes Agassiz, Ojibway-Barlow, and others were formed in the north. A knowledge of these lakes and the history of past drainage systems is prerequisite to interpretations of present-day distributions of aquatic organisms.

With the melting back of the ice, local glaciers were left in the Catskill Mountains of New York, on Mount Katahdin in Maine, in the Shickshock Mountains on the Gaspé Peninsula, in Newfoundland, and in Labrador. The glacier receded faster in the western interior of Canada between the Rocky Mountains and Hudson Bay than it did to the East. There is evidence that the glacier disappeared from the Hudson Bay region while still persisting over the highlands of Quebec and the Labrador Mountains. The last of the glacier still remains on the mountains and plateaus of Baffin, Devon, Ellesmere, and Axel Heiberg Islands, and in Greenland (Flint 1947).

Identification of kinds of pollen and comparative counts of pollen grains from various depths in peat bogs gives us a picture of the predominant vegetation, and consequently the climate, in the vicinity of the bogs at various times in the past (Sears 1942, Deevey 1949). A chronology is given for North America and Europe in Table 21-1. The time scale is determined, in part, by measuring the radioactivity of carbon, C^{14}, obtained from samples taken at various depths in glacial deposits. Radioactive carbon disintegrates in non-living matter at a progressive rate;

its half-life is 5760 years. The age of any sample can be determined on the basis of the extent to which it has degenerated (Libby 1960).

The clisere

As the glacier retreated, vast areas were freed for reinvasion by plants and animals (Adams 1905, Gleason 1922). The land must have been a barren, sterile expanse of raw parent soil material, deficient in nitrogen. The first plants to invade were probably species the root nodules of which bore bacteria, fungi, or actinomycetes capable of fixing nitrogen from the air, thereby enriching the soil (Lawrence 1958). The recession rate of the glacier was probably faster than the advance of vegetation and animal life. A belt of tundra developed; coniferous forest broadened to a much greater width than existed at the peak of glaciation. Deciduous forest, requiring a better soil, amelioration of climate, and competitive displacement of the already established coniferous forests, moved northward rather slowly. There is evidence that this northward movement of the biota is still in progress, and that the great belts of vegetation are not yet stabilized in respect to each other and to the climate.

Fossil or pollen evidence for the existence of tundra along the retreating glacial front is scant in North America, except for certain areas in Maine; existence of tundra is better established in Europe. Special difficulties are involved in the identification of tundra pollen in core samples from bogs. Furthermore, deep kettles in which bogs later formed sustained large blocks of ice, well insulated by being nearly buried in glacial till, for a long time after the main mass of ice had withdrawn northward. Deposits of pollen could not settle in the kettles until the ice blocks had melted, which was usually not until spruce-fir coniferous forests had become the prevailing vegetation of the region. This is doubtless the reason for the almost universal occurrence in North America of spruce-fir pollen in the deepest layer of peat cores. The tundra belt may have been 160 km (100 mi) wide as the ice retreated through New England, but was probably much narrower West of the Appalachians. Presumably, however, forest vegetation continued to advance onto the tundra along its southern margin, but at a rate slower than the tundra expanded northward as the glacier retreated. Tundra gradually, therefore, became more extensive in the North, and permitted its fauna to expand to its present-day form.

FIG. 21-5 **The Great Lakes at the time of the Valders glaciation (Hough 1958).**

The occurrence of pine pollen in peat cores above the spruce-fir indicates the emergence of a warmer climate, drier as well. Beginning with the first appearance of deciduous tree pollen, there is differentiation of the pollen spectrum in different parts of the country, the nature of which apparently reflects a drier climate in the Mid-western states and a more humid one in the East.

During the warm moist *climatic optimum,* when conditions for forest growth were most favorable, eastern hemlock spread from the northern Appalachians and became firmly established in New Jersey, New York, New England, and, to a lesser extent, in Ohio. Beech appeared early in New Jersey and spread through New York and Ohio. Animal species extended their ranges northward and withdrew from

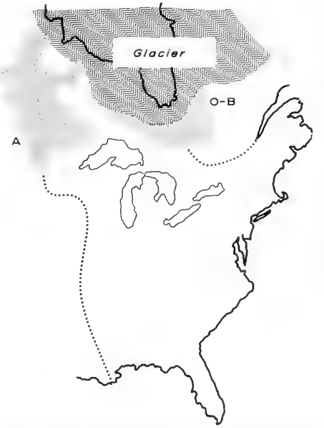


FIG. 21-6 **Glacial Lakes Agassiz (A) and Ojibway-Barlow (O-B), and the outlets of each (after Flint 1947).**

TABLE 21-1 **Late glacial and post-glacial chronology (modified from Deevey 1949, Deevey and Flint 1957, Flint 1957).**

Time		Climate	Northeastern U. S. A.	Ohio	Wisconsin and Minnesota	North Germany	Baltic Basin	
1,000 AD		*Sub-Atlantic* cooler, moister	oak, chestnut	oak, beech	return of spruce at some localities	beech, oak	Baltic Sea	Mya
0								Limnaea
1,000 BC	*Hypsithermal (thermal maximum)*	*Sub-boreal*	oak, hickory	oak, hickory	pine declining	oak, beech		
2,000 BC		warm, dry (xerothermic period)						
3,000 BC								
4,000 BC		*Atlantic*	oak, hemlock	oak, beech (hemlock)	pine, oak, elm	oak, elm, linden	Littorina Sea	
5,000 BC		warm, moist						
6,000 BC		(climatic optimum)					Ancylus Lake	
7,000 BC		*Boreal* warmer, dry	pine	pine	pine	pine, hazel		
8,000 BC		*Pre-boreal*	spruce, fir	spruce, fir	spruce, fir	birch, pine	Yoldia Sea	
9,000 BC		cool, moist	pine, oak			park-tundra pine, birch	Baltic ice lake	
10,000 BC								
11,000 BC		*Sub-arctic*	park-tundra spruce, pine, birch			tundra park-tundra		
12,000 BC		deglaciation						
13,000 BC			tundra			tundra		
14,000 BC								

the South. When later forced to withdraw from over-extended ranges to the North, some species left relict populations, which persist to the present time.

Following the climatic optimum came a warm, dry climate, called the *xerothermic period*. The forest vegetation prevailing from the Mid-west into New England consisted of aridity-tolerant oaks and hickories. The most part of beech withdrew from Ohio, but became well established in the East, where hemlock suffered for want of moisture. A prairie peninsula penetrated at least as far as Ohio, and probably scattered patches of prairie occurred beyond. Grassland animals penetrated far to the East (Schmidt 1938, Smith 1957). Boreal forest retreated northward; sugar maple-basswood forests extended far into Manitoba (Jenkins 1950). In Saskatchewan and Alberta, the northward withdrawal of coniferous forest left groves of aspen trees in the moister and more sheltered locations, while grassland invaded the drier areas (Moss 1944). The numerous lakes in the Great Basin shrank in size or entirely dried up, and desert biota spread both far to the North and high up onto the mountains. Northern species were eliminated from the tops of many southern mountains.

With the coming of cooler, moister climate in the subsequent Sub-Atlantic period, the prairie peninsula receded, leaving populations of biota, relict today, behind. Beech once again spread westward, followed by hemlock; hemlock re-established its dominance in the Northeast. In the northern states there is some evidence that spruce again spread southward. Many of the lakes of the Great Basin refilled with water.

Within historic time, smaller fluctuations in climate are known to have occurred. These have been determined from growth rings of the giant sequoia trees, lake levels, records of past civilizations such as that of the Maya of Yucatan, as well as inferences from historical documents. In western United States these fluctuations have been dated as follows (Brooks 1949):

Wet, 500–250 B.C.
Dry, 250–100 B.C.
Wet, 100 B.C.–A.D. 200
Dry, A.D. 300–800
Wet, A.D. 900–1100
Dry, A.D. 1100–1300
Wet, A.D. 1300–1400
Dry, A.D. 1450–1550
Wet, A.D. 1550–

Mountain glaciation, especially in the Alps and Iceland, was extensive between 1600 and 1850, but glaciers all over the world have been shrinking since then at a very rapid rate. During the last hundred years, mean annual temperatures have increased 0.5° to 2.2°C, and the sea level has risen about 6 cm (2.5 in.) (Flint 1947, Baum and Havens 1956). This amelioration of climate has permitted the northward dispersal of birds and other animals in recent years into Ontario (Urquhart 1957), Iceland (Gudmundsson 1951), northern Europe (Kalela 1949, Haftorn 1958), and in the sea (Taylor *et al.* 1957). Other species will doubtless follow in the future; northern communities are not presently saturated with the variety of species they could support. This is true of aquatic communities as well as terrestrial ones. For instance, the fresh-water fish fauna of North America is most highly developed in the Mississippi River system. The impoverished variety of the fish fauna northward and northeastward is in large part due to the failure of fish species to bypass land barriers and to disperse into otherwise suitable waters in these regions since the retreat of the glacier. A northward movement of fauna may be expected to continue until the carrying capacity of the ecosystems is reached, or until there is another reversal in the climate.

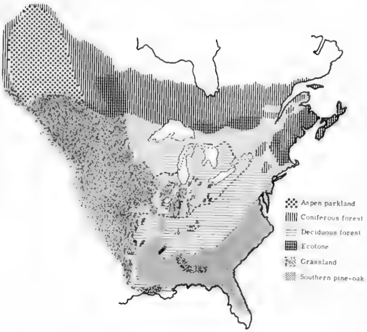


FIG. 21-7 **Conjectural map of vegetation during the xerothermic period in eastern North America (from information given by Transeau 1935, Clements 1942, Jenkins 1950, Halliday 1937). The broken line shows the probable extent to which the prairie massasauga dispersed eastward during this period (Schmidt 1938).**

SUMMARY

At the beginning of the Tertiary Era, 60–70 million years ago, the North American continent was widely covered with epicontinental seas, marshes, and lakes. Scattered mountain ranges occurred in the Rocky Mountain region, but these had been greatly eroded by Oligocene time. Rainfall was heavy and temperatures mild. Tropical conditions extended across the continent to 49° North latitude in the West, and 37° North latitude in the East; temperate climates obtained nearly to the North Pole.

Three principal floras occurred during early Tertiary time. The Neotropical-tertiary flora was coextensive with the tropical climate. The Arcto-tertiary flora consisted of a temperate unit, largely deciduous forest, and a boreal unit, preponderantly coniferous species; this flora extended to within eight degrees latitude of the North Pole and across the Bering land bridge into Eurasia. The Madro-tertiary flora first appeared during the Eocene in scattered dry sites on the lee sides of high ridges in northern Mexico and southwestern United States, but did not become well developed until the Miocene.

Beginning in the Miocene and increasing in intensity through the Pliocene into early Pleistocene,

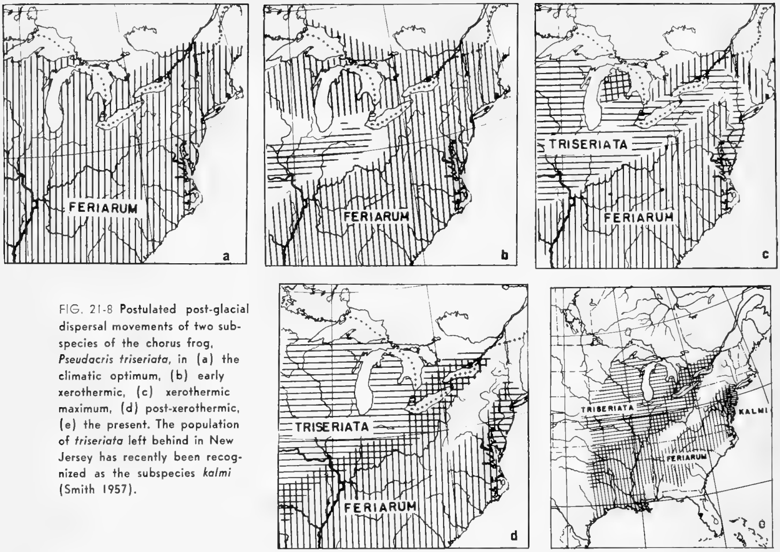


FIG. 21-8 **Postulated post-glacial dispersal movements of two subspecies of the chorus frog, *Pseudacris triseriata*, in (a) the climatic optimum, (b) early xerothermic, (c) xerothermic maximum, (d) post-xerothermic, (e) the present. The population of *triseriata* left behind in New Jersey has recently been recognized as the subspecies *kalmi* (Smith 1957).**

mountain-building was extensive in the Rocky Mountains, Appalachians, Ozarks and Ouachitas, Cascades, Sierra Nevada, and Coast Ranges. The epicontinental seas receded. The climate in the rain-shadows of the mountain systems became increasingly arid, particularly in the Southwest, Great Basin, and on the Great Plains. Concurrently, the climate became progressively cooler, a trend culminating in the severe glaciation of the Pleistocene.

As a result of these changes in physiography and climate, the Neotropical-tertiary flora retreated to the present tropics to constitute the tropical forest and tropical savanna biomes of today. The Arcto-tertiary forest withdrew southward and eastward to form the temperate deciduous forest, coniferous forest, and tundra biomes. Into the areas vacated by these two floras the Madro-tertiary flora expanded to form the woodland, chaparral, grassland, and desert biomes.

At maximum glaciation during the Pleistocene, the tundra biome was greatly restricted in North America and the coniferous forest biome was mostly destroyed, except in refugia in Alaska, the northern Appalachians, the northern Rocky Mountains, and on the Pacific coast. Everywhere it extended to lower elevations in the southerly mountain areas. The deciduous forest was modified by intrusion of coniferous forest species, but was not otherwise greatly disturbed, either in its extent or its composition. Because of heavy precipitation, grassland was more widely distributed through the Great Basin and the Southwest.

With the retreat of the glacier in post-Pleistocene times, the tundra and coniferous forest biomes reoccupied most of northern North America. In the northern states from Minnesota and Illinois eastward, pollen data indicate changes of climate from cool-moist to warm-moist to warm-dry, then back to the cooler, moister conditions of the present time. Accompanying these climatic changes was a succession of vegetation from spruce-fir to pine to oak-hemlock-beech to oak-hickory and the prairie peninsula, then back to oak-beech.

Comparable changes in climate and vegetation occurred in Europe throughout the Tertiary and Quaternary eras. These changes in climate and vegetation had a profound effect both in Europe and North America on the evolution and dispersal of animals; and, by so much, on the development of present-day animal communities.

22

Geographic Distribution of Communities:

Temperate Deciduous Forest Biome

In this and the following chapters we will try to gain an understanding of the geographic distribution of animals as it occurred in primeval time before the colonization of the continent by white man, using biomes as our units of analysis. Each biome will be considered in respect to its distribution, vegetation, and plant associations; the constituents of its various biociations; the relative abundances of the principal animal species, especially mammals and birds; the adaptations and adjustments, especially behavioral, to the biome as demonstrated by the predominant animals; and human uses made of it. We will devote most of our study to biomes of North America, but the rest of the world will not be neglected. A general reference which the reader will find invaluable is *The Naturalist's Guide to the Americas* (Shelford 1926).

The temperate deciduous forests of North America, western Europe, eastern China, and Japan are related as developments of the Arcto-tertiary flora which at one time was practically continuous around the world in North Temperate climates. In North America, the deciduous forest is best developed in the Eastern United States, although elements of it are mixed with conifers in the North, West, and through the mountains of Mexico into Guatemala (Sharp 1953). The deciduous forest of southern Chile is derived from the Antarcto-tertiary flora, discussion of which we must forgo.

Mean annual precipitation for the biome in North America varies from 75 to 125 cm (30–50 in.); mean annual precipitation for the Gulf states is occasionally as high as 150 cm (60 in.). For the most part, rain falls periodically throughout the year; in many places, precipitation also falls as snow in wintertime. Mean monthly temperatures from North to South vary from January minima of —12° to 15°C (10° to 60°F) to July maxima of 21° to 27°C (70° to 80°F). Average mid-day relative humidities during July range from 75 per cent in the East to 50 per cent where the biome contacts prairie in the West. The annual frost-free period varies from about 150 days in the North to as much as 300 days in the South (Kincer 1941).

The climax of the deciduous forest biome is a community dominated by broad-leaved trees that are leafless during the winter over most of the area. In the South, the dominant trees are mostly evergreen. The trees usually form relatively dense forests with a closed canopy, but where the biome verges on prairie, the forest gives way to savannas containing scattered groves. The shrub stratum is often but poorly developed within the forest because of the deep shade there, but is well-formed at the forest-edge. The herb stratum has a rich variety of flowering plants, which are especially conspicuous in the spring. All seasonal aspects are well defined. The leaves of the trees and shrubs, as well as those of most

FIG. 22-1 **Frequent ground fires prevent the southeastern pine forests from succeeding into a deciduous forest climax (courtesy U.S. Forest Service).**

herbs, are intolerant of freezing temperatures overwinter and hence are shed in the North during the autumnal aspect. Consequently there is considerable seasonal change in forest microclimates, to which animal life must respond. The growing season is sufficiently long to permit full development of new foliage and maturation of seed each year, although the size of the seed crop, upon which many animals depend, varies greatly from year to year.

PLANT ASSOCIATIONS IN NORTH AMERICA

The principal plant communities are the following (Braun 1950, Shelford MS).

***Liriodendron-Quercus* association:** mixed mesophytic forest. Centrally located on unglaciated Appalachian Plateau. Contains a rich mixture of tree species, white basswood and yellow buckeye are best indicators of the association.

***Quercus* (*Castanea*) association:** formerly called oak-chestnut forest but chestnut now largely destroyed by blight and its place in canopy taken by oaks and other species, best developed in Appalachian Mountains (Woods and Shanks 1959).

***Quercus-Carya* association:** oak-hickory forest. Center of distribution in Ozark and Ouachita Mountains but radiating far into the prairie along river valleys and into Gulf and South Atlantic states.

***Fagus-Acer* association:** beech-maple forest. Mostly northern in distribution; two principal climax dominants only.

***Acer-Tilia* association:** maple-basswood forest. Occurs mainly in Wisconsin and Minnesota and southward to northern Missouri.

***Tsuga-Pinus*-northern hardwoods ecotone:** mixture in southern Canada and in the Appalachian Mountains of beech, sugar maple, and basswood with eastern hemlock, various northern species of pine, and yellow birch.

Pinus-Pinus associes: southeastern pine forest. Southern species of pines, often mixed with oak. Form extensive subclimax stands in the south Atlantic and Gulf states. Where fire is prevented, this community is succeeded by oak-hickory, beech, or magnolia-oak forest.

***Magnolia-Quercus* association:** magnolia-oak forest. Found in southern portions of Gulf states and most of Florida. Dominant trees are coriaceous, broad-leaved, and evergreen; forests often dense, with deep shade, with Spanish moss and other epiphytes hanging from branches; grading southward into tropical forest (with royalpalm) in Everglades and Florida Keys. Early seral stages include freshwater marshes and cypress swamps, pine flatlands, scrub oak, patches of prairie, coastal dunes, and salt marshes (Davis 1940).

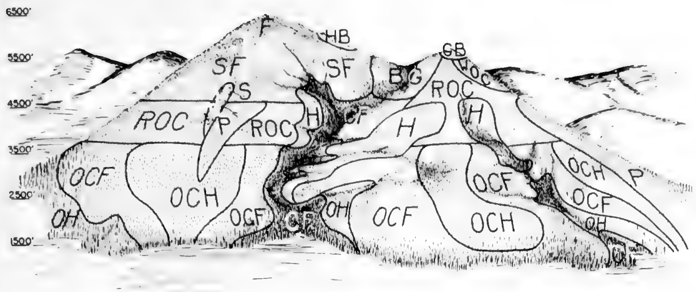


FIG. 22-2 **View of an idealized mountain and valley of the Great Smoky Mountains, looking east: (Whittaker 1956).**

BG **beech gap forest**
CF **cove forest**
F **Fraser fir forest**
GB **grassy bald**
H **hemlock forest**
HB **heath bald**
OCF **oak (chestnut) forest**
OCH **oak (chestnut) heath**
OH **oak-hickory forest**
P **pine forest and pine heath**
ROC **red oak (chestnut) forest**
S **spruce forest**
SF **spruce-fir forest**
WOC **white oak (chestnut) forest**

ZONATION

Climate varies with altitude in kind as it does with latitude; most notably, air temperature varies inversely with altitude. Because of this, there are corollary changes in vegetation such that conspicuous *zonation* is apparent. Zonation of vegetation and differences in climate profoundly affect animal distributions.

In the Great Smoky Mountains of eastern Tennessee, there are two zones, differentiated essentially by temperature. Each is characterized by a circumferentially heterogeneous vegetation different from that of the other. On north slopes of the mountains the demarcation between them is approximately the 1400 m (4500 ft) elevation. The lower zone is mostly deciduous forest, grading laterally from moist mixed mesophytic or cove forest on the north slopes through oak-hickory and oak (chestnut) to southern pine forest and grassy balds on the warm, dry, south slopes (Fig. 22-2). The vegetation of the upper zone also changes, north to south, as moisture conditions change: gray beech forest on the north and in the moist mountain gaps gives way to spruce-fir forest, which in turn changes into heath balds on the exposed southern slopes (Whittaker 1952, 1956).

Contrastingly, each of the several zones of New York's Catskill Mountains is characterized by a circumferentially homogeneous vegetation different from that of the other zones. Below 230 m (750 ft) deciduous forest prevails; between 230 m and 610 m (2000 ft) there is an ecotone of beech-maple-hemlock; then comes a zone where hemlock drops out and the forest is principally gray beech, sugar maple, and yellow birch. Above 980 m and extending to 1280 m (3200 to 4200 ft), the deciduous forest is replaced by spruce-fir coniferous forest (Kendeigh 1946).

ANIMAL COMMUNITIES

North American deciduous forest biociation

This biociation occurs in the climax and late seral stages throughout the deciduous forest proper. It extends into the pine-hemlock-hardwoods ecotone, although locally within the ecotone there is rather sharp segregation of many animal species according as they are frequenters of deciduous or coniferous forest (Kendeigh 1946, 1948). The community is represented as a biocies in the aspen-birch seral stage of the boreal forest. The biociation penetrates well into the magnolia-oak association in the Gulf states, but becomes progressively more impoverished southward as species drop out. To the West, the community occurs in the wider strips of forest along the streams, but as the forest diminishes in density westward, the forest-edge biociation replaces the forest biociation.

Mammal species that occur or formerly occurred through the deciduous forest biociation include:

Eastern mole
Mountain lion
Bobcat
Gray fox
Black bear
Gray squirrel
Southern flying squirrel
Eastern chipmunk
Raccoon
Oppossum
Short-tailed shrew
White-footed mouse

FIG. 22-3 **Two predators of the deciduous forest biociation: the timber rattlesnake, and the great horned owl (courtesy U.S. Forest Service).**

The mountain lion, bobcat, and black bear are also common in other biomes but the other species listed are characteristic inhabitants of the deciduous forest. Seton (1909) estimated original populations of mountain lions and bears at one per 26 sq km (1 per 10 sq mi), and gray foxes at one per 10 sq km (1 per 4 sq mi). Gray squirrel populations vary greatly by time and place, but when common may average 2.5+ per hectare (1+ per acre). Chipmunks vary in numbers from year to year, depending on the abundance of nuts and seeds that they can store in their underground burrows to supply them over winter. In beech-maple forests of northern Ohio they average 25 or more per hectare (10 per acre) during the autumnal aspect of good years (Williams 1936). The combined autumn populations of mice and shrews vary from less than 25 per hectare (10 per acre) in poorer forests having little ground humus to ten times as many during good years in a good habitat. A gradient of increasing populations, from West to East, depending largely on moisture availability as well as abundance of humus, is marked in shrews (Wetzel 1949).

Birds prominent in the deciduous forest biociation include, in declining order of abundance,

Ovenbird
Red-eyed vireo
Redstart
Wood thrush
Eastern wood peewee
Tufted titmouse
Cerulean warbler
Scarlet tanager
Great crested flycatcher
Acadian flycatcher
Downy woodpecker
Black-capped chickadee
Yellow-throated vireo
White-breasted nuthatch
Hairy woodpecker
Red-bellied woodpecker
Whip-poor-will
Ruffed grouse
Barred owl
Great horned owl
Pileated woodpecker
Broad-winged hawk (formerly)

The ovenbird and red-eyed vireo are usually the two most abundant species in deciduous forest stands. An average population of each is 35 to 40 pairs per 40 hectares (100 acres). A 40-hectare plat of average deciduous forest supports approximately 200 pairs of birds, representing all species, as an average. The breeding ranges of most of the species listed above coincide rather closely with the deciduous forest, although some species, such as the downy woodpecker, are distributed more widely and are represented by different subspecies in other biomes (Pitelka 1941).

Reptiles and amphibians are represented by:

Timber rattlesnake
Copperhead
Black rat snake
Red-bellied snake
Five-lined skink
Box turtle
Marbled salamander
Slimy salamander
Red-backed salamander
Common newt
Wood frog
Tree frogs

Invertebrates are too numerous and varied to be mentioned specifically (see Chapter 9). Snails and slugs are especially abundant in the moist mixed mesophytic forests of the southern Appalachians, but decrease in abundance and variety as the forest becomes drier and approaches the prairie (Shimek 1930). Millipedes are numerous in the rich humus of the forest floor. Insects and spiders are represented by a multitude of species in all strata.

North American deciduous forest-edge biociation

Eastern North America, prior to white colonization, had thousands of kilometers of contact between deciduous forest and prairie, with tongues of forest extending far into the prairie along the river valleys. Deciduous forest even bordered the prairie on the north where the aspen grove ecotone intruded in front of the boreal forest. A characteristic forest-edge type of vegetation and distinct animal community occurs along these contacts and where the forest confronts ocean or large lakes. The forest-edge community also permeates the deciduous forest in the role of a seral community or biocies on rock, sand, abandoned fields, and around water (Chapters 8, 9).

A different faciation of the forest-edge biociation occurs west of the Great Plains. As the interior of the continent grew arid in the Miocene and Pliocene, many species of deciduous trees together with their associated animals were able to persist in local habitats throughout the western part of the country. A distinct plant community—riparian woodland—of willows, cottonwoods, sycamores, aspens, alders, and other broad-leaved deciduous trees presently occurs along streams, bodies of water, and elsewhere. It appears to be seral to coniferous forest or woodland over most of the West, but reaches out into grassland and desert in a manner similar to the tongues of forest in the East, thus greatly extending the linear distance of the forest-edge.

The animal species composition reflects the relationship obtaining between the riparian woodland in the West and the forest-edge community in the East. Nearly half of the species listed below pervade both faciations, albeit represented by different subspecies. Several species are confined to one or the other faciation as indicated. Speciation among forest-edge forms was doubtless encouraged by the virtual isolation of both faciations when the grassland biome evolved. Common species (Ingles 1950, Miller 1951):

FIG. 22-4 **White-tailed deer in forest-edge habitat (courtesy U.S. Forest Service).**

Mammals

Eastern mole (East)
Gray wolf
Red fox
Long-tailed weasel
Wapiti
Mule deer (West)
White-tailed deer (East)
Fox squirrel (East)
Woodchuck (East)
Eastern cottontail (East)
Striped skunk

Birds

Turkey vulture
Sharp-shinned hawk
Cooper's hawk
Red-tailed hawk
Swainson's hawk (West)
Red-shouldered hawk (East)
Sparrow hawk
Bobwhite (East)
Mourning dove
Yellow-billed cuckoo
Black-bellied cuckoo (East)
Screech owl
Common nighthawk
Chimney swift (East)
Ruby-throated hummingbird (East)
Hummingbirds (several spp., West)
Red-headed woodpecker (East)
Yellow-shafted flicker (East)
Red-shafted flicker (West)
Eastern kingbird (East)
Western kingbird (West)
Cassin's kingbird (West)
Barn swallow
Violet-green swallow (West)
Common crow
Blue jay (East)
Black-billed magpie (West)
House wren
Catbird (East)
Brown thrasher (East)
Eastern bluebird (East)
Robin
Chestnut-backed chickadee (West)
Cedar waxwing
Loggerhead shrike
Starling
Warbling vireo
Bell's vireo (West)
Yellow warbler
Yellowthroat
Yellow-breasted chat
Brown-headed cowbird
Bullock's oriole (West)

- Brewer's blackbird (West)
- Indigo bunting (East)
- Rufous-sided towhee
- American goldfinch
- Black-headed grosbeak (West)
- Chipping sparrow
- Field sparrow (East)
- Song sparrow

Reptiles

- Blue racer
- Smooth green snake
- Milk snake
- Brown snake
- Garter snake
- Ribbon snake

Southeastern mixed biocies

A number of animal species have their centers of distribution in the south Atlantic and Gulf states and are associated with the southeastern pine forest, the magnolia-oak forest, or with seral stages. There is, doubtless, more than one community involved, but until more detailed analysis can be made the species may conveniently be listed together. Common terrestrial vertebrates of the southeastern mixed biocies are:

Mammals

- Southeastern shrew
- Florida least shrew
- Eastern spotted skunk
- Florida skunk
- Southeastern pocket gopher
- Eastern harvest mouse
- Oldfield mouse
- Cotton mouse
- Golden mouse
- Florida mouse
- Pine mouse
- Hispid cotton rat
- Marsh rice rat
- Eastern wood rat
- Round-tailed muskrat
- Marsh rabbit
- Swamp rabbit

Birds

- Black vulture
- Swallow-tailed kite (formerly)
- Mississippi kite (formerly)
- Turkey
- Carolina parakeet (formerly)
- Chuck-will's widow
- Red-cockaded woodpecker
- Ivory-billed woodpecker
- Scrub jay
- Fish crow
- Carolina chickadee
- Brown-headed nuthatch
- Carolina wren
- Mockingbird
- Blue-gray gnatcatcher
- White-eyed vireo
- Prothonotary warbler
- Swainson's warbler
- Parula warbler
- Yellow-throated warbler
- Pine warbler
- Prairie warbler
- Hooded warbler
- Orchard oriole
- Boat-tailed grackle
- Summer tanager
- Cardinal
- Painted bunting
- Seaside sparrow
- Bachman's sparrow

Reptiles and Amphibians

- Rough green snake
- Chicken snake
- Corn snake
- Kingsnake
- Southern hog-nosed snake
- Eastern fence lizard
- Six-lined racerunner
- Brown skink
- Chameleon
- Spadefoot toad

In addition to these species, many of those listed for the deciduous forest and forest-edge are also common, but frequently represented here by different subspecies than occur in the North. The seral relations of many of the mammals (J.C. Moore 1946, Pournelle 1950), birds (Nelson 1952), as well as certain insects (Rogers 1933, Friauf 1953) have been worked out for various areas of northern Florida.

Several of these species of mammals, birds, reptiles, and amphibians have dispersed from the Southeast far into the deciduous forest and forest-edge communities. Their distributional ranges, in many cases, extend westward into Texas and southward into Mexico. The closest related forms of some of the more restricted species also lie to the West and South, for instance the scrub jay. The evidence is inferential that this biociation and the corresponding plant associations did not originally belong to the deciduous forest biome. It seems more likely, rather, that they belonged to the sclerophyllous woodland and pine forests, derived from the Madro-tertiary, and to the Neotropical-tertiary floras. During the Pliocene or earlier, Madro-tertiary biota may have been continuous around the north side of the Gulf of Mexico (Pitelka 1951a), but later separated into eastern and western portions by the development of grassland through Texas to the Gulf of Mexico.

The terrestrial fauna indigenous to the southern tip of Florida is predominantly deciduous forest-edge species; species of the southeastern mixed biocies are represented, and there has also been some invasion of tropical species. Among birds, the white-crowned pigeon, zenaida dove, smooth-billed ani, gray kingbird, black-whiskered vireo, as well as races of nighthawk and yellow warbler, are recent newcomers from the West Indies (Robertson 1955). There is also a rich and varied aquatic avifauna that is for the most part tropical in origin. The manatee and the alligator formerly extended from Florida around the north side of the Gulf of Mexico; the crocodile was limited to southern Florida.

European deciduous forest biociation

Dominants of the plant associations in Europe are different species of the same genera that occur in North America, particularly beeches, maples, oaks, hornbeams, and basswood. Many mammals and birds of the European deciduous forest and seral stages also belong to the same genera as North American species. The similarity in genera may be traced back to the continuity of the Arcto-tertiary forest between the two continents during the Tertiary; the dissimilarity of species to divergent evolution since the two communities became separated.

Mammals common to the European forest and forest-edge include both the common and white-toothed shrews, European mole, common hare and European rabbit, several mice, wolf (same species as in North America), red fox (perhaps the same species as in North America), weasels, wildcat, wild boar, two deer, and European bison.

The bird fauna (European fauna of Stegmann, 1938) includes some falcons, kites, and eagles, a pigeon and a cuckoo, owls, several woodpeckers, a jay, crows, several tits, a nuthatch, a creeper, a wren, several thrushes, a rich variety of Old World warblers only poorly represented in North America, an Old World flycatcher not found in the New World, an oriole, and various finches. Absent are the tyrant flycatchers, vireos, and wood warblers that are so prominent in the North American deciduous forest (Lack and Venables 1939, Turček 1951, 1952, 1955). Lists of invertebrates, especially of ground animals, are given by Kühnelt (1944). It is possible that Pleistocene glaciation disturbed this biociation much more than that in North America (Moreau 1954).

Asiatic deciduous forest biociation

The broad-leaved deciduous forest of eastern China, Formosa, Korea, and Japan contains many species of plants and animals belonging to the same genera as occur in Europe or North America. During the early Tertiary, this forest was in direct contact, via the Bering land bridge, with that in North America, and deciduous trees still maintain a narrow and tenuous contact along the southern edge and in seral stages of the coniferous forest with the deciduous forest of Europe. In addition, there are some endemic genera of animals confined to the area. A number of Indo-Malayan species penetrate into the biociation as far as northern China and Japan. Stegmann (1938) gives a list of bird species occurring in this area that belong to what he calls the Chinese fauna, but he does not distinguish between those characteristic of forest, forest-edge, and seral communities.

ANIMAL ADJUSTMENTS

Animals are adapted structurally, functionally, and behaviorally to live in or under trees. They may use the trees directly as lookouts, singing posts, nest-sites, for cover and protection, and as a source of food; or they may simply take advantage of the rich humus created by the annual fall of leaves, or the shade, greater humidity, and equable temperatures of the forest habitat. Some animals, for instance the eastern chipmunk, die within a few minutes if exposed directly to the sun. Snails and slugs are most active and carry on their reproductive activities during the moist vernal aspect, but may be conspicuous throughout the summer when they are able to maintain the necessary water balance.

Special adaptations for arboreal habits and for climbing are the sucking discs on the toes of tree frogs, the sharp claws and opposable toes in woodpeckers and squirrels, the prehensile tails of opposums and white-footed mice, the parachutes and bushy tails of squirrels as well as the movable scales of some of the snakes, the many legs of the millipedes, and the slimy feet of slugs and snails.

Hearing and voice are well developed in many forest animals, although vision is less perfected since visibility is limited anyway. The rich and almost constant singing of forest birds throughout the breeding season is well known, but the voice, or songs, of squirrels, chipmunks, and wolves are also well developed for mammals. The loud singing of tree frogs is noteworthy, and the nightly chorus of insect voices, especially those of orthopterans, is remarkable. Most of these sounds serve to attract mates or advertise territories.

The regular and pronounced changes in photoperiod and temperature bring full development of the breeding season of most animals to its peak during the spring and early summer. Deer, bats, and a few others, however, characteristically mate during the autumn, and some of the squirrels and owls during the winter.

All species must meet the severe winter conditions of short days, low temperatures, and scarcity of food in one way or another. In those forms of mammals and birds that remain active over winter and in those insects that hiberate in exposed situations there is considerable increase in resistance to cold by internal physiological adjustments, and they live either on kinds of food that are not usually concealed by snow or on food cached when it was plentiful. Mammals den up in hollow logs or trees during short severe cold periods, coming out again when the weather is mild. Flocking is common in most birds during the winter season in contrast to their isolation in territories during the breeding season. Flocks commonly seek shelter on the lee side of forest areas or in river valleys to get protection from cold winds. Populations and variety of birds are supplemented during the winter as northern species come South.

Those species of birds, mammals, reptiles, amphibians, insects, and snails that cannot maintain activity in winter conditions either migrate or hibernate. Migration among birds commonly reduces the population to less than one-third the number of individuals present during the early summer, but during the spring and autumn migratory periods, populations are temporarily greatly increased. Various insect species, including the monarch butterfly, migrate many miles southward. Other species move much shorter distances from open country into the forest-edge preparatory to hibernation (Weese 1924).

Woodchucks, bats, and possibly chipmunks hibernate in the true sense; the black bear enters a pseudo-hibernation state, remaining quiescent over winter but maintaining temperature and other body functions at near normal. Reptiles and amphibians bury themselves in decaying stumps or logs, in the ground below the frost line, or in the mud bottom of ponds. Nearly all insects and other invertebrates migrate out of the trees, shrubs, and herbs to the forest floor where they hiberate. Some species move up and down in the soil to keep below the frost line. Other species overwinter only in the egg or some other immature stage. Further south, especially in the magnolia-oak forest where there is less need, hibernation and migration of populations that breed in the region are much less pronounced.

The original condition of the forest and its wildlife has, of course, been greatly modified by man. The American Indian should probably be considered a native inhabitant of the deciduous forest, and the modifications he produced (Day 1953) as a normal influence comparable to that of other large mammals. The white man, however, is equipped with a large variety of tools that renders his influence extreme. As a consequence, some forest and forest-edge species, such as the mountain lion, gray wolf, eastern bison, wapiti, passenger pigeon, Carolina parakeet, probably the ivory-billed woodpecker, and others have become extinct. With agriculture and lumbering, seral stages have become more prevalent, so that there has been considerable shift in the relative abundance and importance of species from what occurred originally (Bennett and Nagel 1937, Allen 1938).

HUMAN RELATIONS

White man finds in the climate of the deciduous forest biome conditions favorable for the highest efficiency of his various activities, for his greatest health and energy, for maintenance of high population densities, and for high development of modern civilization (Huntington 1924). The chief and most profitable occupations of man in the deciduous forest biome are agriculture, mining, and industry. In eastern Asia, the broad-leaved deciduous and evergreen forests are occupied by Mongolians, and like the white man this yellow race early developed a high degree of civilization and large populations.

Forests early became essential to white man as a source of lumber, fuel, and raw materials of industry. Trees furnish him shade from the hot summer sun and protection from the cold winter winds. In the early settlement of North America, forests were cleared for farming purposes with difficulty, but forest land was considered more fertile than grassland because it grew trees instead of grass. As man dispersed westward across North America into the grassland biome, he first built his home in the fringes of forest along the streams or in outlying groves (Hewes 1950). As settlement increased, however, surplus people were crowded onto the prairie as they were crowded also into other biomes. It is of interest that in his invasion of grassland man planted trees around his home and thus tried to bring the forest environment with him.

SUMMARY

The temperate deciduous forest biome is derived from the Arcto-tertiary forest and is best developed in eastern North America, western Europe, and eastern Asia. In those places, precipitation is moderate and temperatures mild during the summer growing season, but the winter season is generally unfavorable for the activity of most organisms.

Animal communities of major significance are the North American deciduous forest biociation, North American deciduous forest-edge biociation (often a biocies), southeastern mixed biocies, European deciduous forest biociation, and Asiatic deciduous forest biociation.

Animals are adapted and adjusted in various ways to live in and under trees. Reproduction takes place principally in the spring and early summer. The severe winter season is adjusted to by increase in physiological hardiness, hiberation, or migration.

23

Geographic Heritage of Communities:

Coniferous Forest, Woodland, and Chaparral Biomes

CONIFEROUS FOREST BIOME

The coniferous forest is a continuous, often dense, forest of needle- or scale-leaved evergreen trees. The sclerophyllous leaves prevent excessive evaporation of water during winter and dry periods, and are adapted to withstand freezing. The evergreen leaves take full advantage for photosynthesis of short summer growing seasons, intermittent warm periods of autumn and spring, and the warm winter rains of the Pacific coast. The flexible branches bear snow-loads without breaking; snow-loads tumble easily off the cone-shaped tree. The dead, dry needles which cling to the trees feed devastating crown fires, much more common in coniferous than deciduous forest.

DISTRIBUTION AND ORIGIN

Coniferous forests are largely confined to the northern hemisphere. They are transcontinental in Canada (Halliday 1937) and in higher elevations on the mountains through Mexico and Guatemala, into Honduras and Salvador. In Eurasia there is also a northern transcontinental coniferous belt with disjunct patches of coniferous forests on all higher mountains southward. The main mass of coniferous forest species is doubtless derived from the boreal element of the Arcto-tertiary flora, and is much older geologically than is the deciduous forest. There is some evidence, however, that the eastern hemlock is a segregate from the temperate rather than the boreal unit of the Arcto-tertiary flora (Braun 1950, Oosting and Bourdeau 1955, Whittaker 1956), and that the western arid-tolerant ponderosa pine and Mexican pines come from the Madro-tertiary flora.

CLIMATE

In the transcontinental forest of North America, precipitation varies between 38 and 100 cm (15–40 in.) and is mostly summer rain. Mean monthly temperatures vary from a winter low of about —30°C to a summer high of 20°C (—20° to +70°F). The summer period between killing frosts varies from 60 to 150 days. On the Pacific slope of the high western mountains, because of the westerly winds coming from the warm Japanese current, precipitation is higher (125 to 225+ cm, 50 to 90+ in.); most of it falls as winter rain. Mean monthly temperatures are more uniform (2° to 18°C, 35° to 65°F) and the frostless season is 120 to 300 days long. Humidity is high, and fogs are frequent in this region. In the northern Rockies, Cascades, and Sierra Nevada, heavy winter precipitation falls as snow that accumulates to several meters in depth; winter temperatures are considerably lower. Snowfall is not as heavy in the central Rockies, and declines steadily, southward.

PLANT ASSOCIATIONS OF NORTH AMERICA

Pinus-Tsuga **association** (pine-hemlock forest): Eastern hemlock is the climax, but eastern white, red, and jack pines are of wider distribution; northern white-cedar and yellow birch are prominent. The forest has been badly disturbed by logging and fire, factors which, with climatic succession, have permitted a wide penetration of hardwoods to form an ecotone between deciduous forest and boreal forest. The association extends from Minnesota to New England, and south into the Appalachian Mountains.

Picea-Abies **association** (boreal forest): White spruce and balsam fir most prominent (related species in Appalachians), but black spruce and tamarack also prominent; extends across southern Canada to the northern Rocky Mountains, north into Alaska, and south in Appalachian Mountains; alder thickets common in wet areas and heath shrubs in forest openings; quaking aspen and paper birch occur extensively as seral stages. *Aspen groves,* or *parklands,* form a broad ecotone between forest and grassland from Minnesota to the Rocky Mountains (Bird 1930). In the northern coniferous forest reaches lies a zone extending to the tree line in which the forest decreases in height and density, its floor carpet of lichens and mosses increases in depth and extent, and it becomes interspersed with numerous bogs or muskegs. Lichen woodland is especially well developed east (Hare and Taylor 1956) and muskegs west of Hudson Bay. This whole area is *forest-tundra,* as distinguished from the denser, taller boreal forest; it is equivalent to the Hudsonian zone of Merriam *et al.* (1910).

Picea-Pinus **association** (petran subalpine forest): Extends southward at higher elevations in Rocky Mountains to Arizona, New Mexico, and higher peaks of Mexico; contains Engelmann and blue spruces, subalpine fir, and several species of pine.

Tsuga-Pinus **association** (Sierran subalpine forest): Occurs chiefly in Cascade Mountains and Sierra Nevada; mountain hemlock as well as various pines, subalpine larch, and red fir prominent; trees tall and narrowly cylindrical at lower elevations but dwarfed, gnarled, and misshapened at tree-line; aspen and lodgepole pine extensive as seral stages after fire in both Sierran and petran subalpine forests.

Pinus-Pseudotsuga **association** (petran montane forest): At lower elevations in the Rocky Mountains; ponderosa pine, Douglas-fir, and white fir most important; ponderosa pine most aridity-tolerant; trees often widely spaced with grass stratum underneath, sometimes forming savannas.

Pinus-Abies **association** (Sierran montane forest): Contains species listed for petran montane forest and also sugar pine, incense-cedar, and giant sequoia (central Sierras); chaparral develops after fire.

Pinus-Pinus association (Mexican pine forest): An extension of montane forest, chiefly pines, at higher elevations in Mexico.

Thuja-Tsuga **association** (coast forest): A luxuriant humid forest on the Pacific slope of mountains from northern California to Alaska; western hemlock, western redcedar, Alaska-cedar, Douglas-fir, Sitka spruce, and redwood most characteristic; trees sometimes 90 m (300 ft) high and to 6 m (20 ft) diameter; deep shade in climax forest but in openings there may be dense tangles of shrubs, lianas, tall ferns; moss often thick over ground and fallen logs; forest in North extends to west slopes of Rocky Mountains in Idaho, Montana, and British Columbia to form a *Coast forest ecotone* with petran montane and subalpine forests, in which grand fir, western white pine, and western larch are prominent.

ANIMAL COMMUNITIES

There are three principal biociations in this biome, two in North America and one in Eurasia. There is overlap in their species compositions. Species occurring in seral or climax stages of both North American biociations, although less common in the Mexican pine forests, include

Mammals

Water shrew
Snowshoe rabbit
Red squirrel
Northern flying squirrel
Deer mouse
Porcupine
Gray wolf
Black bear

Birds

Goshawk
Pigeon hawk
Ruffed grouse
Great horned owl
Saw-whet owl
Yellow-bellied sapsucker
Hairy woodpecker
Black-backed three-toed woodpecker
Traill's flycatcher

FIG. 23-1 Left, montane forest in Oregon—a virgin stand of ponderosa pine. Below, forest, tundra in northern Manitoba, composed of spruce and tamarack with the ground covered with a thick layer of moss and lichens (courtesy W. P. Gillespie).

Olive-sided flycatcher
Gray jay
Common raven
Red-breasted nuthatch
Brown creeper
Winter wren
Hermit thrush
Swainson's thrush
Golden-crowned kinglet
Ruby-crowned kinglet
Solitary vireo
Nashville warbler
Wilson's warbler
Purple finch
Pine grosbeak
Pine siskin
Red crossbill
Lincoln's sparrow

North American boreal forest biociation

This biociation extends from the Atlantic Ocean to the Rocky Mountains in Canada and south on the Appalachian Mountains to northern Georgia (Shelford and Olson 1935, Kendeigh 1947, 1948, Munroe 1956). There is a broad overlap or fusion between the boreal and montane forest biociations in the northern Rockies where species of one biociation penetrate into the other (Rand 1945, Drury 1953).

Characteristic mammals that occur generally through the boreal and pine-hemlock forests, in addition to those listed in the above section, are:

Arctic shrew
Masked shrew
Smoky shrew
Pigmy shrew
Star-nosed mole
Hoary bat
Least chipmunk
Northern bog lemming
Gapper's red-backed mouse
Ungava phenacomys
Rock vole
Meadow jumping mouse
Woodland jumping mouse
American marten
Fisher
Ermine
Least weasel
Wolverine
Lynx
Moose
Woodland caribou

Bird species found in this biociation are listed in Table 23-1. This biociation is especially notable for the large representation of wood warblers in the avifauna, each with its own specialized niche (MacArthur 1958). In northern Ontario, warblers constitute 69 per cent of the breeding bird population in the spruce-fir forest; in northern Maine, 63 per cent.

As one proceeds south from Ontario and Maine into Minnesota, Michigan, New York, and along the Appalachian Mountains to Tennessee, species both of mammals and birds drop out, apparently as they reach limits of tolerance to climatic factors. Perhaps

TABLE 23-1 Comparison of avifaunas and population densities (number per 40 hectares, or 100 acres) of breeding birds in the Black Sturgeon Lake area of northern Ontario (Kendeigh 1947), in Aroostook County, northern Maine (Stewart and Aldrich 1952), and in the Great Smoky Mountains of eastern Tennessee (Fawver 1950).

Bird species	Northern Ontario spruce-fir	Northern Maine spruce-fir	Eastern Tennessee	
			Spruce-fir	Eastern hemlock
Goshawk	+	0	0	0
Broad-winged hawk	+	+	0	0
Pigeon hawk	+	0	0	0
Spruce grouse	1	+	0	0
Ruffed grouse	2	+	+	+
Yellow-shafted flicker	4	2	0	1
Pileated woodpecker	+	+	0	+
Yellow-bellied sapsucker	4	+	0	0
Hairy woodpecker	2	2	3	3
Downy woodpecker	2	+	0	0
Arctic three-toed woodpecker	2	+	0	0
American three-toed woodpecker	+	0	0	0
Yellow-bellied flycatcher	2	5	0	0
Acadian flycatcher	0	0	0	7
Least flycatcher	6	+	0	0
Gray jay	4	+	0	0
Blue jay	1	3	0	0
Common crow	0	+	0	0
Black-capped chickadee	2	4	2	7
Boreal chickadee	2	8	0	0
Red-breasted nuthatch	3	8	20	10
Brown creeper	9	+	38	3
Winter wren	5	4	34	7
Robin	0	6	3	4
Wood thrush	0	0	0	22
Hermit thrush	1	4	0	0
Swainson's thrush	4	21	0	0
Veery	0	+	18	7
Golden-crowned kinglet	8	12	38	2
Ruby-crowned kinglet	2	8	0	0
Solitary vireo	2	9	24	39
Red-eyed vireo	7	6	0	1
Black and white warbler	0	+	0	0
Tennessee warbler	59	9	0	0
Nashville warbler	8	8	0	0
Parula warbler	0	5	0	0
Magnolia warbler	6	55	0	0
Cape May warbler	28	28	0	0
Black-throated blue warbler	0	2	6	64
Myrtle warbler	3	20	0	0
Black-throated green warbler	6	+	0	55
Blackburnian warbler	6	22	0	44
Chestnut-sided warbler	0	+	2	0
Bay-breasted warbler	92	69	0	0
Ovenbird	10	2	0	48
Mourning warbler	2	+	0	0
Canada warbler	0	1	0	28
Scarlet tanager	0	+	0	6
Rose-breasted grosbeak	0	+	0	2
Evening grosbeak	+	0	0	0
Purple finch	2	4	0	0
Pine grosbeak	0	2	0	0
Pine siskin	1	2	0	0
Slate-colored junco	3	10	125	29
White-throated sparrow	18	8	0	0
Totals	319+	349+	310+	389+

the elimination of these competing species, or possibly the change in climatic conditions, makes other species more abundant. This is especially noticeable among birds—the red-breasted nuthatch, brown creeper, winter wren, golden-crowned kinglet, solitary vireo, black-throated green warbler, blackburnian warbler, Canada warbler, and slate-colored junco attaining much larger populations in the Smoky Mountains of Tennessee than in northern Ontario. In addition the veery, black-throated blue warbler, and often black and white warblers become numerous. This constitutes a variation in the boreal forest biociation (Stewart and Aldrich 1952) which may be designated the *Appalachian faciation.*

When hemlock, which reaches its best development in the Appalachian Mountains, and spruce-fir forests occur in the same region, some bird species adaptable to both show a definite preference for one over the other. In Table 23-1 it is evident that the red-breasted nuthatch, brown creeper, winter wren, veery, golden-crowned kinglet, and slate-colored junco prefer the spruce-fir forest, while the black-capped chickadee, possibly the solitary vireo, black-throated blue warbler, black-throated green warbler, blackburnian warbler, and Canada warbler prefer hemlock forests. A similar differentiation of bird populations in these two forests is also evident in Algonquin Provincial Park in southern Ontario (Martin 1960). This may be a reflection of the difference in paleo-ecological history of hemlock and spruce-fir forests. The long association of hemlock with deciduous forest may also have permitted the invasion into the former of the Acadian flycatcher, wood thrush, ovenbird, and scarlet tanager.

FIG. 23-2 Species common in the coniferous forest biome: (a) porcupine, (b) gray jay, (c) moose, boreal forest, (d) wapiti, western forest (courtesy U.S. Forest Service).

Spruce-fir forests occur at higher elevations in the mountains, and in some areas at least, as in the Catskill Mountains of New York, a zone of deciduous forest intervenes the hemlock and spruce-fir forests. Elsewhere, as in the Cheat Mountains of West Virginia (Brooks 1943), the two coniferous forests come into direct contact. Apparently because of the close interrelations between hemlock and the northern

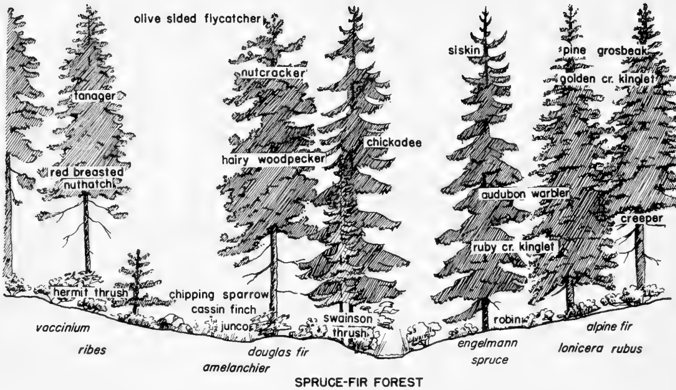


FIG. 23-3 **Foraging niches of birds in the western forest biociation of the central Rocky Mountains (Salt 1957).**

hardwoods, several warblers and other species normally characteristic of coniferous forest have learned to occupy niches in the deciduous forests as well, and attain high populations therein (Saunders 1936, Brooks 1940, Kendeigh 1945). The species composition of foliage insects in the coniferous forests of the Smoky Mountains is essentially similar to that of the deciduous forest (Whittaker 1952). Such general intermingling of species in an ecotone is to be expected, and may be considered characteristic of the Appalachian faciation.

Perhaps some species listed above reach larger populations in a seral shrub or forest-edge biocies (Adams 1909). The Philadelphia vireo, palm warbler, Wilson's warbler, rusty blackbird, and Lincoln's sparrow are largely limited to shrubs or second growth; the northern waterthrush occurs in bogs; the savannah sparrow, in marshes and grassy areas; and the white-winged crossbill, irregularly through the climax. These species extend to the northern tree-line. Seral aquatic stages in the boreal forest contain beaver, muskrat, and nesting horned grebe, black duck, common goldeneye, Canada goose, and the common and hooded mergansers (Hanson *et al.* 1949). Actually, the coniferous forest does not develop a recognizable forest-edge along its southern border because these borders grade by steps into deciduous forest, aspen parkland, woodland, and chaparral. The closest resemblance to an edge are shrubby openings within the forest or the subseres that develop in bogs, burns, and logged areas. The aspen parkland contains a fauna in which boreal, grassland, deciduous forest, and deciduous forest-edge biociation species are represented (Bird 1930) and is essentially an ecotone. Invertebrate composition of the seral stages bears a strong resemblance to that occurring in seral stages of the deciduous forest.

Along its northern border, the coniferous forest comes in direct contact with open tundra to form a broad ecotone. Boreal forest biociation species reach their northern limits of distribution and tundra species begin to appear. There are no distinctive mammals, but several birds are characteristic of this subarctic, lichen woodland and muskeg, Hudsonian, or (most apt) *forest-tundra faciation* (Manning 1952, Harper 1953, 1956, Preble 1908):

Solitary sandpiper
Lesser yellowlegs
Rough-legged hawk
Boreal owl
Hawk-owl
Great gray owl
Northern shrike
Gray-cheeked thrush
Bohemian waxwing
(west)
Blackpoll warbler
Pine grosbeak
Hoary redpoll
Common redpoll
Tree sparrow
Harris' sparrow
White-crowned sparrow
Fox sparrow

The pine grosbeak, white-crowned and fox sparrows extend to the southward at tree-line on the western mountains and the gray-cheeked thrush and blackpoll warbler extend southward at high elevations in the northern Appalachians.

North American montane forest biociation

This biociation, considering the forest-interior and forest-edge together, occurs principally in the coast forest (Storer, *et al.* 1944, Miller 1951, Macnab 1958) and is less developed in the montane and subalpine forests of the Rocky Mountains, Cascades, and Sierra Nevada. There appear to be no important subdivisions related to the several plant associations that it covers (Rasmussen 1941, Hayward 1945, Munroe 1956, Snyder 1950). Because of the mountainous terrain and the many possibilities for populations to become partially or wholly isolated from each other, there are many local subspecies and species of mammals and birds (Findley and Anderson 1956). The following lists include only common species of wide distribution through the biociation.

Mammals

Shrews
Mountain beaver
Yellow-bellied marmot
Golden-mantled ground squirrel
Western chipmunks
Douglas' squirrel
Bushy-tailed wood rat
Red-backed mice
Heather vole
Long-tailed vole
Western jumping mice
Grizzly bear
Western marten
Mountain weasel
Wolverine
Mountain lion
Bobcat
Mule deer
Wapiti

Birds

Golden eagle
Blue grouse
Flammulated owl
Pygmy owl
Calliope hummingbird
Williamson's sapsucker
White-headed woodpecker
Hammond's flycatcher
Western flycatcher
Western wood pewee
Steller's jay
Clark's nutcracker
Mountain chickadee
Pigmy nuthatch
Varied thrush
Mountain bluebird
Townsend's solitaire
Audubon's warbler
Townsend's warbler
Hermit warbler
Western tanager
Evening grosbeak
Cassin's finch
Oregon junco
Gray-headed junco

Additional species from the chaparral biociation penetrate this community, particularly into shrubby stages. The orange-crowned warbler is noteworthy in this respect.

In general, the population of breeding birds is less than one-sixth what it is in the boreal forest (Snyder 1950). In the northern Rockies there is considerable mixture with species from the boreal forest biociation, both in birds and mammals, but these species drop out progressively southward and very few of them cross the Cascades into the Coast forest. The woodland caribou, for instance, ranges only to northeastern British Columbia and the moose to central British Columbia, eastern Idaho, and western Wyoming. The western facies of the deciduous forest-edge biociation penetrates widely as a seral stage through the western forest biociation, and certain of its species may persist into the climax.

Eurasian boreal forest biociation

The dominants of the Eurasian plant associations are different species but the same genera of pines, firs, larches, spruces, poplars, and birches that occur in North America. This biociation is best developed in Asia, from whence the biota is dispersed across the northern part of the continent into Europe (Berg 1950, Jahn 1942, Kalela 1938, Palmgren 1930, Pleske 1928, Stegmann 1932, 1938, Haviland 1926, Schäfer 1938, Soveri 1940, Turček 1956).

The mammal fauna contains shrews, a varying hare, flying and red squirrels, a chipmunk, red-backed mice, the wolf and red fox, a brown bear, martens, weasels, wolverine, lynx, a moose, and a deer. Several of these species (wolf, red fox, wolverine, lynx) are considered by some taxonomists to be conspecific with North American forms (Rausch 1953).

This biociation is equivalent to the Siberian bird fauna of Stegmann (1938) and includes several species of grouse, owls, woodpeckers, crows and jays, and tits, a creeper, several thrushes, several Old World warblers, kinglets, a wagtail, waxwings, and several finches or sparrows. The wood warblers, abundant in the boreal forest of North America, are absent.

PALEO-ECOLOGY

In early Tertiary we may suppose that the boreal unit of the Arcto-tertiary forest had a fairly uniform animal composition from eastern Canada into Asia and Europe. As the forest progressed southward during the middle and later Tertiary, a large segment became separated in consequence of the submergence of the Bering land bridge, becoming the Eurasian biociation. Forms now peculiar to the Eurasian and to the North American biociations must have evolved after this separation took place (Udvardy 1958).

In North America, as the Arcto-tertiary biota retreated southward with the progressive chilling of the continent, it was separated into two portions by the northward invasion of grassland over the Great Plains, except as it had contact through the boreal forest across Canada in the north. During the Pleistocene even this northern contact was broken (Fig. 21-2) with each major advance of the glacier. Furthermore, the western part of the continent was thrown up into mountains beginning in the Miocene, and the climate there became more diversified and rigorous. Plant and animal species tended to segregate into either the western or the eastern section of the forest, depending on where habitat conditions and community coactions were more favorable to them, and isolation encouraged divergent speciation. The western section continued to have sporadic contact with the Eurasian biociation, especially during the Pleistocene, but the eastern section was too far away. Hence came the differentiation of the boreal forest biociation in the eastern lowlands of the continent and the western forest biociation in the western mountains and on the Pacific coast.

In this connection it is of interest that 52 per cent of the breeding bird species in the boreal forest biociation are of Old World origin and 30 per cent of North American origin, compared with 65 and 17 per cent, respectively, for the western forest biociation in Colorado (Snyder 1950). The difference is even more striking when comparison is made between the breeding populations. In the boreal forest biociation, only 20 per cent of the breeding pairs belong to species of Old World origin while 79 per cent belong to species of North American origin. In the western forest biociation of Colorado the percentages are 98 per cent of Old World origin and only 2 per cent of North American origin.

Pleistocene glaciation enhanced the differentiation of boreal and western forest biociations since it allowed independent subspeciation and even speciation in the four refugia (Fig. 21-2). The boreal forest became compressed with each glaciation into the Appalachian refugium, but the western forest was segregated three ways into the Rocky Mountain, Pacific, and Alaskan refugia. At these times the Alaskan refugium was probably connected by the Bering land bridge to Asia.

The present-day distribution of the four subspecies of moose suggests that they were isolated during at least Wisconsin glaciation in the Appalachian, Rocky Mountain, and Alaskan refugia, and in the unglaciated area of Wisconsin, Minnesota, and Illinois. This area probably served also as the refugium for the western subspecies of the woodland caribou, while the eastern subspecies was isolated in the Appalachian refugium (Vos and Peterson 1951). Different subspecies of arctic shrews had refugia to the south and east of the glacier and in Alaska. The American marten and the red squirrel apparently survived in the Appalachian refugium; the western marten and Douglas' squirrel, in the Pacific refugium. Of the red-backed mice, *Clethrionomys gapperi* has apparently dispersed from the Appalachian refugium, *C. dawsoni* from the Alaskan refugium, and *C. wrangeli* from islands off the coast of British Columbia (Rand 1954).

Various subspecies or closely related species of birds apparently differentiated as populations were isolated in one or more of the four refugia. This seems to have occurred with the spruce grouse, sapsucker, gray jay, boreal chickadee, myrtle and Audubon's warblers, slate-colored and Oregon juncos, and white-crowned sparrow (Rand 1948, Drury 1953).

In each interglacial period, the coniferous forest fauna previously isolated in the Appalachian, Rocky Mountain, Pacific, and Alaskan refugia doubtless dispersed centrifugally from each center until they came into contact with each other. Such segregation and dispersal of the biota must have occurred four times during the Pleistocene; the dispersal from refugia after the Wisconsin glaciation is still going on. The four subspecies of moose have come into contact with each other (Peterson 1955), the least chipmunk has entered Ontario and Quebec (Peterson 1953), and the evening grosbeak has spread across Canada from the western mountains only within the past hundred years.

Some of these changes in range may have been hastened as a result of human interference. The woodland caribou was formerly the principal large ungulate present in the boreal forest (Vos and Peterson 1951), but as logging and fires opened up the forest, the caribou has greatly declined in numbers and the moose has become more abundant. The white-tailed deer has also spread from the deciduous forest well into the boreal forest in recent years, and other species of mammals and birds appear in the process of doing so.

ANIMAL ADJUSTMENTS

Animal adaptions for life in coniferous forest are similar in many ways to those for life in deciduous forest. Ecological niches in these two forests are similar, although the species that occupy them are different. Important differences are the stiff needle-shape character of conifer leaves and their arrangement around all sides of the twigs, which hinder the movements and feeding of some birds, and the poor decomposition of the shed leaves that accumulate on the ground, not favorable to high populations of many species of small animals. In contrast to the aspects of the deciduous forest, the vernal and autumnal aspects are less well developed since most of the trees retain their foliage throughout the year.

The woodland caribou is largely restricted to the climax forest where it feeds on reindeer moss, a ground lichen, and on tree lichens. Moose are found throughout seral stages as well as in the climax. During the summer they commonly feed on water lilies, pondweeds, sedges, and grasses; during the

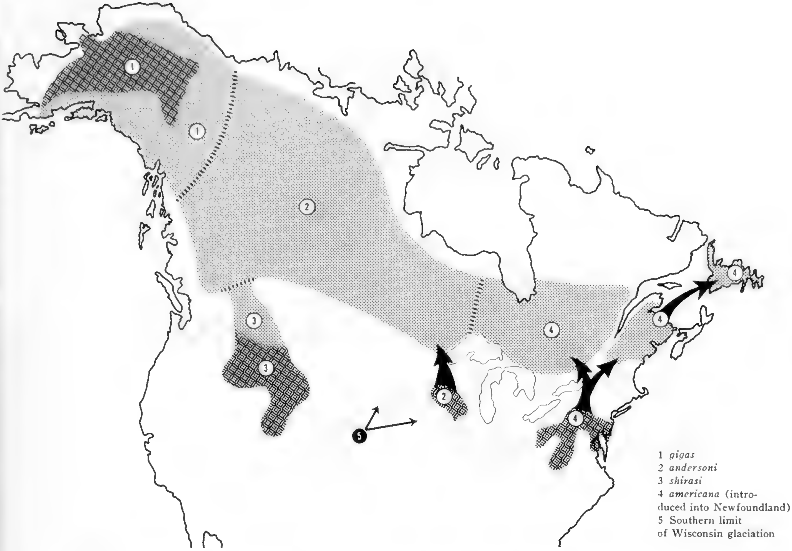


FIG. 23-4 **Present distribution of four subspecies of moose in North America. Post-Pleistocene dispersal routes from distributions at the time of Wisconsin glaciation are shown by arrows (from Peterson 1955).**

winter, on the tips of birch, aspen, cedar, balsam fir, and various other shrubs and small deciduous trees (Shelford and Olson 1935). Small mammals are abundant. In northern Michigan, the populations of two species each of mice, chipmunks, and shrews varied from 6.2 individuals per hectare (2.5/acre) in jack pine to 12.5 (5.0/acre) in black spruce, 16.0 (6.4/acre) in hemlock, 19.5 (7.8/acre) in a white-cedar swamp, and 28.2 (11.3/acre) in white birch (Manville 1949).

Perennial animals that remain active over winter have a high tolerance of low temperatures and use food not readily obscured by snow (Snow 1952). The large mammals become browsers in the winter. Wapiti chew bark patches off aspen trees when other forage is difficult to find. Scars thus formed are ideal sites for the development of fungus disease (Packard 1942). Birds feed on seeds extracted from the cones of the coniferous trees, on buds, and on bark insects. When the seed crop fails, large numbers of pine siskins, pine and evening grosbeaks, red crossbills, and white-winged crossbills emigrate southward into the United States. Small ground and subterranean animals are well insulated under the snow where temperatures even in the far North may drop only a few degrees below freezing (Pruitt 1957). Some birds, such as the grouse, roost at night in cavities formed in snowbanks.

Less than half of the nesting bird population of the western forest biociation migrates for the winter, and then only to lower altitudes on the mountains. In contrast, the birds of the boreal forest are acclimatized to warm climate, and over 80 per cent migrate hundreds of kilometers to the south. A few mammals also migrate, such as the hoary bat in the East and the wapiti and mule deer down the mountain slopes in the West.

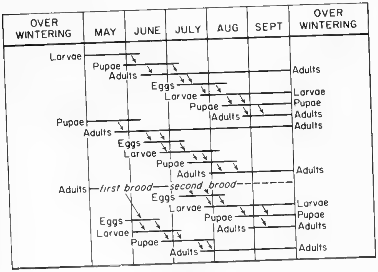
Insects virtually dominate the forest, at times. Vast numbers of mosquitoes and flies force moose to spend much of the summer submerged in water, and are generally annoying to other animals and man. The larch sawfly has spread across Canada and the

FIG. 23-5 **Gallery pattern of a bark beetle in lodgepole pine: (a) nuptial chamber, (b) egg gallery, (c) egg niche (Reid 1955).**

northern states during the last 75 years and caused considerable defoliation and destruction of tamarack (Coppel and Leius 1955). The spruce budworm (a lepidopteran larva) feeding on the leaves has killed balsam fir and spruce trees on vast areas at repeated intervals in the past: 1807–18, 1870–80, 1904–14 (Swaine and Craighead 1924), and again in the 1940's. Several kinds of bark beetles, wood borers, and long-horned beetles are also destructive forest insects.

Beetles, ants, aphids, jumping plant lice, leafhoppers, and spiders, and invertebrates—notably snails, annelids, and millipedes—are not numerous over most of the biome (Rasmussen 1941, Hayward 1945, Blake 1945). Most ground invertebrates have higher population densities in the seral aspen and birch stages than in the coniferous climax (Hoff 1957). Reptiles are few, only the garter snake extends very far north. The northern wood frog, leopard frog, and mink frog are widely dispersed in suitable habitats throughout the boreal biociation. Because of its greater humidity and more equable temperatures, invertebrates and cold-blooded vertebrates are generally more numerous in the Coast forest than elsewhere through the biome.

FIG. 23-6 **Seasonal history of a bark beetle (Reid 1955).**



HUMAN RELATIONS

Only the lower, warmer portions of the coniferous forest biome are permanently inhabited in large numbers by white man throughout the year. Logging for pulpwood and lumber is an important occupation. Over the more rugged northern portions of the coniferous forest, the population is scattered and, in North America, there are more Indians than whites, at the present time. The Indians engage in hunting and fur-trapping for support. Larger settlements of white men occur where minerals may be mined or oil obtained. These regions, as well as the higher conifer-clad mountains, are resorted to for fishing and other recreational activities during the warm summer months.

WOODLAND BIOME

In contrast to forest, woodland is an open stand of trees with an intervening good growth of grasses or shrubs. The trees are usually short, 6 to 15 m high (20 to 50 ft), but may have a dense crown. In favorable local habitats, the trees form a closed canopy, but in arid situations they are scattered. The trees vary widely in leaf structure, but nearly all species are evergreen and tolerant of low moisture. In North America, woodland of different types extends from Washington and Wyoming well down into Mexico. A similar type of broad-leaved, evergreen sclerophyllous woodland, together with chaparral, occurs around the Mediterranean Sea in Eurasia and Africa.

CLIMATE

In Utah, precipitation in this biome ranges from 4 to 6 cm (10 to 15 in.) per year, and mean monthly temperatures from −5°C to 21°C (23° to 69°F) (Woodbury 1947). Precipitation is often higher in Mexico, but this is offset by a higher rate of evaporation. West of the Sierra Nevada precipitation comes principally during the winter months, as it also does in the Mediterranean region.

PLANT ASSOCIATIONS IN NORTH AMERICA

Pinus-Quercus **association:** pine-oak woodland. On mountain slopes of central and northern Mexico; oak scrub, mostly evergreen, at lower elevations grades into pine-oak woodland with some juniper at higher elevations and then into the Mexican pine forest; contains a rich variety of species (Gentry 1942, Leopold 1950, Marshall 1957).

Quercus-Quercus **association:** oak woodland. Broad-leaved mostly evergreen oaks with Digger pine in certain habitats (Miller 1951); mostly west of the Sierra Nevada but extending north into Oregon and Washington.

Pinus-Juniperus **association:** piñon-juniper woodland. Pines and junipers of several species from eastern slopes of Sierras and Cascades across Great Basin to Wyoming and New Mexico (Woodbury 1947, Woodin and Lindsey 1954).

PALEO-ECOLOGY

The various types of woodlands in North America were probably derived from the mixed pines and oaks of the Madro-tertiary flora. The piñon-juniper woodland is a segregation that became adapted to the cold winter climates of the Rocky Mountains and Great Basin. It was more widely dispersed and found at lower altitudes during the pluvial Wisconsin glacial period than it is at present. The oak woodland during lower Pliocene was widely distributed over the central and southern portions of the Great Basin but with the trend toward colder winters and decreased rainfall, the oak woodland came to be restricted to the moister mountain habitats within the desert and to Pacific coast regions with winter rain and mild temperatures (Axelrod 1950, 1957). There is also some evidence that woodland vegetation including oaks extended around the north side of the Gulf of Mexico as far as Florida (Pitelka 1951).

WOODLAND BIOCIATION

The animal life of woodland communities in western North America is not highly distinctive. The trees, being broad-leaved or needle-leaved, attract species from the adjacent deciduous forest-edge (riparian woodland) and montane forest biociations. Since the trees are sometimes scattered, interspersed with grass or shrubs, chaparral, grassland, and desert species may penetrate well into the community. In respect to species composition, therefore, the woodland in North America to a large extent is an ecotone.

FIG. 23-7 **Piñon-juniper woodland in Utah.**

Mammals

Of larger mammals, the mule deer, mountain lion, and coyote commonly occur during the winter months in the piñon-juniper woodland of Utah and Arizona, although most of these species spend the summer high in the mountains. The bobcat also occurs and the grizzly bear was formerly not uncommon. The rock squirrel, cliff chipmunk, desert and dusky-footed wood rats and piñon mouse are found in both the piñon-juniper and the petran bush but show preference for broken country, rocky hillsides, and cliffs (Woodbury 1933, Rasmussen 1941). In southern New Mexico, four species of mice—deer, brush, rock, and piñon—occur more or less together (Dice 1942). The open floor of the oak woodland in California is relatively devoid of mammal life, with only the California and brush mice common in the vicinity of brushy growth. The western gray squirrel is probably most common in this community (Vaughan 1954).

Birds

Certain bird species appear to be more characteristic of woodland than are mammals. Species occurring rather widely in northern Arizona (Rasmussen 1941), Utah (Hardy 1945), California (Miller 1951), and Mexico (Marshall 1957) are:

FIG. 23-8 **Petran bush in Utah.**

Band-tailed pigeon
Acorn woodpecker
Lewis' woodpecker
Nuttall's woodpecker
Ladder-backed woodpecker
Ash-throated flycatcher
Gray flycatcher
Coues' flycatcher
Scrub jay
Piñon jay
Plain titmouse
Common bushtit
Blue-gray gnatcatcher
Scott's oriole
Western bluebird
Hutton's vireo
Black-throated gray warbler
Grace's warbler
Olive warbler
Painted redstart
Hepatic tanager
Lawrence's goldfinch

Rattlesnakes, lizards, and horned toads invade from the desert but are not particularly characteristic of the woodland itself. Invertebrate populations are relatively low, and consist principally of spiders, ants, termites, jumping plant-lice, and a sprinkling of ichneumonids, flies, leafhoppers, beetles, and banded-wing locusts (Rasmussen 1941).

CHAPARRAL BIOME

Chaparral, in the strict sense, consists of xeric broad-leaved evergreen bushes, shrubs, or dwarf trees, usually not more than 2.5 m (8 ft) high, and occurring in more or less continuous stands. Beneath the bushes and shrubs there may be abundant ground litter. Chaparral is less dense where there are rock outcroppings and grass. Most species readily produce sprouts after their tops are destroyed by fire, provided fire does not occur too frequently; germination of some seeds is hastened by the heat of the fire. Chaparral tends to spread as a seral stage into areas of montane forest and woodland when the latter is destroyed by fire. Although chaparral is doubtless seral over much of its range, it appears to be climax over fairly large areas in southern California and northern Baja California, and a narrow belt on the slopes of the Sierra Nevada and southern Rockies. Broad-leaved evergreen chaparral also occurs, with woodland, around the Mediterranean and elsewhere on other continents.

PLANT ASSOCIATIONS IN NORTH AMERICA

Coastal chaparral occurs from southern Oregon to northern Baja California and eastward into Nevada and Arizona (Weaver and Clements 1938). This region is one of winter rains, and consequently the vegetation consists chiefly of evergreen bushes and shrubs with leaves that are glutinous, odorous, or hairy. Coastal chaparral occurs in more massive stands than does petran bush.

Petran bush occurs as a lower zone on the mountains from South Dakota to Texas and westward into Nevada and Arizona. This association has been called petran chaparral, but the shrubs and bushes are mostly deciduous.

Both associations are derived from the Madro-tertiary flora (Davis 1951) and have a phylogenetic history similar to the oak woodland and piñon-juniper woodland respectively, with which they are closely associated.

CHAPARRAL BIOCIATION

There are no mammals peculiar to the chaparral in North America, although in Utah the bobcat, rock squirrel, and cliff chipmunk reach relatively large populations in the petran bush (Hayward 1948). In California, the brush rabbit and the dusky-footed wood rat are numerous in heavy brush, along with other mammals also found in woodland (Vaughan 1954). There may be 6 to 12 occupied houses of the white-throated wood rat per hectare (2–5/acre) in southern Arizona (Hanson 1957). The mule deer becomes common (about 10/sq km or 25/sq mi) during the winter when it migrates down from the higher elevations in the mountains. The chaparral fauna, like that of the woodland, is largely ecotonal between montane forest and grassland or desert scrub.

The coastal chaparral is extensive enough, however, so that these birds show preference for it (Miller 1951):

Mountain quail
California quail
Anna's hummingbird
Allen's hummingbird
Wrentit
Bewick's wren
California thrasher
*Orange-crowned warbler
*MacGillivray's warbler
*Lazuli bunting
*Rufous-sided towhee
Brown towhee
Rufous-crowned sparrow
Black-chinned sparrow

TABLE 23-2 Climate in different zones on the west slope of the Wasatch Mountains, Utah (Price and Evans 1937).

Community	Elevation, meters	Depth of snow on March 1, cm	Total precipitation, cm	Per cent precipitation as snow	Frost-free period, days	Mean temperature		
						May-Oct. °C	Oct.-May °C	Annual °C
Piñon-juniper woodland	1,700	3.8	29.7	45	-	17.0	2.0	8.3
Petran bush	2,333	63.2	44.4	-	90	14.4	-0.2	5.9
Petran montane forest	2,698	120.1	74.9	70	87	11.7	-2.6	3.3
Petran subalpine forest	3,078	134.4	71.1	80	80	8.7	-5.7	0.3

Those species marked with an asterisk are found also in the petran bush of Utah and, in addition, the broad-tailed hummingbird, gray vireo, Virginia's warbler, and green-tailed towhee are characteristic there (Hayward 1948). The petran bush, even more than the coastal chaparral, contains many species from the deciduous forest-edge and montane forest biociations.

No snake or lizard is particularly characteristic of chaparral, although at times they may be numerous. For the most part, the reptiles occurring in chaparral belong more properly to the desert or grassland and reach their upper altitudinal limits in this biome. Among invertebrates in the petran bush, mites, ants, leafhoppers, locusts and grasshoppers, beetles, aphids, and flies are conspicuous, and large numbers of parasitic and gall-forming hymenopterans depend on the oaks for completion of their life-cycles. A few millipedes and centipedes are to be found under rocks, but snails are scarce (Hayward 1948). In the coastal chaparral of southern California, the period of greatest activity for most invertebrate species comes in March and April, towards the end of the winter rains, and is correlated with the flowering season of plants and the period of greatest soil moisture. During the hot dry summer many invertebrates aestivate (Ingles 1929).

ZONATION

With increase in elevation there is a decrease in temperature and increase in wind velocity, depth of snowfall, and total precipitation (Table 23-2). Mean annual temperature tends to drop about 0.6°C (1.0°F) for each rise of 100 m (325 ft); hence, by going up a mountain a few hundred meters one encounters similar, but not identical, climates and biota as occur at lower elevations many kilometers northward on the continent. In deep valleys and canyons, on the other hand, there is often cold air drainage at night, so that colder types of vegetation and fauna occur than on the nearby ridges.

Alpine tundra and coniferous forest at the higher elevations represent southward dispersal of the Arcto-tertiary flora, while woodland, chaparral, grassland, and desert at lower elevations represent northward dispersal from the Madro-tertiary flora. These dispersals doubtless began as these western mountains became elevated in mid-Tertiary time. During the Pleistocene period, glaciation occurred extensively in the higher mountains and forced all communities to lower elevations. Pluvial climates generally accompanied glaciation so that grassland and desert in the lowlands were succeeded by coniferous forest. More continuous zones of forest in foothills and through valleys encouraged wide latitudinal dispersal of animals. With recession of the glaciers and rewarming of the climate, the forest and alpine tundra again withdrew to higher elevations, and mountain ranges assumed the isolation from each other that we see at the present time. This isolation has induced considerable speciation, but the similarity or relationship between animal life in different mountain regions is explicable from the paleo-ecological history of the area.

SUMMARY

Coniferous forests are largely confined to the Northern Hemisphere. Over most of the area, the summer growing season is short and the winter long and cold. On the Pacific coast of North America, however, precipitation occurs mostly during the winters, which are mild.

Some mammal and several bird species occur widely through the biome, but the following animal communities are recognized: North American boreal forest biociation, North American montane forest biociation, and Eurasian boreal forest biociation. Appalachian and forest-tundra faciations of the North American boreal forest biociation are well-marked for birds.

In early Tertiary, the boreal unit of the Arcto-tertiary forest doubtless had a fairly uniform fauna from eastern Canada across the Bering land bridge to western Europe. This fauna became differentiated into the three biociations with the disappearance of the Bering land connection between Alaska and Asia, and the separation of the North American fauna into western and eastern sections by the northward penetration of grassland and the southward movements of the Pleistocene glaciers. Differentiation at the subspecies and species levels was further encouraged by the segregation of the North American fauna during Pleistocene glaciation in the Appalachian, Rocky Mountain, Pacific, and Alaskan refugia.

Animal adaptations are similar to those in the deciduous forest, but often more extreme. Boreal species, for instance, must have greater physiological tolerance to cold to remain active over winter. Migration is also more extensive, although in mountainous areas migration is largely altitudinal rather than longitudinal. Browsing is more common, for the ground during winter months is generally covered with snow. Insects often cause considerable damage to forest trees, and mosquitoes and flies are annoying both to animals and man.

White man is relatively less numerous in this biome in North America than are Indians. Chief occupations are logging, hunting and trapping, and mining.

Woodland and chaparral biociations have some distinctive animal species but in many areas tend to be ecotonal between coniferous forest and grassland or desert.

The zonation of communities on mountains depends principally on decrease in temperature with increase in elevation. In western North America, desert or grassland, woodland or chaparral, coniferous forest, and alpine tundra occur at successively higher elevations.

In the Western mountains the following examples of zonation of communities are of interest, the elevations given being the mean lower limits of the communities. It is evident that identical communities occur at lower elevations in the North than in the South.

Locality	**Northern Arizona**	**Idaho**
Authority	Merriam 1890	Larsen 1930
Desert or grassland	below 1830 m (6000 ft)	300 m (1000 ft)
Piñon-juniper woodland	1830 m (6000 ft)	absent
Petran montane forest	2135 m (7000 ft)	300 m (1000 ft)
Coast forest ecotone	absent	615 m (2000 ft)
Petran subalpine forest	2800 m (9200 ft)	1700 m (5500 ft)
Alpine tundra	3500 m (11,500 ft)	2300 m (7500 ft)

Locality	**California**	**Washington**
Authority	Hughes & Dunning 1949	Taylor 1922
Coast forest	absent	sea level
Grassland	below 150 m (500 ft)	absent
Oak-woodland and coastal chaparral	150 m (500 ft)	absent
Sierran montane forest	760 m (2500 ft)	absent
Sierran subalpine forest	1980 m (6500 ft)	1385 m (4500 ft)
Alpine tundra	3350 m (11,000 ft)	2000 m (6500 ft)

24

Geographic Distribution of Communities:

Tundra Biome

Tundra typically extends from tree-line to the line of perpetual snow and ice, both in the far North and at higher mountain elevations. It is essentially similar in North America and Eurasia (Berg 1950). Very little tundra occurs on Antarctica.

CLIMATE, SOIL, AND TOPOGRAPHY

Arctic regions in North America have an annual preciptation less than 4 cm (10 in.), although east of Hudson Bay it occasionally reaches 8 cm (20 in.). Most of it comes as rain during the summer and early autumn; snowfall is generally light (Koeppe 1931). Humidity is high and evaporation low during the summer.

Mean monthly temperatures vary between extremes of —35°C and +13°C (—30° and 55°F). The July isotherm of 5°C (41°F) is sometimes used to separate the so-called high arctic and low arctic, and the isotherm of 10°C (50°F), which corresponds closely to tree-line, to separate the low arctic from the sub-arctic. Frost may occur at any time in the North, but there is usually a frost-free period of about 60 days in the South.

During the summer, the surface of the ground commonly thaws to a depth of only a few centimeters; permanently frozen soil, *permafrost,* underlies (Ray 1951). The soil becomes wet and soggy, and the accumulation of water in depressions forms numerous shallow ponds. Freezing and thawing are potent forces in arctic regions, since they may occur daily for long periods of time. This action fragments large boulders into small rocks; forms polygon shapes on level ground surfaces varying in diameter from a few centimeters to several meters; develops large ground ice or peat mounds or smaller hummocks (frost heaving); causes downward slumping of soil on slopes to form terraces, or, a gradual creep of rocks and soil downslope with the consequent rounding off of ridges and other irregularities in the topography. The general moulding of the landscape by frost action is called *cryoplanation* and is of ecological importance because it makes the soil unstable and limits the kind of vegetation that can develop on it.

During the winter, the soil freezes down to the permafrost, except under streams, on stream banks and narrow flood-plains, and in sandy areas. Lakes are frozen for nine months of the year with ice a meter or more thick. Under the ice, oxygen almost disappears so that conditions are usually critical for animal survival (Andersen 1946). Ponds less than one or two meters deep freeze to the bottom.

In the spring, absorption of solar radiation causes the mean temperature of the surface of the soil to rise above freezing three or four weeks before the mean temperature of the air, and it is at this time that plants and ground animals renew their growth and activity (Sorensen 1941). Below the surface, ground temperature rise lags behind rising air temperature. Temperature just below the surface is higher than at greater depths in the summer, but lower in the winter, the turnover coming in April or May in the spring and September or October in the autumn (Beckel 1957).

Photoperiods north of the Arctic Circle vary from zero hours during mid-winter to twenty-four hours during mid-summer. Elsewhere, the length of periods depends on latitude. Even in the summer, however, light intensity is low compared with tropical latitudes.

In contrast to the arctic plains, alpine habitats on the higher mountain slopes are on rugged, often precipitous, terrain. Each mountain top is an island isolated from other mountain tops by intervening forested lowlands. High plateaus may have more or less level surfaces, but the size of such tundra-covered areas, except for the Tibetan plateau of Asia, is generally very limited. These alpine habitats also lack a permafrost in the subsoil, except in the far North, and the extreme change in photoperiod during the year that arctic regions experience. Soils are thin and unstable except in small pockets on the slopes, in valleys, or on protected flat surfaces. Average temperature is low, but the range between daily maximum and minimum during the summer is sometimes as great as 32°C (58°F). North slopes are colder than south slopes. The length of the growing season between killing frosts is similar to what it is in the arctic. Precipitation and humidity are commonly high, and the mountain tops are frequently shrouded in fog. Snowfall in some areas, as in the Cascades, may reach 18 m (60 ft) and is generally much greater than in the arctic. Water runoff is rapid because of the severe topographic relief. Winds are strong. On clear days, light intensity, notably ultraviolet, and evaporation may be high because of the thin air. A unique characteristic of the alpine habitat not shared by the arctic is low barometric pressure and oxygen concentration, which probably does not affect plants as much as it does some animals. Altogether, the alpine environment imposes greater severities on plant development than does the arctic environment (Bliss 1956), and this is doubtless true for animal activities also.

VEGETATION

Tundra has the appearance of short-grass plains, but differs in that the vegetation consists of sedges, rushes, lichens, mosses, ericaceous or decumbent shrubs, and flowering herbs as well as grasses. The plants are generally of small size, stunted growth, and compact structure adopted to resist desiccation and mechanical abrasion from wind, snow, and sand. Germination of seeds is poor, and most species require several years to produce the first flowering. Most tundra plants are therefore perennials, and vegetative reproduction is important. Seral vegetation varies in composition depending on whether it develops around ponds, in low wet places, or on clay, sand, gravel, or rock. Flowering herbs are often abundant with different species coming into bloom progressively during the year (Sorensen 1941, McClure 1943).

Succession has been studied in only a few areas, and the true nature of the climax is unknown over much of the arctic. There is doubt as to whether or not a stable climax, as understood for southern latitudes, actually develops (Raup 1951, Sigafoos 1951, Britton 1957). This is due to the instability of the soil, varying depths to which the soil thaws out in the summer, depth and duration of the snow cover, exposure to wind, and grazing and trampling by animals. Although tundra associations are not recognized in this book, we do make a primary division of the biome into arctic tundra and alpine tundra.

Arctic tundra

The so-called barren grounds of the far North are divisible into four significant types in respect to animal distribution. *Bush* or *mat tundra* contains dwarf trees, decumbent shrubs, or heath, usually mixed with mosses and lichens. Near Churchill in northern Manitoba, much of the area is muskeg; but climax vegetation is interpreted as a mixture of low Ericaceae heath and *Cladonia* lichen growing in a mat of sphagnum and other organic material 7 to 10 cm (3–4 in.) thick. This climax develops on wet ground, clay, sand, and on gravel and rock ridges (Shelford and Twomey 1941). A variety of dwarf shrub-lichen-grass-sedge types have been described in Alaska (Hanson 1953, Churchill 1955) and in the eastern arctic (Polunin 1934–35, 1948, Holttum 1922).

Grass tundra is largely limited to deeper mineral and organic soils. The soils are more fertile, and in places thaw out in the summer to a depth of one meter. Different species of grasses and sedges are dominant in recognizable seral and climax stages (Hanson 1951). *Lichen-moss barrens* (Tanner 1944, Hanson 1953) have been called desert tundra or rock desert by various investigators. The soil is thin, and there is much exposed rock. Vegetation is scant and consists of crustose and foliose lichens, mosses, and scattered short herbs or very small shrubs. In the low arctic, this may be a seral stage, but in the high arctic it is often the only vegetation able to tolerate the severe climate. In the extreme North there is *perpetual snow and ice,* a polar desert; vegetation is practically absent, and animal life is restricted to marine forms along the ocean coast. The slight development of tundra in the antarctic is of the lichen-moss barrens; most of the antarctic continent is covered with ice (Lindsey 1940).

Alpine tundra

Tundra extends into the tropics on the high Western mountains and into New England on a few of the higher Appalachian peaks. This alpine tundra consists chiefly of grasses and sedges without conspicuous development of Ericaceae or the great masses of foliose lichens and mosses found in parts of the arctic (Cox 1933, Daubenmire 1943, Hayward 1945). About 37 per cent of 170 vascular species collected in the alpine tundra of the Colorado Rockies also occur in the arctic, and about half of these are circumpolar in distribution. Most of the remaining species are endemic to North America, and many species are uniquely endemic to the Rockies (Holm 1927). The taxonomic composition of alpine vegetation varies greatly from place to place, but most of the plants are perennials. The dwarfness of the shoots in proportion to the flowers and fruits that they bear is very striking. As one ascends the mountain slopes, the grass tundra gives way to lichen-moss barrens, and then to perpetual snow and ice. On the downslope side, there is often bush tundra and at tree-line the trees are dwarf and misshapen (*krumholz*) from the wind and cold. Flowering herbs are often abundant and conspicuous.

The occurrence of krumholz is evidence that trees have extended up the slopes of mountains as far as they are able under present climatic conditions (Griggs 1946). The alpine tree-line is usually very irregular. Outlying trees may occur at some distance in advance of the forest proper if they can secure the protection of an embankment, or find other suitable microhabitats. In some mountain areas trees advance to higher altitudes on ridges than in valleys because snow accumulates to greater depths in the valleys and takes longer to melt.

Origin

The origin of the tundra flora is uncertain (Raup 1941), but the species involved may be segregates from seral stages, especially bogs, of the Arcto-tertiary flora that were tolerant of arctic and alpine environments. With the cooling of the continent and the coming of the glaciers we may suppose that these species were left behind when the rest of the flora retreated southward. During Pleistocene glaciation, these species survived in the Alaska refugium (Hultén 1937), in possibly unglaciated islands of the Arctic Archipelago, and along the southern margin of the glacier. Pollen profiles indicate that climate and vegetation in the Alaska refugium were not greatly different then than now (Livingstone 1955). During the warm interglacial periods, tundra was probably limited to far northern regions and high mountains, with forests covering much of what is now the low arctic.

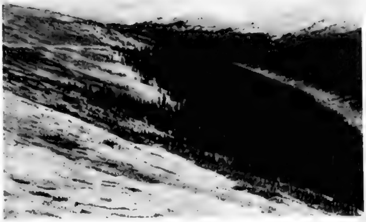


FIG. 24-1 Tree-line in Rocky Mountain National Park, Colorado. Sub-alpine forest below, alpine tundra above.

When the glaciers retreated in post-Pleistocene time, there appears to have been a period when many tundra species were continuous in distribution from the arctic plains onto the mountain slopes in the northern Rockies. Probably at this time also arctic species were able to disperse farthest southward, as alpine tundra occurred more extensively at lower elevations, and intervening forests were less extensive (Daubenmire 1943). As the forests dispersed northward through the valleys and lowlands and then gradually up onto the mountains, alpine vegetation retreated to the higher elevations and became separated from the arctic tundra proper. This northward dispersal of coniferous forest was especially rapid during the thermal maximum period, but in some localities, as in Alaska, it is not yet complete (Griggs 1936). On the other hand, the tree-line may be retreating southward at the present time in other areas (Raup 1941). The coming of the forests interrupted the complete colonization of alpine slopes by arctic species, but the forests brought a new element into the mountain flora derived from refugia south of the glacier (Raup 1947). Since the coniferous forest contained seral grassy stages with species intruding from the grassland biome, some of these species also penetrated the alpine vegetation and became part of it. Furthermore, tundra and grassland probably came into direct contact during the glaciation periods, so there is intermingling of tundra and grassland species in arctic as well as alpine regions (Hayward 1945).

ARCTIC TUNDRA BIOCIATION

Origin

The tundra fauna probably began to evolve late in the Tertiary, along with the tundra flora, as the continent cooled and the Arcto-tertiary flora retreated southward. The true arctic fauna is apparently derived from previously wide-ranging forms able to tolerate cold climates (Johansen 1956–58) and from coniferous forest and grassland, fresh-water marshes, the seacoast (Stegmann 1938), and mountainous or upland regions (Larson 1957). Adaptations in the avifauna proceeded along lines either of toleration of the many hours of darkness and severe cold of the winter climate, or to the development of extensive migrations, sometimes far into the southern hemisphere as in some shorebirds and terns.

During glacial periods of the Pleistocene, the tundra of the Alaska refugium was isolated from the tundra south of the glacier but in direct contact over the Bering land bridge with the unglaciated tundra of Asia. During this time there was doubtless an exchange of fauna with emphasis on invasion of Eurasian forms into North America. With recession of the glacier and disappearance of the land bridge, the Alaska tundra again became isolated from Asia and connected to the North American tundra. This has allowed Asiatic species to disperse over North America to varying degrees (fresh-water triclads: Kenk 1953, birds: Cade 1955). Some species, such as the grizzly bear, doubtless invaded the tundra from the western coniferous forests, perhaps since Pleistocene time. Other species now on the tundra are probably derived from refugia in the Arctic islands and from south of the glacier (Rand 1954, Johansen 1956–58).

Composition

There is enough uniformity in the animal life of the arctic tundra in North America and Eurasia so that only one biociation is presently recognized. Circumpolar distribution is characteristic of both vertebrates (Udvardy 1958) and invertebrates (Netolitzky 1932). Common animals of the tundra are those listed below, which are conspecific or represented by equivalent species on the two continents. Marine or strictly coastal species and those of more limited distribution are omitted (Bailey 1948, Banfield 1951, Bee 1958, Harper 1953, 1956, Manniche 1910, Manning 1946, 1948, Porsild 1943, Preble 1908, Rausch 1953, Salomonsen 1950–51, Soper 1944, 1946, Stegmann 1938, Taverner 1934, Taverner and Sutton 1932):

Mammals

Masked shrew
Arctic shrew
Arctic hare
Arctic ground squirrel (suslik)
Tundra vole
Brown, European, Siberian lemmings
Collared lemming
Gray wolf
Arctic fox
Grizzly bear
Polar bear (limited to coast)
Ermine
Wolverine (glutton)
Barren ground caribou (reindeer)
Peary's caribou (limited to North)
Muskox

The muskox, formerly of wide distribution, is now restricted to North America and Greenland. The tundra in North America is richer in species, both of mammals and birds, west of Hudson Bay than it is eastward, and richest in Alaska.

The most abundant mammals on the tundra are lemmings, and in peak years their numbers are enormous. Among the larger animals the caribou form large herds and are important in the food and economics of Eskimos and Indians. Seton (1912) estimates their original number at 30 million, but they are much reduced at the present time. There are also fewer muskox now (C.H.D. Clarke 1940).

Birds

Yellow-billed loon
Arctic loon
Red-throated loon
White-fronted goose
Oldsquaw
Common scoter
Rough-legged hawk
Gyrfalcon
Peregrine falcon
Willow ptarmigan
Rock ptarmigan
Sandhill crane
Semipalmated plover
Black-bellied plover
American golden plover
Long-billed dowitcher
Whimbrel
Ruddy turnstone
Knot
Sanderling
Baird's sandpiper
Pectoral sandpiper
Purple sandpiper
Dunlin
Red phalarope
Northern phalarope
Pomarine jaeger
Parasitic jaeger
Long-tailed jaeger
Herring gull
Glaucous gull
Arctic tern
Snowy owl
Horned lark
Common raven
Water pipit
Lapland longspur
Snow bunting

In addition to these species, the *North American faciation* contains the whistling swan and snow goose in the north; Canada goose and semipalmated, least, and white-rumped sandpipers rather generally distributed; and in the west, the Eskimo curlew (now probably extinct), Hudsonian godwit, stilt and buff-breasted sandpipers, and Smith's longspur. The *Eurasian faciation* also contains some species limited to it: two species each of swans and geese, several plovers and sandpipers, and another pipit and bunting.

Less than one-third of the above species of birds are entirely terrestrial in their life requirements. Many species get their food from the fresh-water ponds and lakes or on the margins of these bodies of water, so characteristic of at least the low arctic tundra. On Banks Island in the high arctic, one study (Manning *et al.* 1956) gave the following population per square mile (260 hectares): 38 Lapland longspurs, 15 sandpipers and plovers of several species, 4 horned larks, 1.5 ptarmigans (2 species), and less than one snow bunting.

Reptiles and amphibians are poorly represented where not absent, and the invertebrate fauna is comparatively restricted in variety. In the ponds on the west side of Hudson Bay occur a stickleback fish, a flatworm, a leech, an annelid, a few snails, a couple of phyllopods, a few species each of Cladocera, Copepoda, Ostracoda, and Amphipoda; a good representation of dytiscid and hydrophilid beetles, and an abundance of midge fly larvae. Since the lakes and rivers thaw out for only a few weeks, annual productivity is low (Frey and Stahl 1958). Fish are more numerous in rivers, and are largely migratory salmonids. Pond life in the Alaskan tundra is essentially similar to that near Hudson Bay (Johansen 1922).

On land, the snails *Succinea* and *Vertigo* are found in wet tundra on the west side of Hudson Bay. Spiders and mites are well represented. Springtails and flies are especially numerous among the insects, and there are a few species of Lepidoptera, Coleoptera, and Hymenoptera, but species of Hemiptera, Homoptera, Orthoptera, Odonata, and Neuroptera are scarce or absent. Ants are scarce on the tundra but bumblebees are conspicuous. Especially noteworthy are the vast devastating hordes of mosquitoes, black flies, and deer flies that reach a peak of numbers in mid-July (Seton 1912, Shelford and Twomey 1941, McClure 1943). The invertebrate life of western Greenland is essentially similar (Longstaff 1932). Quantitative studies of the soil fauna in eastern Greenland showed that springtails and mites, especially Oribatidae, reached populations of 780,000 per sq m in bush tundra, but only 3000 per sq m in the lichen-moss barrens (Hammer 1937). Seven different societies of invertebrate fauna have been differentiated here (Macfadyen 1954).

In comparison to the arctic, the antarctic supports a limited fauna. Among the invertebrates, one study found several peculiar species of Protozoa, 16 species each of rotifers and tardigrades, two fresh-water crustaceans, mites, and at least 18 species of insects. Vertebrates are primarily marine although several species, especially birds, nest on land (Lindsey 1940).

Food is more abundant along the shores of northern oceans; the association of sea and land provides niches for various species not found abundantly inland (Freuchen and Salomonsen 1958). During the winter the sea is covered with ice, there is little or no light, and phytoplankton is scarce or absent except for reproductive spores and eggs. However, nutritive salts, such as nitrates and phosphates, accumulate in large supply, so that in May when the ice disappears and light returns there is an almost explosive development of phytoplankton followed by microcrustaceans and other zooplankton. This is the key to the teeming abundance of fish, sea birds, and marine mammals that occur at this time. Large colonies of fulmars, cormorants, auks, murres, guillemots, gulls, and others nest on ledges of precipitous cliffs or in some cases on islands or shores down close to the water. Eider ducks and other waterfowl are frequently numerous. Vegetation is best developed in and around these colonies because of the rich nutrient added to the soil from the excreta of the birds. One of the most common seals is the ringed seal which remains over winter, even in the high arctic, by keeping blow-holes open through the ice. The harbor seal and harp seal overwinter in the more open waters of the low arctic. Other species of seals, whales, walruses, and polar bears occur during the summer throughout most of the maritime areas of the arctic.

Animal adjustments

White coloration is common, especially over winter, in several mammal species (artic hare, collared lemming, gray wolf, arctic fox, polar bear, ermine, Peary's caribou) and in a few birds (willow and rock ptarmigans, snowy owl). When the ground is covered with snow, white coloration, of course, conceals both the prey and predators. Many of these species acquire darker coloration during the months

FIG. 24-2 **Rock ptarmigan males: left, summer plumage; right, winter plumage (courtesy Bert Babero).**

between May and September. The white winter color apparently does not give special protection against heat loss from the body, as has sometimes been thought (Hammel 1956).

A major habitat problem that tundra animals must solve is tolerating or avoiding the long severe cold of the winter season. Cold-blooded animals are generally acclimatized so that they remain active at temperatures down to freezing much better than their relatives in temperate and tropical zones. This is particularly true for aquatic species (Scholander *et al.* 1953, Bullock 1955). Invertebrates commonly pass the winter in the larval or pupal stage that is especially resistant to freezing, although beetles, spiders and some other forms may overwinter as adults. Rotifers, tardigrades, midge fly larvae, and dytiscid and hydrophilid beetles may be frozen in the ice for months or even years, yet resume activity immediately on thawing (Lindsey 1940, McClure 1943, Andersen 1946). Because of the short growing season and slow development, many tundra insects require two or more summers to complete their development.

The larger mammals and over-wintering birds have good insulation in long, dense pelage or plumage, and in fat. Heat production in their bodies is not greatly increased until very low air temperatures are reached (Scholander *et al.* 1950). The tarsi and legs of ptarmigan and snowy owls become well feathered in the winter.

Voles, lemmings, and ermines escape the winter cold by staying in their runways and nests under the snow. The ptarmigan also digs tunnels into snowbanks where it roosts protected from the cold (Wetmore 1945), sometimes for days at a time. Only the arctic ground squirrel truly hibernates. This it does by excavating burrows into sandbanks or hills which, because of exceptional drainage, possess an area that remains unfrozen between the deep permafrost and the winter frost at the surface (Mayer 1953). The bears den up during the cold weather but remain active to the extent of giving birth to their young in the middle of the winter.

Those species that cannot tolerate or escape the winter cold and lack of food migrate. The barren-ground caribou on the mainland migrates in long strung-out armies to the southern portions of the tundra, even well beyond the tree-line into the forest-tundra, to pass the winter, and their trails remain conspicuous throughout the year (C.H.D. Clarke 1940, Harper 1955). The caribou on Greenland, Spitzbergen, and the northern islands of the Canadian Archipelago are necessarily resident throughout the year. Migration of the bird fauna in this biociation is nearly complete; during the winter only an occasional hawk, ptarmigan, raven, or owl will be encountered over the land, although marine birds occur wherever there is open sea. When the birds return in the spring they are quick to get nesting started. Often they are already mated, carry through their nesting cycle quickly, and then leave promptly again for southern latitudes.

In general, the melting of the snow and the breakup of ice is the signal of transition from winter to summer. Although it is possible to recognize all of the four aspects (Sørensen 1941), the change from winter to summer and back again to winter is so rapid that all aspects are abbreviated except the hiemal and aestival. May is the usual month of parturition among the larger mammals, and the peak of bird nesting comes in late June and early July.

Owls, hawks, water birds, and some passerine species do not breed in those years in which scarcity of food or delayed freeing of nesting grounds of snow and ice are detrimental to survival. Failure of hawks and owls to breed occurs especially in years when the lemming population is low (Marshall 1952).

Ptarmigan, hare, voles and lemmings, and their predators, particularly the fox and snowy owl, are subject to oscillations in abundance that come at intervals of either 3–4 or 9–10 years. These oscillations are more pronounced in the arctic tundra than in any other biome.

The food coactions of the herbivorous animals are of interest. Caribou feed on lichens, including reindeer moss, especially in the winter, which they uncover by pawing through the snow. During the summer they also consume shrubby growth and sedges (Harper 1955). Grass is the principal food of the muskox, but it also eats willow brouse and, less frequently, lichens and mosses (Jackson 1956). Ptarmigan feed on plant material left behind by these large animals. The chief food of ptarmigan, however, is the buds, leaves, and tender branches of willow and other shrubby plants not easily obscured by snow. Their winter food appears to be richer in fats and contains less protein than the food they consume during the summer (Gelting 1937). Gulls are known to eat warble fly larvae rising from the skin of caribou (Scalon 1937) but depend mainly on dead fish that they find in open water, or on carrion. Most of the small passerine birds are seed-eaters or mixed seed- and insect-eaters. Berries become abundant in August, and are much sought after by birds. Exclusively insectivorous land birds, such as warblers, would find great difficulty in surviving and reproducing on the open tundra. Shorebirds are largely insectivorous but depend largely on aquatic forms for food.

Although the continuous arctic summer light permits activity throughout the twenty-four hour day, most mammals and birds need periods of rest, which they take at any time. Birds appear to rest most frequently in the hours before midnight, but the periods of rest are shorter than in southern latitudes (Armstrong 1954, Cullen 1954). In one study conducted above the Arctic Circle, adult robins fed their young for 21 hours per day and the young birds grew so rapidly that they left the nest in 8.8 days instead of the 13 days usual in more southerly latitudes (Karplus 1949). During the winter, there is at least a faint glow of light for an hour or two at noon. It is during this period that ptarmigan and probably other birds feed most heavily (Gelting 1937). As a rule, northern birds also tend to lay larger clutches of eggs than their closest relatives in southern latitudes (Lack 1947–1948). Related to their nesting is the tendency for many species to have flight songs, sometimes given high in the air, for announcing the possession of territories and for soliciting mates. This development of behavior is related to the lack of high song posts and is similarly developed in the grassland biome.

A final characteristic of these northern animals is their fearlessness of man. The few Eskimos, Indians, and white men who inhabit the tundra are so scattered that animals in general have not learned to fear them. To a certain extent this is true also of some boreal forest species; snow buntings, snowy owls, grosbeaks, crossbills, and other species may be approached closely before they are moved to flee. Among mammals, individual arctic foxes not infrequently linger close to human habitation for days at a time.

Human relations

The arctic is the home of Eskimos in North America and of the Lapps in Eurasia (Hadlow 1953, Freuchen and Salomonsen 1958). The Eskimos are concentrated along the coast as much of their food comes from the sea: fish, walrus, seal, and polar bear. During the summer, caribou flesh, bird eggs, and berries are eaten. Caribou fat and seal oil are burned in the Eskimo igloos to furnish light and heat, and pelts from these animals are made into clothing and blankets. Meat is eaten either cooked, dried, or raw, and some of it is frozen and buried in the ground for the winter days of scarcity. The Eskimo gets his transportation during the summer in light boats made of sealskin stretched over frameworks of driftwood or bone, and during the winter in sleds drawn by dogs. Fur trapping is the chief source of income.

The Lapp lives much like the Eskimo, although he more commonly lives in a tent made of reindeer skin than in an igloo made of snow. The reindeer is used by the Lapp for pulling his sled, for meat, and for milk. The Lapp may also keep goats. Lapps move up and down the mountains in summer and winter in search of pasture for their animals, northwards and southwards with the seasons for fishing; below tree-line they occasionally grow meager crops.

ALPINE TUNDRA BIOCIATION

Tibetan faciation

The largest alpine areas of the world lie on the Tibet Plateau and in the adjacent Himalayan Mountains of Asia (Hingston 1925, Schäfer 1938). Occurring here are related forms of pikas, pipits, rosy finches, and horned larks also found in mountain areas of the western hemisphere, while the marmot and sheep may be conspecific with North American forms (Rausch 1953).

Stegmann (1938) gives a long list of birds especially characteristic of the Tibetan fauna. The Tibet Plateau may represent an important center of origin of alpine species, some of which then became dispersed into the higher mountains of Europe and North America. The Tibetan fauna evolved independently from that of the Arctic tundra and there are few or no bird species common to the two. There is some overlap of species, however, with the Asiatic grassland (Mongolian fauna), Asiatic deciduous forest (Chinese fauna), and Ethiopian desert (Mediterranean fauna) biociations which suggests their possible remote derivation.

North American faciation

Because of its small total area, rugged terrain, and discontinuity between mountain peaks, there are only a few species characteristic of the alpine tundra in North America.

Mammals are conveniently divided into two groups. Those occurring in the high tundra from Alaska to British Columbia are the collared pika, hoary marmot, singing vole, barren ground caribou, mountain goat, and Dall's sheep. Species limited to the southern mountains are common pika, yellow-bellied marmot, and mountain sheep. The common pika is differentiated into over thirty subspecies in the various mountain areas. Shrews, bears, coyotes, weasels, badgers, mice, wapiti, and mule deer of the western montane biociation range up into the alpine tundra during the summer. Ground squirrels and pocket gophers reach this community south of Canada by extending their ranges from the low elevation grasslands through seral stages in the intervening coniferous forests.

Of birds, the white-tailed ptarmigan, water pipit, and gray-crowned rosy finch are characteristic and widely dispersed. In the central and southern Rocky

FIG. 24-3 **Columbia ground squirrel in alpine tundra, Glacier National Park (courtesy R.L. Day).**

Mountains the brown-capped and black rosy finches replace the gray-crowned rosy finch. Rock wrens and horned larks are occasional summer visitors. In the alpine meadows of the far North, savannah sparrows and upland plovers are common, although they belong principally to the prairie biociation and grassland seral stages of the boreal coniferous forest. Also in the North, around ponds, occur lesser yellowlegs, herring gulls, short-billed gulls, and Bonaparte's gulls (Drury 1953).

Except for the caribou and pipit, the alpine and arctic tundra biociations have no important species in common. There appears less taxonomic relation to arctic tundra with animals than plants. Probably most of the species listed above are of northern origin and, entering North America over the Bering land bridge, dispersed southward on the mountains as they became elevated and the alpine tundra differentiated.

Reptiles and amphibians are uncommon. In contrast to the arctic tundra, flies are comparatively few except in the vicinity of ponds, but there is an abundance of springtails, ground-dwelling beetles, leafhoppers, grasshoppers, true bugs, butterflies, ants, bumblebees, mites, and spiders (Hayward 1945, 1952).

Alpine ponds have an impoverished fauna. In a small pond at 3507 m (11,500 ft) in the Colorado Rockies of maximum depth one meter and which freezes solid in the winter, plankton was scant during the summer after the ice melted, but midge fly larvae reached populations of over 1900/m^2, *Pisidium* fingernail clams, 1470/m^2, and tubificid worms, 168/m^2. A fairy shrimp was the most characteristic metazoan in the open water, although a small number of aquatic insects occurred along the shoreline (Neldner and Pennak 1955). Phyto- and zooplankton tend generally to be represented by fewer species and a smaller number of individuals than in temperate or tropical lakes (Thomasson 1956).

Animal adjustments

As in the arctic tundra, most of the residents in the alpine tundra that remain active over winter are white in color: mountain goat, mountain sheep, Dall's sheep, and white-tailed ptarmigan.

The pikas inhabit masses of loose rock rather than the climax meadow itself and also occur well below tree-line. During the summer they gather stacks of tundra vegetation and during the winter subsist on this hay. Pocket gophers spend most of their existence in underground burrows feeding on roots and bulbs and hence are well protected from winter cold. The hoary and golden-mantled marmots and ground squirrels hibernate. Wapiti and deer migrate to the lower mountain slopes and valleys for the winter as do most of the birds. There is often some downslope movement of mountain sheep and goats for the winter, but it is not so extensive as with the wapiti and deer (Hayward 1952). The behavior and interrelations of wolves, Dall's sheep, caribou, and other species in the high tundra of Alaska are described in detail by Murie (1944). It is of interest that subspecies of mountain sheep formerly occurred regularly on the Great Plains and in desert regions at low altitudes (Buechner 1960).

Low temperature slows up the development of insects and other invertebrates and reduces the number of generations possible during the year. Animals, however, are generally acclimatized to be active at low temperatures. For example, springtails are sometimes abundant on the snow, where they freeze at night and thaw out during the day. An interesting food-chain occurs with their feeding on conifer pollen falling on the snow and being fed upon by mites.

Because of the usually strong winds, insects and even birds stay close to the ground and fly as little as possible. Many insects are wingless. Birds commonly feed and build their nests on the sheltered side of obstacles, or they crawl into holes and crevices. When in the open, they persistently face the wind (Hingston 1925).

In the Colorado Rockies, grasshoppers are among the most numerous species. However, of 28 species recorded, only 11 are truly alpine species, the rest being found only as adults which have flown or been blown up from lower altitudes and do not reproduce successfully there (Alexander 1951). In Tibet, grasshoppers go as high as 5540 m (18,000 ft); bees, moths, and butterflies to 6460 m (21,000 ft); and spiders to 6770 m (22,000 ft) (Hingston 1925).

During the late spring, south slopes on the mountains become free of snow before the north slopes because they get direct radiation of the sun. Consequently, plant and animal life become active on south slopes before they do on north slopes. Individuals of the same species will also begin growth and reproduction on the lower slopes before they do on the higher slopes. Birds appear to construct more compact nests, as insulation against cold, at high than at low altitudes, and they build these nests on the exposed south sides of thickets or trees where they benefit from the heat of the sun (Heilfurth 1936).

The low oxygen pressure at high altitudes appears to be more critical for the warm-blooded mammals than it is for birds, which are adapted to fly at high elevations anyway, or for invertebrates and plants that have much lower rates of metabolism and oxygen requirements (Hall 1937, Kalabuchov 1937). Mammals moving up to high altitudes may become temporarily acclimated through increases in rate of respiration, in rate of heart beat, in number of red blood cells, and in hemoglobin, but these adjustments are seldom as effective as in those species which are permanent residents at high altitudes. Species acclimatized to low oxygen pressures are affected in a reverse manner when they move to low altitudes. Some mammals that have a wide altitudinal range, particularly the pocket gopher *Thomomys,* are, like plants, smaller in size at high than at low elevations with a continuous gradation between the extremes (Davis 1938).

Human relations

There are few humans living permanently in the high mountainous regions of North America, but white man goes up there, taking sheep and goats to summer pasture, and for recreational or sight-seeing purposes. Man does occupy the Tibetan plateau of Asia. There, he depends on the yak to plough his fields and to furnish meat, butter, and milk. Although much of the plateau is too rugged and cold for crops, millet, corn, and wheat are grown in sheltered valleys.

SUMMARY

The tundra biome extends beyond the tree line in the far North and on high mountains. It has low precipitation, low temperatures, a short growing season, and, in the arctic extreme seasonal changes in length of day and night and a permafrost in the ground. Vegetation is bush or mat tundra, grass tundra, or lichen-moss tundra. Perpetual snow and ice occur in extreme areas. The tundra flora is probably derived from seral stages in the Arcto-tertiary flora which became segregated as the continent cooled in the Pliocene and Pleistocene.

The arctic tundra biociation is fairly uniform faunistically in North America and Eurasia, although two faciations are distinguishable. Mammals, birds, mosquitoes, and flies are the most conspicuous animals with springtails and mites predominant in the soil. White color is common among mammals and birds, especially during the winter. Acclimatization to cold is highly developed in many resident forms. Some small mammals remain active under the insulating cover of snow during the winter months. Most birds migrate. Cycles of abundance are pronounced in several species. The Eskimo and Lapp mainly hunt and fish for a living.

The alpine tundra biociation is best developed in the Tibetan plateau in central Asia. Only a few species of mammals and birds are peculiar to the biociation. Mammals are physiologically adjusted to the low oxygen pressure. Man finds habitation in this area difficult except during the summer months, when he brings his sheep and goats for pasture or comes for recreation.

25

Grassland Biome

Grassland presently occurs on all the continents, and at one time covered 42 per cent of the earth's surface. Grasslands everywhere possess marked similarities in points of climate, physiognomy, and animal mores. In Russia this community is termed the *steppe,* in Hungary, the *puszta,* in South Africa, the *veld,* and in South America, the *pampas* (Carpenter 1940). In North America the tall, dense grasslands with their rich fertile soils in the eastern portion of the biome are called *prairie;* in the West, the short grasses and shallow soil characterize the *plains.*

In North America, grasslands extend from northern Saskatchewan and Alberta and central British Columbia to central Mexico, and from Indiana to California. The eastern portion is a huge expanse, continuous except for forest strips in the river valleys, but the continuity of the western portion is broken by the many mountain ranges. In general, the terrain is flat or rolling, green in summer and brown in autumn and winter (Weaver and Clements 1938, Clements and Shelford 1939).

CLIMATE

Precipitation in North America may be as high as 100 cm (40 in.) per year adjacent to deciduous forest, but trees cannot spread into the grassland because of high rates of evaporation, late summer and autumn droughts that are particularly severe and prolonged during some years, and intermittent fires that kill seedling trees but from which grasses quickly recover. Rainfall decreases and becomes more irregular and evaporation increases in a gradient from East to West or Southwest, because of the general pattern of air circulation over the continent (Kincer 1923, Borchert 1950). An isohyet of 2–3 cm (5–8 in.) precipitation separates grassland from desert.

Few species of grasses can tolerate the entire range of precipitation, and differences in the moisture requirements of species is the main reason for the subdivision of the biome into its various plant associations. There is little snow even in northern portions of the grassland, but winds are normally heavy, and there occasionally are severe winter blizzards.

Temperature is not as critical a factor as moisture, as is evident in the great North-South distribution of grasslands. Temperature, however, helps to separate temperate grasslands from tropical grasslands. In the North, mean monthly winter temperatures drop to —15°C (5°F), while summer temperatures in the South may exceed 32°C (90°F). There are great seasonal and daily ranges of temperature. The frostless period in the North may be only 100 days long, but in the South frost rarely or never occurs. In the California and bunch grass prairies, most of the rainfall comes in the winter months, and in southern California some grasses start their growth in late autumn and come into bloom in December, although others wait until spring.

VEGETATION

Grassland owes its characteristics to the perennial grasses that constitute the dominant climax vegetation. Annual grasses are largely confined to seral stages. These climax grasses may be *tall* (1.5–3 m), *mid* (0.5–1.5 m), or *short* (less than 0.5 m) and grow in *bunches* or as *sod*. Forbs occur mixed with the grasses, and variation in the time of blooming of these broad-leaved and mostly perennial herbs as well as of the grasses gives the grassland a variety of aspects like the forest (Weaver 1954, Weaver and Albertson 1956). The prairie has beauty, character, and a history all its own (Craig 1908a, Weaver 1944).

Grasses grow quickly after the onset of warm and rainy weather and are adapted for long quiescent periods of dryness and cold. The leaves or tops of the grasses die down during unfavorable seasons, but underground buds regenerate new growth during the next favorable period, even if this be delayed for some years. After dry-season fires in tropical climates, new shoots sprout from perennial grass bases. These provide a sparse forage for grazing animals, a forage that, except for the fires, would not be present until the rainy season (Vesey-Fitzgerald 1960). The grasses and forbs are deeply and extensively rooted, except in arid climates, where a hardpan occurs near the surface (Fig. 11-4). Competition is primarily for the limited water supply and only secondarily for light. Since grasses grow from the base of the leaf, they can tolerate considerable grazing by large herbivorous animals, and this is an important factor in their dominating the prairie.

Several of these, the most important genera of grasses in the North American grasslands, occur also in other parts of the world (Clements and Shelford 1939):

Mostly tall and mid grasses

Andropogon—blue stem
Agropyron—wheat grass
Elymus—wild rye
Festuca—fescue
Koeleria—June grass
Panicum—panic grass
Poa—blue grass
Sporobolus—drop-seed
Stipa—needle grass

Mostly short grasses

Aristida—triple-awned grass
Bouteloua—grama grass
Buchloë—buffalo grass

PLANT ASSOCIATIONS OF NORTH AMERICA

Stipa-Sporobolus **association** (true prairie): Mostly tall and mid grasses in a long strip extending north and south in the eastern more humid part of the biome next to deciduous forest. Much of this prairie was marshy and poorly drained before white man came (Hewes 1951). Oak-hickory forests occur as scattered groves in better drained areas on hills, in sandy areas, and along streams making a savanna. The coastal prairies of Texas constitute a faciation of this community.

Stipa-Bouteloua **association** (mixed prairie): Mid grasses confined to the moister low areas; short grasses, to drier hillslopes.

Bouteloua-Buchloë **association** (short grass plains): On Great Plains east of Rocky Mountains. The climate here is so dry that mid grasses are inconspicuous except during wet years. Pronghorn and bison in former days consumed mid grasses as fast as they appeared, in preference to the short grasses, and hence should be considered co-dominants along with the grasses (Larson 1940).

Agropyron-Festuca **association** (bunch grass prairie): In northern half of the Great Basin and into British Columbia, mostly isolated from rest of biome by mountains and desert. Precipitation comes chiefly as snow and rain during winter months. Dominant species mostly mid grasses which grow as bunch grasses. Overgrazing by domestic animals has permitted the less palatable sagebrush and related species to spread widely and give character to the landscape.

Stipa-Poa **association** (California prairie): Located in central valley of California almost completely isolated from rest of grassland, dominants are mostly mid and bunch grasses. This is a region of winter rains. Much of area is now cultivated or overgrazed and contains many weedy annuals and exotic species.

Aristida-Bouteloua **association** (desert plains): Most arid of grasslands, composed mostly of short and bunch grasses. It occurs from southeastern Texas to southern Arizona and extends well down into Mexico. Because of overgrazing and control of fire, desert and tropical shrubs, such as mesquite, creosote bush, *Opuntia* cactus, are conspicuous throughout the association. The sugary pods of mesquite are eagerly eaten by cattle although the bony seeds resist digestion and are dispersed widely.

PALEO-ECOLOGY

Grasses did not evolve until the Upper Cretaceous period of the Mesozoic, and did not become important in North America until the elevation of the Western mountains in mid-Tertiary produced a semi-arid climate in the middle of the continent. Several of the mid grasses are circumpolar in distribution and may have constituted seral stages in the Arcto-tertiary flora. They probably segregated out to form the true, mixed, and bunch grass prairies when the forests belonging to this flora retreated southward and eastward. The close relation of grass species on the prairies of North America and northern Eurasia is doubtless due to their similar derivation from the Arcto-tertiary flora. The tall grasses of the Andropogoneae may be of tropical origin. The short grasses were probably derived from the Madro-tertiary flora to form the short grass and desert plains. Although one cannot be sure because of the paucity of grasses in the fossil record, it appears that the grassland is of mixed and relatively recent origin (Axelrod 1950, 1952).

During portions of the Pliocene and Pleistocene (Fig. 21-2), rainfall was heavy; grassland probably extended through the Great Basin and into the Mohave desert. There is little information available to indicate whether the California grassland was ever in broad contact with the rest of the biome, but there was probably a narrow and irregular contact through mountain valleys at either or both the southern and northern extremities.

During the post-glacial xerothermic period, grassland doubtlessly retreated in the southwestern states and in Mexico as the desert biome became extended, but it is difficult to draw boundary lines for the extremes of these advances and retreats. In the eastern part of the continent during the xerothermic period, prairie advanced as a peninsula far into the deciduous forest (Fig. 21-7). Relict patches, including the Illinois prairie, still remain after later cool and more humid climate permitted the forest to recover much of the area it had previously lost. Doubtless the prairie also advanced northward into the area now dominated by the boreal forest of central Canada during the xerothermic period, where relict patches of grassland may still be found. Reinvasion of prairie areas was slow at first because of frequent fires caused by lightning and Indians and to poor drainage, but since settlement of the area by white man and artificial lowering of the water table it has become rapid (Gleason 1922).

In spite of its vast extent, only a single grassland biociation can be recognized at present in North America, although it varies in composition between different regions.

NORTH AMERICAN GRASSLAND BIOCIATION

The North American grassland biociation extends in reduced form as a biocies or seral stage into the deciduous and coniferous forest biomes. Common species are the following, sometimes replaced locally by related species:

Mammals

Masked shrew
White-tailed jack rabbit (North)
Black-tailed jack rabbit (South)
Eastern cottontail (East)
Desert cottontail (West)
Nuttall's cottontail (South)
Black-tailed prairie dog
Ground squirrels
Northern pocket gopher
Plains pocket gopher
Pocket mice
Banner-tailed kangaroo rat (South)
Harvest mice
Deer mouse
Northern grasshopper mouse
White-throated wood rat (South)
Meadow vole
Prairie vole (East)
Meadow jumping mouse
Coyote
Swift fox
Long-tailed weasel
Black-footed ferret
Badger
Prairie spotted skunk
Pronghorn
Bison

Birds

Ferruginous hawk
Great prairie chicken
Lesser prairie chicken
Sharp-tailed grouse
Long-billed curlew
Upland plover
Burrowing owl
Short-eared owl
Horned lark
Sprague's pipit (North)
Bobolink
Western meadowlark
Dickcissel (East)
Lark bunting
Savannah sparrow
Grasshopper sparrow
Vesper sparrow
Lark sparrow
McCown's longspur (North)
Chestnut-collared longspur (North)

In addition to the more strictly grassland species above, many species from the deciduous forest-edge biociation extend their ranges varying distances into the open country. Many desert species also extend their ranges into the grassland biome, especially where sagebrush, mesquite, and other shrubs come into overgrazed areas. Because of these various influences, the long North-South range through various temperatures, and the isolated nature of some portions of the grassland, several faciations may be recognized (Carpenter 1940). They have not yet been clearly defined but may correspond to the biotic provinces described by Dice (1943) and Blair (1954); *viz.:* Illinoisan in the East; Saskatchewan in the northern Great Plains; Kansan in the central

TABLE 25-1 **Equivalent species in grassland communities around the world (modified from Allee *et al.* 1949: 470–471).**

Ecological niche	North America	South America	Asia	Africa	Australia
1. Saltatorial (leaping) herbivores					
a. grasshoppers	*Melanoplus spretus* *Melanoplus differentiales* *Melanoplus maculipennis* *Melanoplus ponderosa*	*Schistocerca paranensis*	*Locusta migratoria*	*Locusta migratorioides* *Stauronotus macroccanus* *Schistocerca peregrina*	
b. mammals	jackrabbits		jerboa	springhaas	red kangaroo
2. Fossorial (burrowing) herbivorous mammals					
a. feeding in herb stratum	ground squirrels prairie dogs	viscacha pampas cavy	souslik hamster bobak	African ground squirrels	wombat European rabbit (introduced)
b. feeding in subterranean stratum	pocket gophers	tucotucos	mole rat	golden moles	marsupial mole
3. Cursorial (running) herbivorous birds		rhea		ostrich	emu
4. Cursorial gregarious herbivorous mammals	bison pronghorn	pampas deer guanaco	saiga goitered gazelle and other gazelles maral wild ass wild horse	quagga Burchell's zebra eland springbok gazelles (several species) black wildebeest blue wildebeest bubal bontebok 30 other genera of antelopes	pig-footed bandicoot
5. Cursorial predators					
a. snakes	blue racer bull snake prairie rattler	*Cyclagras gigas* *Rhadinea merremii*	common cobra Asian moccasin elaphe	puff adder black-necked cobra rock python	death adder tiger snake
b. mammals	swift fox coyote (wolf) (cougar)	pampas cat red wolf	Pallas cat corsac fox cheetah jackal	lion serval caracal cheetah Cape hunting dog	Tasmanian wolf (marsupial)

Great Plains; Texan and Comanchian in the South; Navahonian in contact with the Southwestern desert; Palusian corresponding with the bunch grass prairie; and Californian, including the California prairie. The student should re-read Chapter 9 which gives additional data on the grassland fauna especially in regard to reptiles and invertebrates.

OTHER BIOCIATIONS

Grasslands in other parts of the world (Brehm 1896, Haviland 1926, Stegmann 1938) are occupied by species ecologically equivalent to those that inhabit the grasslands of North America. The parallel evolution of adjustments and behavior in

FIG. 25-1 **Grassland animals. Clockwise, bison, pronghorn, coyote, badger (courtesy U.S. Forest Service).**

animals that occupy similar habitats, although often quite unrelated taxonomically, is of particular interest and may best be shown in table form (Table 25-1).

ANIMAL ADJUSTMENTS

It is in the grasslands throughout the world that the large herbivorous ungulates reach their largest populations. Their adaptations for feeding on grasses and the high productivity of grasses, which in fact is stimulated by moderate grazing, gives an efficient food coaction of high energy utilization. A forest cannot support such large populations of grazing animals since the herb layer is less luxuriant, composed more of the broad-leaved herbs, and shrub and tree foliage cannot tolerate continued browsing. The evolutionary development of these large ungulate populations had to await the evolution of these extensive grasslands in mid-Tertiary time (Stirton 1947). Previous to the formation of the grasslands in North America, we may suppose that the ancestral forerunners of bison and pronghorn were largely limited to seral grassy stages in the Arcto-tertiary and perhaps Madro-tertiary floras.

It is common for these large ungulates to feed in large herds. The primitive population of bison in North America is estimated at 50–60 million animals, perhaps an average of 6 per sq km (15 per sq mi). Few occurred west of the Rockies even in colonial times, but to the east and north the species penetrated far into forested areas. Herds containing 20,000 individuals were common and an occasional herd reached a population as high as 4 million animals (Seton 1909). When attacked by wolves or other predators the bulls formed a circle facing outward with the cows and calves inside. The animals shed their fur in the summer and were greatly annoyed by flies, mosquitoes, and the penetrating seeds of the needle grass. They relieved their miseries by rolling in wallows, covering themselves with mud. Some calves were killed by wolves, coyotes, bears, and mountain lions. Adults died in consequence of bogging down in sloughs or swamps, breaking through thin ice when crossing rivers in winter, and of old age. Disease apparently was never common. The animals regularly grazed until mid-morning, traveled sometimes 16 km (10 miles) to a water hole, rested and chewed their cud during mid-day, and grazed again in the evening. A herd would graze an area intensively for several days or weeks, then move to some other area. In these movements and migrations, the animals commonly traveled in single file. There is question, however, whether north-south migrations were very regular and extensive (Roe 1951).

The pronghorn antelope occurs in the drier grasslands, including California, and their primitive population is estimated at 4 per sq km (10 per sq mi). They traveled in herds of 100–200, sometimes 2000. When they were scattered in feeding, the approach of a predator was quickly signalled from one to the other by raising the hair in the white rump patch so that it flashed like a tin pan reflecting the sun.

Safety for these animals depended largely upon fleetness of foot, and some of the fastest-running animals in the world occur in this biome (Craig

1908a, Visher 1916). Joined with this ability was long-range vision to discern the approach of danger from a distance. Coyotes could not run as fast as pronghorn, but since the pronghorn usually ran in wide circles, the members of a pack of coyotes would sometimes run in relays until the pronghorn fell exhausted.

Rodents and lagomorphs constitute the other principal groups of mammals. Ground squirrels, pocket gophers, mice, and jack rabbits are common nearly everywhere and sometimes reach plague proportions. Prairie dogs form towns, some in former days large enough to cover several square miles, with each animal feeding on the grasses and herbs only in the vicinity of his own burrow. Prairie dogs are most numerous on the Great Plains where the grasses are shorter, and a century ago they probably numbered in the billions. They as well as other species of rodents have numerous predatory enemies such as coyotes, badgers, ferrets, foxes, weasels, owls, and rattlesnakes. They have good vision, however, and quickly plunge into their extensive underground burrows at the approach of danger (Koford 1958).

Jack rabbits, other small mammals, prairie chickens, as well as most of the small birds, grasshoppers, and other insects rely considerably on their well developed protective coloration—they freeze in the deep grass to escape notice of predators. If the predator comes too close, they take to running, jumping, or flying with such a burst of activity so as to startle the intruder momentarily and give them a head start in their flight.

The development of hopping locomotion among

grassland and desert animals is of special interest. We see it expressed in jack rabbits, kangaroo rats, pocket mice, and grasshoppers in North America; all these species have short forelegs and long, strong, hind ones. Hopping enables the animals to get above the level of the grass for locomotion and is of advantage also in allowing greater visibility.

There is a nearly complete absence of animals above ground in the winter. Bison formerly shifted their main populations from the northern to the southern portions of the grassland, pronghorns sought shelter in the piñon-juniper woodlands and petran bush in the valleys and foothills of the mountains, and most of the birds left for the South. Ground squirrels, prairie dogs, and jumping mice hibernate in underground burrows, reptiles from over large areas aggregate into deep holes or crevices in the sides of hills, and invertebrates pass the winter in a dormant or inactive condition in the soil humus. Many of these animals also become inactive or aestivate during dry seasons, especially in late summer and autumn, and sometimes aestivation proceeds directly into hibernation so that the animals are active for only a short time each year.

Grassland birds are direct, strong fliers and can withstand the fierce winds prevalent in open country. They are adroit in walking and running on the ground. They also appear better able to tolerate the continuous direct rays of the sun, but nevertheless on hot sunny days they commonly seek the shade of the tall grasses, scattered bushes, or line up in the narrow shadow of a fence post or telephone pole. With the absence of trees, many birds make themselves conspicuous during the nesting season by developing loud flight songs which they give high in the air. Flight songs are much more characteristic of grassland than of forest birds. Contrary to the herd instinct in mammals, flocking is not particularly characteristic of grassland birds, although prairie chickens and grouse exhibit gregariousness in their mating performances. Birds are usually widely spaced with their nests well concealed in the grass (Kendeigh 1941a).

The more humid portion of the grassland is studded with small ponds or potholes. These ponds are surrounded with marsh vegetation. Here are found numerous ducks, grebes, herons, bitterns, coots, rails, terns, and other marsh birds as well as muskrats. Animal life is especially concentrated around these water holes (Brehm 1896), although larger species roam widely through the upland for feeding purposes.

HUMAN RELATIONS

Tall grass prairie is highly productive agricultural land for corn, wheat, soybeans, and cereal crops in general. This is evident both in North America and Europe. Hogs are raised on the corn that is grown. The more arid short grasslands, such as are found on the Great Plains and the northern Great Basin of North America and on the Russian steppe, are more hazardous to cultivate, as crops, mostly wheat, often fail during the dry years of climatic cycles. Plowed or overgrazed ground, destitute of grass or crop cover, is whipped up by strong winds to produce the great dust storms that have become so well known in recent years. Dry farming for wheat is a common practice in some areas, where land is cropped only every two or more years and left idle between times to accumulate ground moisture, or there may be crop production under irrigation (Weaver 1927). Man has not always used grassland intelligently (Shelford 1944) especially during the war years when the demand for food supplies was so great, because he has plowed up land where the grass cover should have been left intact. Arid grassland in the Great Plains had best be used only for stock raising, especially of beef cattle and sheep, and this is done extensively on our western ranches. In the arid parts of Asia, many different peoples have a nomadic existence in a never-ending search of pasture for the cattle, sheep, goats, camels, and horses that serve their everyday needs (Hadlow 1953).

The history of early exploration and settlement on the North American grassland is of considerable interest (Malin 1947). Before the advent of white man, Indians were scarce over the grassland because of difficulties in transportation and in hunting large game animals. With the escape of horses from the early Spaniards and their rapid multiplication, the Indians soon learned to use them, and several tribes took to the prairies and plains.

The white man was, at first, somewhat reticent about invading the prairies and kept his settlements to the forested areas along the streams. The prairies that he first encountered along the forest-edge in the East were flat, very wet in the spring, and poorly drained. The grass roots made a tough sod difficult to plow with the primitive equipment then available. There were difficulties in obtaining drinking water. Prairie flies were a nuisance, and the prairie fires that occasionally swept across the country were dangerous. Furthermore, he was accustomed to using timber for buildings, fences, and fuel, and the forest gave him protection from cold winter winds (Vestal 1939). In the course of time, however, and under the pressure of increasing populations, he learned to surmount these difficulties. Ditches were dug to drain the land and the streams were deepened. Better plows and other farm equipment made cultivation easier. Construction of roads, bridges, and railroads brought building equipment for homes, supplies, and other comforts of life. At the present time the tall grass prairie is the so-called bread basket of our modern civilization.

SUMMARY

Grasslands occur on all continents and are marked by low amounts of precipitation and high rates of evaporation. Climax grasses are mostly perennial and are characteristically tall, medium, or short in stature. Since their leaves grow at the base, they tolerate grazing by animals, and it is in this biome that ungulate mammals and rodents attain large population densities.

The large herbivorous ungulates commonly go in herds, are fleet on foot, and have long-range vision. Some species of rodents form large colonies and dig extensive underground burrows. Locomotion by hopping occurs in several mammals and some insects. Protective coloration is well developed in many kinds of animals. Upland birds are strong fliers and commonly have flight songs. Scattered ponds surrounded by marsh have concentrations of many nesting species of birds and are the source of drinking water for the large mammals. Migration is well developed among birds and hibernation among small mammals, reptiles, amphibians, and invertebrates so that there is a nearly complete absence of animals above ground during the winter months. Only one biociation is recognized in North America and in each of the other continents.

The more humid grassland areas make very fertile and productive agricultural land for man while the drier portions are best used for grazing of domestic animals.

26

Desert Biome

Extreme desert is arid wasteland, with practically no vegetation. In the ecological sense, however, deserts also include arid regions which contain considerable vegetation in the form of bushes, shrubs, and trees especially adapted to tolerate hot, dry climates. Deserts are unique in possessing a large number of different life-forms among the dominants (Shreve 1942).

Deserts, like any other biome, occur in belts at similar latitudes north and south of the equator around the world and they cover about one-fifth of its surface. Prominent deserts occur in southwestern United States and northwestern Mexico; in Sahara, southern Africa, Arabia, central Asia, Australia, and in a narrow strip along the west coast of South America. All these areas are at low elevations. In spite of its arid character, the desert, like other biomes, has a fascination and charm for one who becomes familiar with its inhabitants and their problems (Jaeger 1955, 1957).

CLIMATE

Deserts around the world generally occur on the lee side of high mountains and continents, with respect to the prevailing winds. Average annual precipitation in the desert scrub of North America is usually not more than 5 in. (13 cm) and snowfall is slight (Jaeger 1957). Because of the high rate of evaporation and lack of penetration into the soil, Weather Bureau statistics are not indicative of how much moisture of precipitation is actually available to organisms. Long drought periods are typical, and the little rainfall that occurs is often in the form of short, violent storms or cloudbursts. The ground surface is generally baked hard, and most of the rain runs off; flash-floods are not infrequent (Lowdermilk 1953). Precipitation is slightly greater and evaporation less in the Great Basin. Where rainfall is so slight, dew formation assumes great significance. In the deserts of Israel, dew forms 120–240 nights of the year (Duvdevani 1953).

The yearly evaporation from a pan of water may be 7 to 30 times the actual amount that falls on an area of similar size (Buxton 1923). The high evaporation rate correlates with the low relative humidity which at noon averages less than 25–30 per cent.

There is little cloudiness, and the actually received percentage of possible annual sunshine averages close to 90. Ultraviolet radiation reaches the ground in high concentrations. Winds are more or less continuous.

The mean annual temperature in the Great Basin is approximately 10°C (50°F), but it is over 20°C (68°F) in parts of the desert scrub. Daily maximum summer temperature in the desert is 40°C (104°F) or more. Differences between daily maxima and minima are greater than in any other biome. Frosts are limited to mid-winter; the frost-free period averages more than 280 days. Frost and snow are common, however, in the Great Basin (Kincer 1941); consequently, the Great Basin area is sometimes called the cold desert in contrast to the hot desert adjacent to the south.

The Great Basin is not a single large basin; rather, it is broken up into a number of small ones separated by low mountain ranges running in a north-south direction and seldom exceeding heights of 1800 m (6000 ft). These ranges support piñon-juniper woodland. Water drains from the surrounding hills into these small basins from which there are usually no outlets. High rates of evaporation make the basin lakes very salty or may dry them up to produce alkaline flats.

A characteristic topographic feature of the desert is the alluvial fan of erosion products washed down mountain slopes by the torrential rains. Broad flat basins occur between adjacent mountains. Extensive sand dunes occur in some portions of the desert, and sand and dust storms are spectacular features.

VEGETATION

Desert bushes and shrubs in North America are seldom more than 1–2 meters high and are spaced 3–10 meters apart (Fig. 26-2). Joshua-trees, paloverdes, and saguaros are, however, more conspicuous. The shrubs seldom form a canopy except along washes. The intervening ground between the shrubs is usually a wind-swept desert pavement of either fine texture soil, gravel, or rock, and always with very little humus. The shrubs and bushes have shallow, wide-spreading, many-branched root systems adapted quickly to absorb any surface moisture. There is very little moisture in the subsoil. Stems and branches often bear prickles or thorns and intertwine to form a dense tangle. A rich variety of thorny, succulent cacti occurs in the Western Hemisphere only, and is divisible into tree, cholla, and barrel types. Between the shrubs, a few short annual grasses may grow, but after rains, the ground often becomes thickly covered with a carpet of flowers and grasses that quickly mature, seed, and then disappear in the dry weather that follows.

These desert plants have sclerophyllous adaptations to retard transpiration and survive long periods of drought. Foliage becomes greatly reduced, even absent altogether, during long periods; stems contain the chlorophyll necessary to carry on photosynthesis. Cell walls are thick, highly ligneous, and have thick cuticles. The cell sap increases in osmotic pressure and hydrophilous colloids. Cacti store considerable water in their stems as a reserve for use when there is no water in the soil. Many other kinds of adaptations occur in these xerophytes (Weaver and Clements 1938, Zohary, in Cloudsley-Thompson 1954).

Biotic succession is not conspicuous in the desert because of the low rate of reactions by organisms upon the habitat (Shreve 1942). When the vegetation is disturbed it is usually replaced directly by the same type without intervening seral stages (Muller 1940). Physiographic succession is evident, however, depending upon distances from water channels, differences in elevation, leaching of salts out of the alkali flats, and in sand dune areas. There is considerable variation in the distribution of different species because of local differences in the chemical and physical nature of the soil, soil moisture, and so forth (Shantz and Piemeisel 1924).

PLANT ASSOCIATIONS IN NORTH AMERICA

***Covillea-Franseria* association** (desert scrub): Creosote bush, *Covillea glutinosa,* is generally distributed and with bur sage, *Franseria,* sometimes forms a monotonous, uniform growth on the flat inter-montane plains, relieved only by the larger acacias, saguaros, paloverdes, and mesquites along the washes. The richest variety of vegetation is on the outwash plains and lower mountain slopes, where there is greater penetration and retention of soil moisture. The desert scrub has three faciations (Shreve 1942, Axelrod 1950). The *Mohave desert* to the west is a rolling plain with a monotonous uniform cover of low shrubs, interspersed conspicuously with the curious Joshua-tree. The *Sonoran desert,* sometimes subdivided into Colorado and Arizona deserts (Benson and Darrow 1944), or as many as six sub-units (Jaeger 1957), is much more diversified, with tall shrubs, trees, and succulent cacti of many forms, especially along the washes, and a few grasses. The *Chihuahuan desert* to the east is almost completely separated by mountain ranges from the rest of the desert, and some of the western species are replaced by new ones that come in. The yucca-like sotol is conspicuous (Jaeger 1957).

***Atriplex-Artemisia spinescens* association** (shadscale association); ***Artemisia tridentata-Agropyron* association** (sagebrush association): Shadscale, *Atriplex confertifolia,* and bud sage, *Artemisia spinescens,* as well as other small (less than 1 m high), widely scattered, more or less spinescent, microphyll shrubs are dominant in the southern part of the Great Basin and have contact with desert scrub. Greasewood and a few grasses are important

FIG. 26-1 **Faciations of the desert biome in North America (after Axelrod 1950, Jaeger 1957).**

in some localities. Sagebrush, *Artemisia tridentata,* often occurs in nearly pure stands, but where grazing is limited, several species of perennial grasses, especially wheat grass, *Agropyron spicatum,* become intermixed to form a continuum leading into the bunch grass prairie to the north. Only a few opuntia cacti occur. Sagebrush is widely distributed as a subclimax, because of overgrazing, in the bunch-grass prairie and short-grass plains. Various species of *Artemisia* also extend into central and southern California and together with associated species have been called *coastal sagebrush.* It may be subclimax to chaparral. The original vegetation of these two associations has become greatly modified as result of overgrazing by domestic animals and increased erosion with reduction in grasses and edible shrubs and introduction of exotic species (Fautin 1946, Cottam 1947, Billings 1949).

A *tropical thorn forest* occurs on the west coast of Mexico, in northern Venezuela, and in other scattered localities. It is made up of a dense scrubby growth of small, often thorny and leguminous trees. Cacti are common. Some authors distinguish a thorn forest and a short-tree forest, but there is considerable intergrading between the two (Gentry 1942) as well as with the tropical deciduous forest.

PALEO-ECOLOGY

During early Tertiary, the present desert regions in North America were largely dominated by tropical and warm-temperate forests. Following Eocene, rainfall gradually decreased, and forests were replaced first by grassland, then by desert. Desert began to appear during middle Tertiary on the lee side of high mountain ranges, but did not become extensive until middle and late Pliocene time. The present deserts in North America are therefore of comparatively recent origin.

Desert plants have apparently originated through gradual adaptation to arid climates of more hardy species belonging to all three Tertiary floras. *Artemisia, Atriplex, Eurotia,* and *Suaeda* of the two Great Basin associations are thought to have Arctotertiary affinities. Related species in the same genera occur in the Eurasian deserts at the present time. Species of the desert scrub appear to be derived from

FIG. 26-2 **Joshua trees interspersed through low shrubs of the Mohave desert in California (courtesy U.S. Forest Service).**

the Neotropical and Madro-tertiary floras, and are for the most part unrelated to Eurasian forms. Related species and genera are found, however, in the arid regions of South America. The vegetation of the present Great Basin, Mohave, and Sonoran desert regions was largely woodland and chaparral through much of the Miocene and into the Pliocene. Desert vegetation became differentiated with the increasing aridity of the mid-Pliocene. The Mohave and Sonoran deserts became distinct as cool winters in late Pliocene and Pleistocene restricted the less hardy succulent species to the Sonoran desert. It is probable that the origin and development of deserts elsewhere over the world has followed the same general pattern (Axelrod 1950, Clements 1936).

DESERT SCRUB BIOCIATION

Large mammals, such as the bison and pronghorn, are mostly absent from the desert scrub. The mule deer is present in small numbers both in the desert scrub and in the basin sagebrush, and the mountain lion, bobcat, and badger penetrate to some extent. The most common species of animals are the following (Dice 1939, Huey 1942) although additional species occur farther south in Mexico (Burt 1938, Van Rossem 1945, Baker 1956) (species with asterisks in this and following lists also found in basin sagebrush biociation):

Mammals

*Black-tailed jack rabbit
Desert cottontail
Rock squirrel
Spotted ground squirrel
Round-tailed ground squirrel
*Botta's pocket gopher
Desert pocket mouse
Rock pocket mouse
Merriam's kangaroo rat
Desert kangaroo rat
*Canyon mouse

FIG. 26-3 In the Sonoran desert of Arizona. Saguaro (tree cactus at left), paloverde trees (in middle distance), tree cholla (cactus at right center), organ pipe cactus (upper right), creosote bush (the taller bushes in the foreground), and bur sage (the smaller bushes in the foreground).

Cactus mouse
*Deer mouse
Southern grasshopper mouse
White-throated wood rat
*Desert wood rat
*Coyote
*Kit fox
Gray fox
*Western spotted skunk
Collared peccary
Mountain sheep

In the mesquite vegetation of New Mexico, the mouse and rat populations are highest in May with about 8.5 individuals per hectare (3.4/acre) and with the kangaroo rats the most numerous species. These small desert mammals tend to have larger home ranges than do comparable species in deciduous forest and grassland (Blair 1943). Several of these species extend their ranges well south through the Chihuahuan faciation (Dalquest 1953).

FIG. 26-4 Sagebrush with sparse grass in Nevada (courtesy U.S. Forest Service).

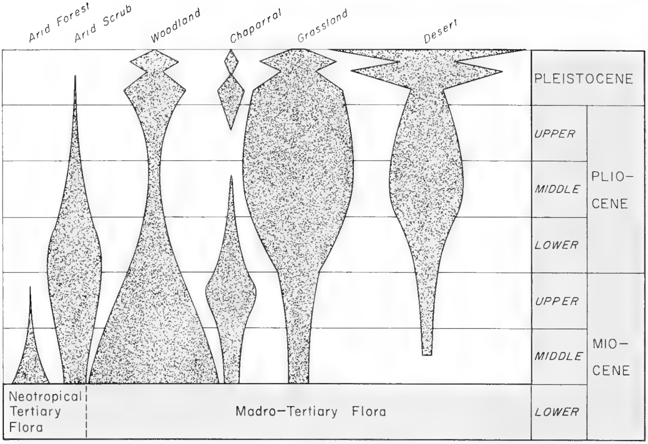


FIG. 26-5 **Changes in the relative proportions of different types of vegetation in the Mohave desert region since Miocene time (from Axelrod 1950).**

Birds

*Red-tailed hawk
Harris' hawk
Caracara
Gambel's quail
Mourning dove
White-winged dove
Ground dove
Roadrunner
*Great horned owl
Elf owl
Lesser nighthawk
Costa's hummingbird
Gilded flicker
Gila woodpecker
Ladder-backed woodpecker
Wied's crested flycatcher
Vermilion flycatcher
Verdin
Cactus wren
Bendire's thrasher
Curve-billed thrasher
LeConte's thrasher
*Crissal thrasher
Black-tailed gnatcatcher
Phainopepla
*Loggerhead shrike
Lucy's warbler
Abert's towhee
*Black-throated sparrow

In addition to these, several species from the deciduous forest-edge, woodland, and chaparral penetrate into the desert. Bird populations are very low in the open desert (0–37 pairs/40 hectares or 100 acres) but may reach 108 pairs per 40 hectares in washes or near water where there is a greater diversity of vegetation (Miller 1951, Hensley 1954, Dixon 1959).

Reptiles

Gopher turtle
Banded gecko
Crested lizard
*Leopard lizard
Chuckwalla
Zebra-tailed lizard
Fringe-toed lizard
Spiny lizards
*Side-blotched uta
Long-tailed uta
Tree uta
*Desert horned toads
Desert gila monster
Night lizard
*Whip-tailed lizard
Western blind snake
Boa snake
Whip snake
Leaf-nosed snake
*Bull snake
Common king snake
Western shovel-nosed snake
Mojave rattlesnake
Diamond rattlesnake
Sidewinder rattlesnake

The list of reptiles is compiled from the studies of Mosauer (1935), Dice (1939), Huey (1942), and Johnson *et al.* (1948). Amphibians are not common, but the red-spotted toad occurs in small ponds. Little quantitative investigation has been made of the invertebrate populations of desert scrub, but grasshoppers and other orthopterans are especially conspicuous (Tinkham 1948), and the scorpion and tarantula spider are much in evidence.

BASIN SAGEBRUSH BIOCIATION

This community inhabits both the shadscale and sagebrush associations. There is considerable overlap of species between the desert scrub and basin sagebrush biociations, as indicated by the species marked with an asterisk in the above lists, but there is a sufficient difference to warrant calling the two areas faunistically distinct. At the subspecies level, the contrast between the two animal communities is more striking. In addition to a strong intrusion of grassland species, the basin sagebrush has the following noteworthy species (Linsdale 1938, Hall 1946, Fautin 1946):

Mammals

Nuttall's cottontail
Pigmy rabbit
Townsend's ground squirrel
White-tailed antelope squirrel
Least chipmunk
Little pocket mouse
Great Basin pocket mouse
Long-tailed pocket mouse
Chisel-toothed kangaroo rat
Ord's kangaroo rat
Dark kangaroo mouse
Northern grasshopper mouse
Sagebrush vole

Rodents, exclusive of ground squirrels and pocket gophers, average about 40 per hectare (16 per acre) in western Utah with deer mice and kangaroo rats most numerous. Ground squirrels are widespread and numerous although sometimes locally restricted. Black-tailed jack rabbits are important constituents of the community and average numbers seen in different plant communities range from less than 0.1 to 0.5 per hectare. The pronghorn was once numerous in the Great Basin sagebrush, but not the bison (Fautin 1946).

Birds

There is greater contrast in the avifauna between the desert scrub and basin sagebrush biociations than in the mammalian fauna. However, more species enter this community from the grassland and forest-edge biociations, such as the Swainson's hawk, prairie falcon, burrowing owl, and horned lark, than venture into the desert scrub. Bird populations are low during the breeding season, averaging only about 25 pairs per 40 hectares (100 acres). The principal avian species in the basin sagebrush in addition to those listed above are (Fautin 1946, Miller 1951):

Sage grouse
Poor-will
Sage thrasher
Sage sparrow
Brewer's sparrow

Reptiles

Collared lizard
Sagebrush lizard
Striped whip snake
Long-nosed snake
Prairie rattlesnake

Lizards are numerous and conspicuous. Counts of only those seen above ground gave an average for the summer season of 6.5 per hectare (2.6/acre). A few amphibians, particularly the western spadefoot toad and western toad, occur near bodies of water (Linsdale 1938, Fautin 1946).

Invertebrates

Actually, only two strata occur in this community, the shrub and ground, since herbs are few and scattered most of the year. In the shrub stratum, arachnids, cicadellids, fulgorids, coccids, chrysomelids, and mirids are most numerous. Grasshoppers feed on the foliage and lay their eggs in open areas of the ground. Arachnids, tenebrionid beetles, and ants are the most conspicuous ground invertebrates. The harvester ant and honey ant build conspicuous mounds, the number of mounds of the former averaging over 15 per hectare (6.2/acre) in the sagebrush community. Invertebrates are most numerous in sagebrush and greasewood and least abundant in shadscale. Maximum populations occur in May on most of the vegetation, after which they decline as temperature increases, but on the greasewoods, which retain their leaves and remain green, populations remain more constant throughout the summer (Fautin 1946).

OTHER BIOCIATIONS

The vegetation and animal life of extreme deserts around the world are impoverished, but in semi-deserts, similar to those in southwestern North America, ecologically equivalent species occur, although they show little taxonomic relationships with each other. These organisms are derived from adjacent, more humid floras and faunas and have many similarities in adjustments and adaptations. Rodents, for example, are generally numerous everywhere. In North American deserts the genera *Dipodomys* and *Perognathus* of the family Heteromyidae are especially important; in the Eurasian deserts, *Gerbillus, Meriones,* and *Dipodillus* belonging to the family Muridae are found; in South Africa *Pedetes,* family Pedetidae, occurs; and in the Australian desert the family Muridae is represented by *Notomys.* All are bipedal in locomotion and have elongated hind legs (Schmidt-Nielsen in Cloudsley-Thompson 1954). It is also of interest that tenebrionid beetles are represented by different subfamilies in different deserts of the world, but, contrary to the prevailing desert colors, these diurnal beetles are predominantly black (Brehm 1896, Buxton 1923, Haviland 1926, Kachkarov and Korovine 1942, Bodenheimer 1953).

Stegmann (1938) recognizes a distinct Mediterranean avifauna of desert grassland, chaparral, and woodland that is best developed in northern Africa but extends north through Spain, Italy, the Balkans, Turkey, and southwestern Asia.

ANIMAL ADJUSTMENTS

The characteristic animals of the desert are the small herbivorous rodents and the reptiles. Large animals, including the carnivores, are relatively scarce, and population levels of the rodents appear determined more by the availability of food and water than by predation. Among birds on the Arizona desert, insectivorous species are most numerous, then seed-eaters, and lastly carnivores (Hensley 1954).

Most adjustments grassland species make to their environment continue to be expressed in the desert and additional ones become conspicuous (Buxton 1923, Sumner 1925, Heim de Balsac 1936, Linsdale 1938, Fautin 1946, Hensley 1954, Schmidt-Nielsen in Cloudsley-Thompson 1954). The two most critical environmental factors are the high temperatures, especially during mid-day, and the lack of water. Reptiles have some advantage in that their scaly skin is adapted to prevent rapid evaporation. Moist skinned amphibians and snails are absent except in the immediate vicinity of springs or other bodies of water.

Animals tend to avoid extreme high temperatures rather than to tolerate them for any length of time. They do this in various ways. The small mammals, snakes, and even insects are largely nocturnal. Birds are active chiefly in the cooler hours of early morning and evening and tend to remain quiet and concealed during the middle of the day. Lizards are the most conspicuous animals during the day. Nearly all animals spend their time above ground in the shade cast by the scattered shrubs or rocks, and it is here that they have their burrows or nests. Bird nests occur most frequently on the east and northeast side of plants, where they are shaded from the hot afternoon sun. The intervening ground, fully exposed to the sun's rays, heats up much higher than the air temperature and may not cool down completely even at night, so that small mammals and other animals scurry quickly from the protection of one bush to another in their travels for food. Ground surface temperatures go well above the upper limit of tolerance of snakes, but some lizards can hold their bodies away from contact with the ground on their long thin legs. Even the grasshoppers come to rest in bushes to avoid the hot ground surface as much as possible. Grasshopper species confined to hot sandy areas have, like the lizards, long slender legs that hold their bodies away from the ground. Many mammals, reptiles, and insects (ants, crickets) burrow deeply into the ground and thereby avoid the surface heat; for example, the burrows of kangaroo rats penetrate 50–65 cm below the surface near Tucson, Arizona (Sumner 1925). On one day when the maximum air temperature in the shade reached 42.5°C (108.5°F), and the temperature of the ground surface was 71.5°C (160.7°F), at a depth of 10 cm in the burrows the temperature was only 40.1°C (104.2°F), at 30 cm 29.8°C (85.6°F), and at 45 cm 27.9°C (82.2°F). The amount of moisture in the air inside these burrows is also more favorable, being 3 or 4 times higher than it is outside (Schmidt-Nielsen in Cloudsley-Thompson 1954). The percentage of mammal species that burrow increases from 6 in forest communities to 47 in short-grass plains, to 72 in deserts. This is in contrast to the decrease in percentage of mammals that are active on the ground level; from 68 to 53 to 28 (Bodenheimer 1957).

Many desert animals are adapted to go a long time without drinking water, but those species that depend on drinking water, which probably includes many of the larger mammals, are restricted to the vicinity of springs, lakes, or ponds. Dew is often a source of water in the early morning. Much of the desert vegetation, particularly the cacti, is succulent and is a source of water to animals. The development of an armor on the plants in the form of thorns and prickles serves as a defense against excessive browsing by animals. The flowers and fruits of such plants as the saguaro are important sources of water to birds and other animals. The blood and body fluids of prey furnish ample water for carnivores. Metabolic water obtained with the oxidation of fats and carbohydrates in the food eaten is apparently sufficient for many species of small size. Even some of the larger game mammals of Africa find green pasture sufficient for satisfying their moisture needs if they can also obtain shade (Vesey-Fitzgerald 1960). Water is conserved in the bodies of birds, insects, and many desert reptiles by kidney wastes excreted as solid uric acid salts rather than as urine. The urine of mammals is more highly concentrated than in non-desert species, and feces are egested in a dry condition, the excess water having been reabsorbed in the large intestine (Schmidt-Nielsen and Schmidt-Nielsen 1952).

After rains sufficient to soak the soil or to refill the shallow ponds, a rapid cycle of events occurs. Herbaceous plants become abundant and bloom. Snails come out of aestivation in the mud. Immature insects and crustaceans become abundant in the water. Termites and ants produce winged forms and mate, and other insects appear in large numbers. Frogs come out of their underground burrows and deposit their eggs; tadpoles hatch quickly, grow rapidly, and metamorphose into adults. Animals previously aggregated around water holes scatter widely over the surrounding country. However, as the rains stop and the ponds again dry up, populations contract sharply, and many species go back into aestivation, sometimes for years, until the next wet period occurs. Not only invertebrates but also birds and mammals largely confine their reproductive activities to the rainy season (Buxton 1923).

In the northern cooler portions of the desert, hibernation over winter is necessary for many cold-blooded forms. Lizards and snakes may hibernate one-half meter or more in sand, under rocks, or in burrows of other animals (Cowles 1941). Rattlesnakes hibernate in natural cavities on hillsides or elsewhere.

Although much of the desert soil is a hard, gravelly pavement, loose soil and sand dunes are not uncommon. Many reptiles have special structural and behavior adaptations to cope with sandy habitats so that a good herpetofauna occurs in such places (Mosauer 1935). The texture and hardness of the soil, its depth, slope, and color influence the niche segregation of small mammals (Hardy 1945). The light gray, yellow, and brown tone of desert soils is reflected in the pale coloration of many desert birds and mammals. Desert animals are generally less heavily pigmented and are smaller in size than close relatives in humid regions (Gloger's rule). It is not certain how much of this is a response to the arid climate (Buxton 1923, Sumner 1925) or high light intensities (Meinertzhagen 1950), and how much is a response to the color of the soil. Deer mice and pocket mice occurring in the White Sands National Monument of New Mexico are very light in color, but a few kilometers away, in the Tularoosa lava beds, their color is very dark (Dice and Blossom 1937). This blending coloration doubtless furnishes protection from the attacks of predators on moonlit nights. Even in humid climates, the dark coloration of animals may be an adaptation to the darker colored vegetation and ground litter (Bowers 1960).

The fish of the desert present features of special interest. The small ponds and pools are widely isolated from each other and are without outlets to the sea. The salt concentration in some of them is high as a result of centuries of continuous evaporation of water. Some spring-fed pools contain only a few dozen or a few hundred individuals, but because of their isolation these individuals have evolved into distinct varieties or species found nowhere else. These various fish populations, however, show a relation to each other. In many cases, particularly in the Great Basin, the ponds are deep holes that persisted after the drying up of large shallow Pleistocene lakes, such as Lake Lahontan and Lake Bonneville. The fish in these ponds are descendants, therefore, of populations formerly widespread throughout the Pleistocene lakes (Hubbs 1940a, Hubbs and Miller 1948).

HUMAN RELATIONS

In semi-deserts, there is production of cattle, sheep, goats, horses, and camels, but the carrying capacity of the land is low. The stock needs to have access to springs, ponds, or rivers which are of course widely scattered. Nomadic primitive people roam the semi-deserts of Arabia, Africa, and Australia in search of pasture for their herds.

Since the scanty rainfall does not wash away the salts, the soil is fertile where irrigation is possible. Vegetable and other crops and fruit can be raised advantageously. Where the ground water table comes close to the surface locally, oases of vegetation occur, even in otherwise extreme desert, and may support small settlements. On the whole, however, man does not find the desert an amenable habitat.

SUMMARY

Deserts, like grasslands, occur in all continents. They develop in areas with very low annual precipitation and generally high temperatures. The vegetation consists of scrubby, sclerophyllous, small-leaved, often widely-spaced shrubs, bushes, or cacti, which are commonly covered with prickles or thorns. Succession is not conspicuous and the prevailing vegetation varies considerably with local soil and moisture conditions. Desert scrub and basin sagebrush biociations are distinguished in North America. These communities commenced to emerge as distinct biotic entities in mid-Pliocene, as organisms became adapted to the increasing aridity of the climate.

The most prominent animals of the desert are small herbivorous rodents and reptiles. Animals tend to avoid extremely high temperatures by becoming nocturnal, spending much of their time in shady places, or burrowing into the ground. Many desert animals are able to go a long time without drinking water, getting what they need from succulent foods and the oxidation of fats and carbohydrates. There is reabsorption of much water from urinary wastes, or uric acid is excreted instead of urea. After periods of rain, there is temporarily a rich expansion of plant and animal reproductive activities. Many reptiles have structural and behavioral adaptations to cope with sandy habitats. There is a general tendency for desert animals to be lighter in color and smaller in size than close relatives in humid regions. Since ponds and lakes are widely isolated, speciation among fishes has developed extensively.

27

Tropical Biomes

Tropical communities and habitats vary from rain forest to desert. The largest continuous mass of tropical evergreen forest lies in the Amazon valley of South America and extends from lower Mexico across northern South America from the Pacific to the Atlantic Ocean. It is interrupted by tropical deciduous forest and savanna, as well as cloud forests in the Andes Mountains. Elsewhere tropical vegetation of various types covers extensive areas in central and western Africa and almost the whole of the Oriental Region. Tropical vegetation also occurs in Australia, New Guinea, and the Pacific Islands.

CLIMATE

The conspicuous features of tropical climate are high, even temperatures throughout the year; uniform lengths of day and night; and seasonal variation in rainfall (Richards 1952). Mean monthly temperatures do not drop below 18°C (64°F) and may rise to 32°C (90°F) or higher. Lowest mean temperatures usually but not always occur during the wet season, but the difference between monthly means may be less than 1°C (1.8°F) and is seldom more than 13°C (23°F). There may be a greater range in temperature at different times of day and night than in mean monthly temperature throughout the year. Mean daily minimum and maximum temperatures are seldom below 10°C (50°F) or above 43.3°C (110°F). As one ascends mountain slopes there is, of course, a drop in temperature.

On the equator, the length of day and night are approximately 12 hours each throughout the year. The seasonal variation increases away from the equator, both north and south, but in an opposite manner. The shortest daylength in the Tropics is about 10.5 hours, the longest about 13.5 hours. In the rainy season, the actual amount of sunshine is low, averaging only five or six hours per day.

In contrast to the uniformity of temperature and the length of daylight is the considerable diversity in rainfall and humidity in different parts of the tropics. Deserts with insufficient moisture to support any vegetation occur at one end of a climatic gradient, while at the other end large areas exist where annual precipitation is between 250 cm (100 in.) and 400 cm (160 in.). Rainfall is largely convectional and results from the cooling of the air that rises from heated land surfaces. Sudden showers are often accompanied by lightning and thunder and may bring a sudden drop of as much as 4°C (7°F) in temperature. These storms commonly occur in the afternoon and may come regularly day after day. Because of this influence of the sun, the rainy season typically occurs when the sun is directly overhead.

Adjacent to the equator, there is considerable rainfall every month in most areas. Between latitudes 3° and 10°–15°, North and South, the two periods of the year when the sun is at its zenith are far enough apart so that there are two rainy and two dry seasons each year. At still higher latitudes there is only one wet and one dry season. What constitutes a dry season is arbitrary, but in the wetter parts of the tropics, it is considered the period when the rainfall is less than 10 cm (4 in.) per month. Under extreme conditions no rainfall may fall during the dry season, while in the rainy season some localities may receive over 100 cm (40 in.) in a single month. During the dry season the soil may become desiccated while during the wet season it may become waterlogged. Grass fires frequently occur during the dry season. The periodic monsoons of India and southeastern Asia result from the outflow of dry winds from a high pressure area that persists in central Asia during the winter and the inflow of moisture-laden winds from the surrounding oceans toward a continental low pressure area during the summer.

In the wettest parts of the tropics, relative humidity is always very high. It seldom drops below 60 per cent of saturation during the hottest part of the day, and may average over 90 per cent for the entire day. On tropical mountains, mean relative humidity rises with increase in elevation until at 1000 m (3300 ft) in some localities there is almost continuous fog and drizzle.

Where rainfall is scant throughout the year (Fig. 20-3), there occurs desert scrub and tropical thorn forest belonging to the desert biome. Climax tropical savanna occurs where rainfall ranges from 90 to 150 cm (36 to 60 in.), but there is a dry season that lasts four or five months. Tropical deciduous forest replaces savanna where the dry season is shorter and less severe. Probably an annual total of 160 cm (64 in.) is the minimum that permits development of tropical broad-leaved evergreen forest. Occasional months may have as little as 6 cm (2.4 in.) but there is no true dry season. In the so-called cloud forests on the mountains, rainfall may not be particularly high, but this is compensated for by almost continuous fog and drizzle, condensation of moisture on all the vegetation, and the very low rate of evaporation.

VEGETATION

Tropical vegetation has been described in detail by Richards (1952). It is essentially a continuum from desert to savanna to tropical deciduous forest to broad-leaved evergreen or rain forest. There is no true lowland climatic grassland in the Tropics except in relatively small areas (Pendleton 1949). Treeless grassland is the result of excessive burning, cultivation, grazing, or unfavorable soil conditions for the growth of trees.

Tropical savanna is, however, extensive. Much

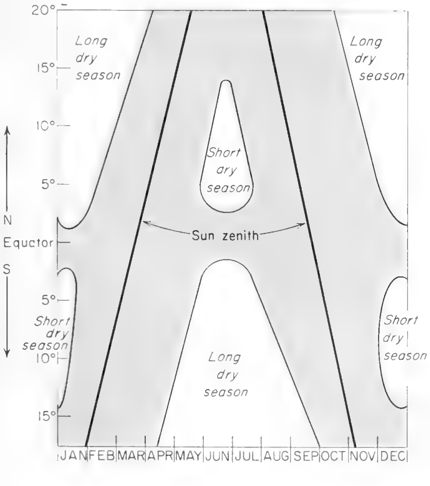


FIG. 27-1 **Wet (indicated by the gray tint) and dry seasons in the Tropics in relation to latitude (from Richards 1952, after E. de Martonne).**

FIG. 27-2 **Tropical rain forest on slopes of Mt. Aoyo, Republic of the Congo (courtesy S. Glidden Baldwin).**

of the savanna in Africa probably represents a climatic climax, but in those areas with a high precipitation, the savanna may be subclimax due to fire, biotic, or edaphic conditions. This latter is the common situation in South America (Beard 1955). Savannas are communities having a *dominant stratum of more or less xeromorphic herbaceous plants, of which grasses and sedges are the principal components, and with scattered shrubs, trees or palms sometimes present* (Beard 1953). The grasses in the savanna may be tall, mid, or short and related taxonomically to those in temperate regions. The grasses and forbs die down in the dry season at the same time that the trees shed their leaves. Sedges are more common than grasses where there is more rainfall. The trees may form a dense narrow stand along rivers—the so-called gallery forest—or may be more or less uniformly scattered through the grassland to give the appearance of a park or orchard (Burtt 1942). The trees are often thorny or xerophilous, crooked in growth, and seldom over 20 m high. There is very little shrubby undergrowth; lianas and epiphytes are scarce. Probably savanna is increasing in extent at the present time because of human influence in destroying or opening up closed stands of the deciduous and evergreen forests.

Tropical deciduous forest, including monsoon forest, is more or less leafless during the dry season, is less lofty than the broad-leaved evergreen forest, but has a higher and more continuous canopy than savanna forest. The forest is rich in woody lianas and herbaceous epiphytes, but not in woody epiphytes. There are usually two tree strata; in the upper stratum the trees are scattered and strictly deciduous. A proportion of the trees in the lower stratum is evergreen, and the number of these broad-leaved evergreen trees increases in both strata as the climate becomes more humid and less seasonal. The deciduous forest is less susceptible to burning than is the savanna, while the evergreen forest is practically immune.

At its height, the tropical broad-leaved evergreen forest is nearly completely evergreen, hygrophilous, 36–55 m (100–180 ft) high, and rich in thick-stemmed woody lianas and in both woody and herbaceous epiphytes. It is commonly called a rain forest because of the continuous high humidity. Seasonal changes are minimal, the aspect being perpetually that of mid-summer. There are usually three strata of trees, one of shrubs and giant herbs, and one of low herbs and undershrubs.

The trees are extremely varied in size, but the dominants tend to be tall, slender, and unbranched except at tops. The bark is thin, smooth, light-colored, and often covered with lichens. Tree bases are commonly provided with plank buttresses or stilts. Palms and tree ferns may be frequent. There is an extreme variety of species; for instance, there are seldom less than 15 and sometimes over 30 species of trees over 30 cm diameter in a single hectare. The Indo-Malayan rain forest is richer in species than either tropical America or Africa; the African forest, the poorest and most uniform in flora.

The undergrowth is not a thick jungle as is popularly supposed. Because of the dense shade cast by the several tree strata, shrubs and herbs are scattered, there is little or no moss on the forest floor, and one can walk through this forest as easily as through one in a temperate climate. It is only where trees are blown down or the forest is undergoing secondary succession that increased light reaches the ground and jungle growth develops.

At Barro Colorado Island in the Panama Canal Zone, light intensity under the dense forest canopy is less than one per cent of the direct rays of the sun, but there are numerous sun-flecks where the intensity is greater. Full intensity of sunlight may reach 20,000 foot-candles. The temperature near the forest floor out of the sun-flecks is nearly constant. In the tree-tops, temperature rises rapidly from a nightly minimum not very different from that on the forest floor to a maximum in the early afteroon. Air movements within the forest are almost nil, and evapora-

FIG. 27-3 **Wildebeest in the tropical savanna of Tanganyika (courtesy S. Glidden Baldwin).**

tion is only about one-half what it is in the open. Animals in the lower strata live in remarkably constant environments, although by climbing into the tree-tops they can enter into environments comparable to those of open plains (Allee 1926, Moreau 1935a).

Tropical America has the richest variety of epiphytes; Africa, the poorest. These epiphytes include lichens, algae, mosses, liverworts, as well as vascular plants. The epiphytes are relatively small in size, have high light requirements, and tolerate a precarious water supply and lack of soil. Often they are more numerous than flowering herbs on the ground. They are important in the community dynamics because their closely overlapping leaves, especially in the bromeliads, enclose large masses of humus and water where mosquitoes and other aquatic animals breed.

On the mountains, the tropical evergreen forest of the lowland gives way to a submontane and then to a montane rain forest. The trees are still evergreen but lower in stature, simpler in structure, and poorer in species. In addition to strictly tropical species, the forest may include many genera and species both of plants and animals that are of temperate origin (Miranda and Sharp 1950, Martin and Harrell 1957). Tree ferns are common. On exposed peaks and ridges, the trees become still more dwarfed and crooked but remain covered with many epiphytic ferns, mosses, and lichens; the whole is aptly, if picturesquely, described as elfin forest. Lianas are scarce in the montane rain forest as compared with the lowland rain forest, the shrub layer is dense, and there are only two tree strata.

Although plant ecologists are gradually working out a detailed classification of tropical vegetation (Beard 1955), we will base our recognition of major communities on the physiognomy of that vegetation which is of importance to animals. Tropical vegetation may be divided, then, into *desert, tropical savanna,* and *tropical forest biomes.* Deserts may be extreme with little or no vegetation present or may be covered with scrub or thorn forest, as already discussed. Savannas represent a forest-edge community in which animals make use both of the trees and intervening grassland to various extent in different species. Animals may well distinguish by their segregation into niches between park savanna and gallery forests and between grassland composed of tall or short bunch-grasses or sedge (Beard 1953). There appears to be no critical dividing line between tropical deciduous and rain forests, but together they give a continuous closed forest contrasting with the open forest or scattered groves of the savanna, and this is of importance to animals. Geographically the tropical forest is separable into American (Dansereau 1947, Leopold 1950), African, and Indo-Malayan units. The family predominance, for instance, of the Dipterocarpaceae in the Indo-Malayan rain forest, and Leguminosae in the American rain forest, and the Meliaceae in some of the west African rain forests is noteworthy. This geographic distinction between the continents in plant life is reflected also in the animal life.

FIG. 27-4 **Zebras in Tanganyika (courtesy S. Glidden Baldwin).**

BIOCIATIONS

Brief attention has already been given to desert and grassland (Table 25-1) animals in tropical regions. We may recognize one or more *tropical savanna biociations* in Africa to include both the more strictly grassland animals and those of the forest-edge. On the basis of differences in bird distribution, Moreau (1952) recognizes Sudanese arid, Somali arid, southwest arid, northern savanna, and southern savanna faunal areas. Among mammals, this community is especially characterized by extensive numbers of wildebeest, zebras, gazelles, antelopes, and lions (Table 24-1) that occur in open country; and the elephant, hippopotamus, rhinoceros, giraffe, wart-hog, and African buffalo that spend considerable time in thickets, swamps, and forests. The habits of many of these animals have been described by Selous (1908), Chapman (1922), and Darling (1960). Moreau (1935, 1937) has worked with the birds. Termites are world-wide in distribution in tropical regions and their large mound nests are conspicuous in some parts of the savanna. Another noteworthy insect of the savanna is the tsetse fly, the vector of a parasite which is a scourge to both man and beast (Buxton 1955). Perhaps another tropical savanna biociation may be distinguished in Australia where a variety of marsupials are characteristic, and there are ecological equivalents for birds and other animals. However, the savannas of South America lack these herds of large mammals so conspicuous in Africa, and this is doubtless due to the savannas of South America being seral in nature and relatively recent in origin. We do not at present recognize a climax savanna biociation in South America. Forest and forest-edge communities have been distinguished for the tropical avifauna of Mexico (Edwards and Tashian 1959).

The animal inhabitants of the tropical forest biome differ so greatly in taxonomic composition on the different continents that they are placed in three different zoological regions. We may therefore designate the *Indo-Malayan, African,* and *American tropical forest biociations.* It would be worthwhile at this point to re-read the discussion of these three zoological regions (Chap. 20) the better to become more acquainted with the more conspicuous kinds of animals that occur in each. Noteworthy studies of the animals of the American tropics are those of Bates (1864), Belt (1873), Beebe *et al.* (1917, 1947), Haviland (1926), Allee (1926), Strickland (1945), Goodnight and Goodnight (1956).

PALEO-ECOLOGY

The tropical forest is of very great age and, along with associated habitats, may represent the center of origin for many modern groups of both plants and animals (Darlington 1957). In past geological ages both on the Western and Eastern Hemispheres, the tropical forest has expanded over great areas when climates were warm and moist and contracted when they became dry and cool. Perhaps, if one were to work out a phylogenetic tree, all other biomes could be traced back in origin to the tropical biota of Mesozoic and Paleozoic times. Arctic communities have been derived from temperate ones, and temperate communities from tropical ones, as organisms became adapted to occupy climatic and environmental conditions that differed more and more from the primitive optimum of tropical regions. This, however, is conjecture.

In the Andes of South America it is apparent that the fauna of the lowland rain-forest (tropical zone) long antedates the elevations of the mountains. After the mountains were formed, they were invaded by those species of plants and animals adapted to the lower temperatures and other differences in habitat moving gradually upward. The animal life

FIG. 27-5 **Lions in the Amboseli Game Refuge, Kenya (courtesy S. Glidden Baldwin).**

of the submontane rain-forest (subtropical zone) is derived almost entirely from the rain-forest at lower elevations. The montane rain-forest (temperate zone) is of more recent origin than the sub-montane forest and consequently derived part of its fauna from it. In addition, the montane forest contains many species of both animals and plants that have dispersed into it from higher latitudes both to the north and south where these species occur in temperate climates at lower elevations. Some very high peaks extend above the tree-line to produce alpine meadow (paramo zone). The fauna and flora of this community are derived almost entirely by lateral dispersal of organisms from extreme southern South America (Chapman 1917).

ANIMAL ADJUSTMENTS

Like the flora, the fauna in the tropical rain forest is very rich in species (Table 27-1). Bates (1864) tells of finding 18 species of swallow-tailed butterflies within 10 minutes' walk of his house in tropical South America. This is to be compared with only about 20 species in all of North America north of Mexico. Apparently, however, the density of individuals in tropical species is low. This is understandable, since the greater the number of species in an area, the greater becomes the competition among them for living space, and each is forced to withdraw

TABLE 27-1 **Diversity of fauna at various latitudes (Dobzhansky 1950).**

Birds		Snakes	
Region	Number of species	Region	Number of species
Labrador	81	Canada	22
New York	195	United States	126
Panama	1,100	Mexico	293
Colombia	1,395	Brazil	210

FIG. 27-6 **A column of army ants moving across the forest floor, and, right, a bivouac of army ants, Barro Colorado Island, Panama Canal Zone (courtesy T.C. Schneirla).**

into those niches to which it is best adapted. The great number of tree and plant species provides a variety of niches, but the availability of niches of each kind is limited so that their animal inhabitants are accordingly reduced in numbers.

In contrast with temperate regions where animal adaptations are so largely concerned with the physical environment and getting food, there needs to be little or no adaptation in the tropical rain forest to winter cold, inclement weather, lack of food, or desiccation. Inter-species competition and struggle, however, is harsh and exacting, and evolutionary forces tend to perfect specializations that enable organisms to fit better into their niches or invade new ones and thus avoid much of the competition and predation (Allee 1931, Mertens 1948, Dobzhansky 1950).

One specialization in this connection is the ability to hang from trees—animals suspended in mid-air are almost inaccessible to attack by predators. Many birds, particularly flycatchers, orioles, and honeycreepers build pendant nests, as do certain solitary wasps. The cocoons of many moths as well as chalcid wasps are suspended by thin threads. Spiders in their webs suspended off the ground are immune from attacks of army ants.

An unusual number of birds nest in holes in trees—trogons, motmots, parrots, toucans, woodpeckers—but this may be to protect them from the

heavy showers as much as from marauders. Stinging ants inhabit the hollow stems of sapling cecropia trees and the swollen bases of leaf petioles of the leguminous tachigalia tree, and for this protection are supposed to defend the trees against the attacks of the leaf-cutting ants.

Many other interesting coactions exist. Collared peccaries on Barro Colorado Island in the Canal Zone make narrow trails through the bushy tangles and dense undergrowth and proceed single-file from one place to another. These well-defined paths are utilized also by the coati, octodonts, and several kinds of marsupials which probably could not otherwise penetrate these areas (Enders 1935). The tapir is a trail-maker in the South American jungle, and the elephant in Africa ploughs its way through the forest by sheer strength. The trails it breaks are followed at later times by the hippopotamus, rhinoceros, buffalo, lion, leopard, hyena, pig, and baboon, which in turn make the trail more passable for lesser forms (Hesse, Allee, and Schmidt 1951).

In contrast with the sporadic occurrences of most species, ants and termites are abundant in the American tropics. The leaf-cutting ants and the insect-eating army ants are especially characteristic (Belt 1873). Termite nests occur in all strata, and the wood-eating habits of these insects hasten the destruction of woody materials. The Hymenoptera, Diptera, and Coleoptera are, in general, the best-represented groups among the insects (Briscoe 1952).

With temperatures high and uniform throughout the year, the developmental period of cold-blooded animals is shortened, and there is a general speeding up of the life-cycle. Insects possessing only a single generation per year in the north temperate zone may complete their life cycle in 3–4 weeks in the Tropics, and may have several generations during the year. On the other hand, high uniform temperatures are depressing for the metabolism and activities of warm-blooded animals, and the pace of their activities is comparatively slow.

Cold-blooded animals, particularly reptiles and arthropods, reach their largest adult sizes in the tropics. In the Amazon forest there is a spider large enough to catch and feed on small birds that are caught in its web (Bates 1864). Some moths have a wing-spread of 30 cm; a millipede reaches a length

FIG. 27-7 **East face of meridian termite nests in Australia. It is characteristic of these nests to be oriented north and south, their broad surfaces presented one to the rising, the other to the setting sun, and the narrow top edge to the hot midday sun (courtesy G.F. Hill and A.E. Emerson).**

of 28 cm, and a slug 20 cm. Birds and mammals, however, are usually smaller than their relatives in temperate regions. Birds also lay fewer eggs in a clutch than they do in temperate regions, but this may be due to the shorter days that tropical birds have for feeding.

Since there is little variation in the duration of light per day throughout the year, photoperiodism is largely absent. In desert regions, the gonads of birds may remain inactive and reproduction inhibited for a succession of seasons during a prolonged drought, but their sexual cycles respond quickly to rainfall, and nesting may begin within a few days after heavy precipitation (Serventy and Marshall 1957). In regions where wet and dry seasons are not developed, bird species may breed throughout the year, although individual birds, after breeding, need a period of rest before they can breed again (Chapin 1932, Baker 1938, Miller 1955). In the evergreen rain forest of Borneo, where precipitation is extremely high, the onset of breeding among mammals appears correlated with the period of the year when precipitation is minimum rather than maximum (Wade 1958).

There is no definite period of dormancy or migration. Movements are largely localized and in quest of ripening fruit or other food supplies. Away from the immediate vicinity of the equator and toward the periphery of the rain forest, where wet and dry seasons become important, the annual cycle of breeding, migration, and other activities becomes more pronounced and important (Baker *et al.* 1936, Davis 1945, Wagner and Stresemann 1950, Moreau 1950).

In dense rain-forest on the equator, the daily rhythm of animal activities is striking. Many naturalists have commented on the great hush of the forest during the middle of the day. The forest appears empty of both birds and mammals. There is an occasional note of a bird, but birds do not have the varied and conspicuous songs that they do in temperate regions. They may be glimpsed in the tree-tops or searched out in the undergrowth moving through the forest in loosely formed groups, each group composed of a few individuals each of several species. These social groups occur at all seasons, although nesting birds must withdraw temporarily from them (Davis 1946). The cicada chorus is often loud and persistent; with the onset of darkness, other orthopteran insects burst into song to which tree frogs, night birds, monkeys, and others add their voices.

Nectar feeding is well developed in some tropical birds, and many flowers depend on birds for their pollination. Hummingbirds are numerous in the Western Hemisphere. Many insects are also nectar and pollen feeding, and these species are largely limited to the tropics. Fruits are an important food for many birds and mammals. Fruit-eating bats are confined to the tropics. Sloths and ant-eaters have powerful claws and long sticky tongues with which they open and plunder the nests of ants. Army ants moving in large numbers over the forest floor in their search for prey often attract a large and varied group of birds, but these birds are after the other insects that the ants stir up rather than the ants themselves (Johnson 1954).

As in most other terrestrial biomes, animals occur in the greatest variety and numbers in the forest floor. Here they are much more numerous during the wet than the dry season. In the Panama Canal Zone during the wet season there are between 4000 and 10,000 animals per m^2, representing 294 species. Of this fauna, mites constitute 25 per cent, springtails

TABLE 27-2 **Stratal distribution of mammals in British Guiana (Haviland 1926).**

Mammal family	Terrestrial species		Arboreal species
	Cursorial	Amphibious	
Marsupiala		*Chironectes* (1)	
Rodentia	agoutis (2) paca (1) spiny rats (2) rats and mice (8)	capybara (1) paca (1)	porcupine (1) squirrels (2)
Edentata	armadillos (4) anteater (1)		sloths (2) anteaters (2)
Carnivora	huntingdog (1)	others (2)	cats (5) raccoon (1) coati (1) kinkajou (1) tayra (1) grison (1)
Ungulata	peccaries (2) deer (2)	tapir (1)	
Primates			monkeys (6) marmoset (1)

34 per cent, ants 25 per cent, and all others 16 per cent. Planaria-like flatworms, a leech, and a land crab are found, although in temperate climates they are usually limited to aquatic habitats. Many different kinds of millipedes are a characteristic feature of the fauna. Centipedes and snails are not abundant (Williams 1941).

Many animals of all sorts have developed an arboreal-living habit although their close relatives outside the tropics are ground-dwellers (Table 27-2). These arboreal species tend to be limited in size and possess opposable toes and prehensile tails. The New-World monkeys have prehensile tails but not the Old-World monkeys and apes. Porcupines, climbing ant-eaters, the coatis, and the kinkajou also possess prehensile tails (Haviland 1926). Some sloths and lemurs hang upside down as they climb around through the branches of the trees. Tree-dwelling snakes and lizards are either long and whip-like or heavy-bodied and with prehensile tails. Parachutes, similar in function to those of the flying squirrels of temperate forests, have developed in such diverse forms as marsupials, lizards, and frogs. Some frogs are entirely arboreal and have sucking discs on their toes to aid in climbing. Some species of frogs lay their eggs in the trees in sacs made of leaves, others glue their eggs to leaves, still others carry them on their backs and the tadpole stage is passed through before hatching. Snails climb to the topmost branches of the trees. Some butterflies fly continuously about the tree-tops and appear never to alight on the ground. There is a group of tree-dwelling tiger-beetles, Odontocheilae. Termite nests located in trees are often connected to the ground by covered passages. Leeches climb into bushes to get onto the bodies of warm-blooded animals more easily. During the wet season, the mosquito *Anopheles gambiae* spends most of its time below 7 meters in the forest, but its close relative *A. africanus* is most abundant at heights of 13 to 25 m. Species of *Anopheles* and *Culex* are mostly crepuscular or nocturnal in activity while the sabethine group and certain *Aëdes* are diurnal (Bates 1949).

Many of the epiphytes, especially the bromeliads, hold small quantities of water within the clump of leathery leaves high up in the trees. These small reservoirs usually contain protozoans, rotifers, flatworms, leeches, annelids, snails, isopods, copepods, ostracods, onychophorans, centipedes, millipedes, scorpions, spiders, a great variety of insects, and small frogs which may spawn here (Haviland 1926).

The true forest inhabitants keep well within the forest shade and, like the monkeys, are quite sensitive to direct exposure to the sun. Animal life is less abundant, however, in the depths of the forest interior than it is on the forest margin. It follows that the fauna is richer both in species and in numbers in the tropical savanna than in the tropical rain-forest itself.

HUMAN RELATIONS

The tropics are the native home of the black or negroid races of man. The death rate of white man in some parts of the humid tropics is increased ten times over what it is in temperate regions, and he can seldom spend more than a few months at a time there without impairment of health and vigor. Relatively little effort is required by the native of the tropics to secure food, and the need for clothing is minimal. The biological environment, however, is harsh and exacting. He must guard against malarial plasmodia, hookworms, and a variety of skin parasites (Dobzhansky 1950).

African natives in tropical savanna are nomads and have herds of cattle, goats, and other animals which furnish them with milk, meat, and blood meals.

This region may some day become a big cattle-raising country if the diseases of nagana and rinderpest can be controlled. Some tribes practice a primitive form of agriculture. Occasional locust swarms devastate both the native vegetation and the cultivated crops.

The monsoon region of India supports a very large population. The land is divided into tiny plots, plowed by donkey, ox, or water buffalo, and cultivated by hand tools. Elephants do some of the heavier work. Tea leaves are harvested from bushes, rice is grown, and teak lumber obtained from the forest. Cattle and goats supply milk.

Natives in the tropical rain forest make their living by hunting and fishing. They live in rude huts made of branches and leaves. Their hunting is done with bows and poisoned arrows, blow pipes, and pits dug in the ground. In better developed equatorial lands they grow manioc from which tapioca and flour are obtained, yams, sugar cane, pineapples, bananas, and cocoa. Cocoanuts are important food in some places. Coffee is cultivated extensively in South America. Sap from which rubber is made was originally collected from scattered naturally growing trees in the forest, but rubber trees are now grown extensively in plantations. The tropics undoubtedly are a potentially rich productive area, but this productivity will not be fully realized until the natives, who are best adapted to live in the area, can be educated and acquire the skills to develop it (Hadlow 1953).

SUMMARY

Noteworthy of tropical climates is the uniformity of temperature and length of daylight throughout the year. Rainfall varies from a distinct seasonal distribution in some regions to constant and very heavy in others. Correlated with the rainfall gradient is a vegetation continuum from desert, to savanna, to tropical deciduous forest, to tropical rain and cloud forests. The biomes recognized are those of desert, tropical savanna, and tropical forest. Aside from deserts there are one or more tropical savanna biociations in Africa and in Australia and the Indo-Malayan, African, and American tropical forest biociations. The tropical forest flora and fauna are of great age and continuity, and it may well be that all other biomes can be traced back in origin to the tropical biota of mesozoic and paleozoic times.

The flora and fauna of the tropical forest is marked by the richness of their species compositions. Correlated with this is the harshness and severity of interspecific competition and predation. On the other hand, except for ants and termites, few species reach high levels of population density. Large herds of ungulate mammals occur, however, in the tropical savanna.

With uniform climate throughout the year, cold-blooded animals may have several generations per year and species of birds, though not the same individuals, may breed during every month. There is no hibernation or period of dormancy, nor is there migration, except in regions of pronounced wet and dry seasons.

Cold-blooded forms, especially reptiles and arthropods, reach a large size in the tropics, but birds and mammals are generally smaller than their relatives in temperate regions. Although animals occur in greatest numbers and variety on the forest floor, many different groups have evolved members largely restricted to the arboreal stratum.

The tropics are the native home of the black races. Originally they made their living by hunting and fishing, grazing of domesticated animals, and a primitive form of agriculture. The tropics are potentially a rich productive area, but this productivity will not be fully realized until disease can be controlled and the natives better educated.

28

Geographic Distribution of Communities:

Marine Biomes

The geographic distribution of organisms in the sea depends on their responses to currents, temperatures, and physical barriers; local distribution is affected by waves and tides, type of bottom, salinity, and depth. Marine ecology is concerned with environmental factors and problems of organismic adjustments quite different from those on land and also different in many respects from those in freshwater. Animals are relatively more conspicuous than plants. Succession is less evident, but such ecological processes as represented by chemical cycles, cooperation and disoperation, food chains, productivity, population dynamics, niche segregation, speciation, and dispersal are fully as important as on land.

Distinct self-contained community units are more difficult to recognize in the sea than on land because of the apparently greater interrelation of benthic species and the freer movement with circulating currents of plankton and nekton. Plankton is everywhere a basic link in food chains, but the general distribution and importance of plankton species in the sea is no more remarkable than that of soil organisms in terrestrial biomes. To consider the entire ocean community as a single biome, as has been suggested by some investigators, is stretching the concept beyond its usefulness. Since we identify biomes by differences in the life-forms and functional adjustments of the conspicuous dominant or predominant organisms, we may properly recognize biomes that occur in the open ocean, on eroding rocky shores, on muddy and sandy beaches, and composing the coral reefs and atolls. Each of these biomes may be subdivided by the taxonomic composition of the predominant organisms into secondary communities equivalent to the biociations that we have recognized on land. Much of the early literature on marine communities has been reviewed by Gislen (1930).

We can only hope in this chapter to present a brief summary of some of the more salient features of marine ecology. For more thorough treatments, the reader is referred to the publications of Sverdrup *et al.* (1942), Ekman (1953), Harvey (1955), Hedgpeth (1957), and Moore (1958).

HABITAT

The marine biocycle is considered to have *benthic* (*bottom*) and *pelagic* (open water) divisions. The *littoral zone* of the ocean shore extends between the limits of high and low tides. The *sublittoral zone* covers the continental shelf to a depth of about 200 m, the approximate depth at which maximum wave action produces any effect. The average depth of the ocean is about 3800 m, but oceanic trenches (hadal zone) extend much deeper; the Marianas Trench in the Pacific Ocean to approximately 11,600 m. The *neritic biochore* is above the continental shelf and is commonly 16–240 km (10–150 mi) wide. The *oceanic biochore* is subdivided vertically with the boundary between the epi- and mesopelagic zones, depending on the extent of effective light penetration.

Tides

The level of water in the ocean rises and falls usually twice each day or at an interval of 12 hours and 26 minutes. In some parts of the world the tides are less regular or there may be but one daily. *Flood-tide* is the period in which the level is rising and covering more and more of the shoreline; *ebb-tide* is the period in which the waters are receding. In the open sea the change in water level is less than a meter, but the change may be much more than this on the shore, depending on its configuration. The Bay of Fundy opens broadly to the sea and tapers to a narrow head landward, and tides may be 6 to 10 or even 15 meters. On the other hand, when bodies of water have only a relatively narrow connection with the sea, as does the Gulf of Mexico with the Atlantic, the range in water level is less than 30 centimeters. Even lakes have a tide, but it is hardly perceptible except in the larger lakes where it may amount to a few centimeters.

Tides are caused by the attraction of the moon and, to a lesser extent, the sun. When the sun's attraction is added to that of the moon, as occurs twice each month at times of full moon and new moon, the fluctuations of the tides are unusually high and unusually low. These are called *spring tides.* When the tidal influences of sun and moon are opposed as happens twice each month, the tides have the least amount of flow and ebb and are called *neap tides.*

Tides have their greatest effect on animals on the seashore, because of the associated pounding of waves and the alternate submergence in water and exposure to the air. However, the organisms appear well adjusted to this rhythmic submergence and exposure (Flattely and Watson 1922, Korringa 1947). For instance, as the stones on which the chiton occurs become exposed, the animals react positively to gravity and negatively to strong light, and move downwards. They travel at maximum speed while the stone is still moist and become aggregated on the damp lower sides of the stones. When the stone again becomes immersed by the returning tide, the animals lose their geotatic orientation, and, since illumination becomes more or less equal on all sides of the stones, they move about at random until they reach the upper surfaces again.

On the other hand some ciliated and flagellated protozoans and diatoms in inter-tidal habitats are active only when the tide is out and become encysted or inactive and attached to surfaces when the tide is in (Fauré-Fremiet 1951). These rhythms in intertidal organisms may persist for days, even when the organisms are placed experimentally under constant conditions (Brown 1959).

Substratum

The pounding action of waves on rocky shore may have tremendous force, estimated in one instance at 15,000 kg/cm^2. Animals occupying exposed rocky shores in the surf belt must be strongly protected and firmly attached (Flattely and Walton 1922). The conical-shaped limpets present a minimum of surface to the waves. Barnacles are protected by heavy shells and grow fast to the rocks, snails and chitons hold themselves by powerful suction apparatus on their feet, mussels like *Mytilus* have a glandular byssus, while some species of sea urchins bore shallow craters into the rock. Advantage is taken of nooks, crannies, and spaces underneath stones and rocks (Glynne-Williams and Hobart 1952). Large depressions in the rock retain water at ebb tide to form tidal pools and thus may contain the more delicate species because of the protection they afford. The various sea weeds absorb some of the wave shock for the animals living with them. The shape, form, and size of corals, sponges, and other colonial types are affected by the amount of wave action to which the animals are exposed. A shell of the *Mytilus* mussel may weigh 58 g where the animal is exposed to a heavy surf but only 26.5 g in more quiet waters.

Sandy beaches occur only where the force of waves is reduced by being spread over a more gentle slope. Even here, especially during storms, the sand makes a very unstable substratum and not many animals except mollusks and some of the echinoderms can keep from being smothered or buried. Mud bottoms occur only in relatively quiet waters. Burrows made in mud hold their form better than in sand, so larger populations of animals can occur in mud.

The sea-floor at greater depths is covered with a variety of sediments. *Terrigenous* deposits of mineral and organic matter derived from the land and from the littoral and neritic biochores are relatively rich in nutrient substances and extend into the bathyal zone. All other deposits on the sea-bottom are *pelagic,* being derived, in part, from the skeletons of dead plankton and other organisms. In the long slow journey of these dead organisms to the bottom of the sea, much of the organic matter decomposes, releasing carbon dioxide, nitrates, phosphates, and the many other elements in the composition of the protoplasm. Even various amounts of skeletal material may dissolve, but enough of the organisms reach the bottom to create a substratum of loose flocculent

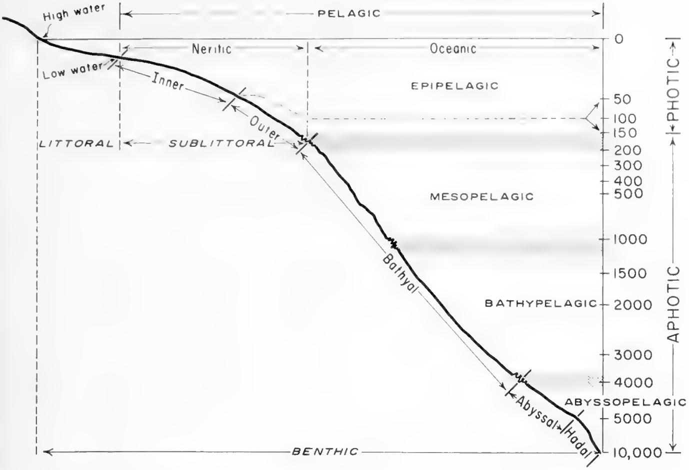


FIG. 28-1 **Subdivisions of the ocean biocycle (Hedgpeth 1957).**

ooze and to furnish food for the living animals that spend their lives in this habitat.

Pelagic deposits that contain less than 30 per cent of organic remains are known as *red clay*. These deposits are the most widely spread of all, especially at the greater depths of the ocean. They are probably derived from wind blown desert dust, terrestrial volcanic dust, and submarine eruptions. The very hard earbones of whales and teeth of sharks are regularly found in red clay. Animal life is scant, consisting only of shellless holothurians and worms, probably because of the poor nutrient content and great depth.

Organic deposits are either calcareous or siliceous, the former being derived from the shells of foraminiferans, small pelagic mollusks, or flagellate coccolithophorids, and the latter from skeletal material of diatoms and radiolarian protozoans.

Pressure

There is an enormous increase in the pressure of water upon the bodies of animals at great depths. This is not, however, an important limiting factor in the vertical distribution of animals in general, as internal pressures closely counterbalance external pressures and life is known to exist at the greatest depths. Adjustments of internal pressures are not so rapid, however, to prevent injury in many species that are dredged at great depths and quickly hauled to the surface. Furthermore, individual species have different limits of pressure tolerance.

Temperature

The temperatures of surface waters vary between the freezing point (—1.9°C) in polar regions and 25°–30°C in the tropics. Seasonal variations are small in polar and tropical waters but somewhat greater in the temperate zones.

Temperature varies with depth, more so in the tropics than elsewhere. At 60°N latitude in the Atlantic Ocean, the mean temperature of the warmest and coldest months at 0 meter is about 10°C, while at a depth of 2000 meters it is 3.5°C. On the equator the temperature at 0 meter is approximately 26°C, at 200 meters 13°C, at 400 meters 7.5°C, at 1000 meters 4.5°C, and at 2000 meters 3.3°C (Ekman 1953). This temperature decrease, known as a thermocline, is a permanent feature of the tropics. A permanent thermocline also exists at mid-depths in temperate and subtropical waters. Superimposed upon it is a seasonal thermocline that develops near the surface during summer and is destroyed in autumn and winter when vertical mixing creates a layer of relatively uniform temperature in the upper 20 to 300 meters.

Currents moving towards the poles from the equator consist of warm water, and currents moving in the opposite direction of cold water. Cold waters flowing towards the equator tend to be deflected to the right and hence bathe the North Atlantic coast of North America and the North Pacific coast of Asia. In the southern hemisphere they come into contact with the west coasts of both South America, Africa, and Australia. Warm waters, on the other hand, bathe the west coasts of Europe and North America and the east coasts of Australia, Africa, and South America.

Organisms living in the intertidal zone on the shore are ordinarily exposed to great variations of temperature twice during each day as they are alternately flooded by the tides and exposed to the air and direct solar radiation. Unusually severe cold spells during the winter have been known to produce extensive mortality of fish and invertebrates in shallow waters off the coasts of Texas and Florida (Gunter 1941). On the other hand, one of the characteristic features of the deep-sea habitat is its low and almost constant temperature.

Light

The character of the radiation, as well as its intensity, varies with depth. Even in the clearest waters and at maximum radiation, the red, orange, and ultraviolet are absorbed in the first 20 m. Green, yellow, and blue wavelengths penetrate farther, depending on the water color. When the sun is not at the zenith, light penetration is reduced, and the maximum penetration in the winter at high latitudes is much less than during the summer (Clarke 1939, Jerlov 1951).

The *compensation point,* or the depth at which the amount of oxygen released in photosynthesis by algae just balances the oxygen needs of the plants for respiration over 24 hours, has been found to vary during the daytime between 1 and 100 m, according to the locality, turbidity, and season. The upper illuminated layer where photosynthesis exceeds respiration is often called the *photosynthetic zone* (Harvey 1955).

Salinity

The salinity of sea water varies from place to place depending largely on the amount that it is diluted by the inflow of fresh water from rivers or melting glaciers or the amount that it is concentrated by evaporation. The Red Sea, for instance, has a salinity of 40°/00 (40 g dry salts in 1000 g sea water) while in some polar seas the salinity is less than 30°/00. The average salinity of the oceans as a whole is commonly given as 35°/00 of which the chloride ion constitutes about 19°/00 and the sodium ion a little over 10°/00. The various major salts occur nearly everywhere in definite and constant proportions. As one would expect, the pH of sea water is high, averaging about 8. There is some similarity in relative proportions and concentrations of the various ions in sea water and in the blood or body fluids of many invertebrate organisms. This may indicate that the sea is the habitat in which living forms first evolved.

The contrast in salinity between sea water (35,000 ppm) and fresh water (15–660 ppm) requires important differences in physiological adjustment of organisms to occupy these two habitats. The problem is one of osmotic regulation (Black 1951). Most marine invertebrates are poikilosmotic in that they are nearly isotonic with sea water, they are highly permeable to water, and gain or lose water according to the concentration of the medium. A few marine segmented worms, flatworms, and crabs and all marine fish and mammals have at least some internal osmotic regulation and tend to be homoiosmotic. All except the elasmobranch fishes maintain body fluids hypotonic to sea water in various ways. The skin has decreased its permeability to the free movement of water back and forth, the necessary water is obtained by swallowing, surplus salts are secreted outside the body, especially through the gills, and there is a general decreased function or atrophy of water secreting organs such as the kidneys. The practical absence of insects and amphibians from the sea is largely due to their inability to secrete salts outwardly. The high osmotic concentration found in elasmobranchs is the result of huge quantities of urea retained in the body tissues and fluids.

Fresh-water organisms, in contrast to marine forms, maintain body fluids hypertonic to the surrounding medium by excretion of water through contractile vacuoles in lower organisms or highly functioning kidneys in higher ones, active absorption of salts from the surrounding water by special cells in the gills, and reabsorption of salts from the urine. There is no swallowing of water, as sufficient amounts are absorbed by osmosis through the gills and mouth surfaces and incidentally with feeding.

Probably the most extensively utilized of the dissolved substances in the sea are the nitrogen compounds (nitrates, nitrites, ammonia salts), phosphates, calcium salts, and silicates. Nitrates and phospates are particularly important as nutrient material for phytoplankton. Calcium is required in large

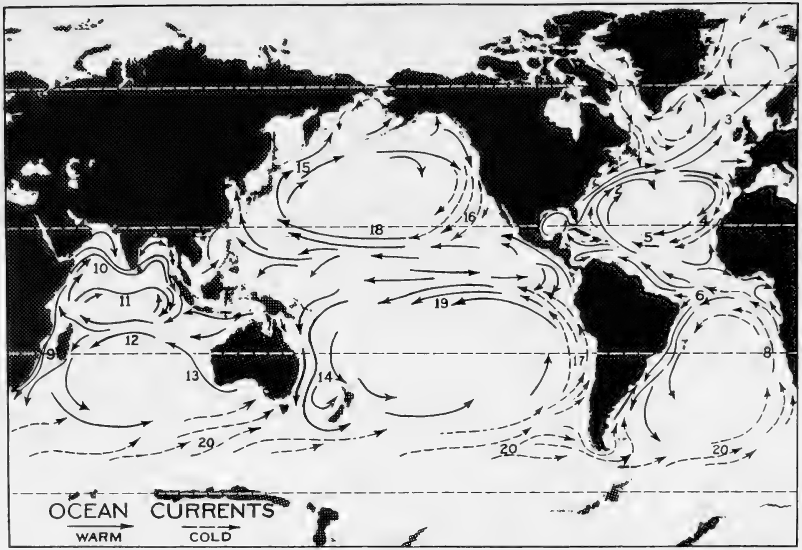


FIG. 28-2 Surface currents of the oceans (after Huntington and Carlson 1934).

1. Labrador Current.
2. Gulf Stream.
3. North Atlantic Drift.
4. Canaries Current.
5. North Equatorial Current.
6. South Equatorial Current.
7. Brazil Current.
8. Brnguela Current.
9. Mozambique Current.
10. Monsoon Drift.
11. Indian Counter Current.
12. Equatorial Current.
13. West Australian Current.
14. East Australia Current.
15. Japan Current.
16. California Current.
17. Peru Current.
18. North Equatorial Current.
19. South Equatorial Current.
20. West Wind Drift.

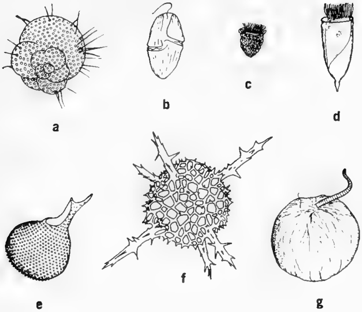


FIG. 28-3 **Characteristic holoplankton (Sverdrup *et al.* 1942). (A) Protozoa: a) foraminifera *Globigerina*, b) dinoflagellate *Gymnodinium*, c) tintinnid *Stenosomella*, d) tintinnid *Flavella*, e) radiolarian *Protocystis*, f) another radiolarian, g) dinoflagellate *Noctiluca*.**

amounts for the shells of mollusks, the skeletons of corals, some protozoans and worms, certain algae, the other organisms and may be precipitated out of the water by bacteria. Silicon is required by sponges, some protozoans, and the phytoplankton diatoms.

These salts keep cycling through the ecosystem, but additions to the supply come continually from the land, being washed into the oceans by the rivers. Neritic waters are especially fertile and support a great mass and variety of animal life because of this land drainage and the pattern of water circulation on the continental shelf. Biological productivity decreases progressively from shallow waters over the continental shelf, to deeper waters, to the open ocean, but is also high over offshore banks and in areas of upwelling. Substantial amounts of nitrogen salts are also swept out of the air by precipitation, and there is nitrogen-fixation by bacteria.

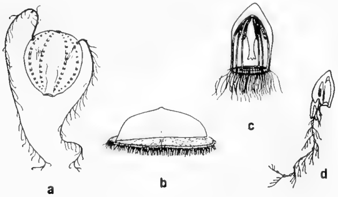


FIG. 28-3 **(B) Coelenterates and ctenophores: a) comb-jelly *Pleurobrachia*, b) siphonophore *Velella*, c) jellyfish *Aglantha*, d) siphonophore *Diphyes*.**

It is of interest that atoms of phosphorus, nitrogen, and carbon occur in sea water in ratios of 1:15:1000 and in plankton in ratios of 1:16:106. This means that there is an overabundance of carbon available in the sea for absorption by the phytoplankton, but phosphorus and nitrogen may be limiting for further increases in the population of organisms (Redfield 1958).

Oxygen

The oxygen supply of sea water comes by diffusion from the air at the surface and from photosynthesis of green plants down to the compensation point. It is continuously used at all depths in respiration of animals and plants and in the decomposition of organic matter.

The oxygen content of sea water (Hedgpeth 1957) is seldom limiting for the occurrence of animals, except in the deeper waters of the brackish Black and Caspian Seas where it is practically absent. Oxygen concentration is especially high on shores where there is splashing of waves. Surface waters of the Atlantic Ocean commonly have 4.5 to 7.5 cc/1 and abyssal regions may run over 5 cc/1. Oxygen is somewhat less abundant in the Pacific and Indian Oceans. Oxygen may be reduced to lower concentrations between 100 and 1500 m, because of its use in animal respiration and in decomposition, than at lesser depths where there is photosynthesis or at greater depths where the abundance of animals is greatly diminished.

Marine animals have a variety of mechanisms and adaptations for respiration (Flattely and Walton 1922). Greatest difficulties occur in shore animals at low tide when they are exposed to the air, but the need for oxygen at this time is decreased in many forms by curtailment of activity. Some crabs, barnacles, snails, and fish have become almost amphibious in being capable of respiring in air, although at reduced rates, as well as in water. Pure mud bottoms may present anaerobic conditions a short distance below the surface, but mud bottoms mixed with sand contain an abundant and diversified fauna.

PLANKTON

Composition

The plankton of the sea includes a great variety of forms, even more than in fresh water (Biglow 1926, Hardy 1956). Rotifers, however, are uncommon in marine plankton and cladocerans are much less important.

The nannoplankton consists mostly of flagellates, algae, bacteria, and a few fungi. The bacteria are largely *periphytic*, in that they are attached to the surfaces of floating plants, animals, and to particles of organic detritus. Very few occur freely suspended in the water (Harvey 1955). Bacteria occur at all depths but are especially abundant in or close to the bottom. They are generally more numerous in the winter than in the summer.

The green phytoplankton is composed primarily of diatoms, dinoflagellates, and small unarmored flagellates, but several other kinds of algae are present and occasionally important. The dinoflagellates *Noctiluca* and *Ceratium* are luminescent and in some regions may give a glow at night to the entire sea. Bioluminescence is not limited to these organisms, however, but occurs also in various forms of bacteria, radiolarians, sponges, coelenterates, ctenophores, nemertineans, worms, crustaceans, brittlestars, mollusks, balanoglossids, tunicates, and fish (Harvey 1952).

The most important groups of protozoan zooplankton, other than the green flagellates which are usually considered with the phytoplankton, are the rhizopod Foraminifera, the actinopod Radiolaria, and the ciliate tintinnids. They may be enormously abundant at times.

Among the Coelenterata, many hydrozoans have medusae and larval floating stages in their life cycle, but only the siphonophores, the best known example of which is the Portuguese man-of-war, are pelagic throughout their life cycle (*holopelagic*). The true jellyfish of the class Scyphozoa are often conspicuous and ctenophores of the related phylum are often abundant. Some of these forms are so large they are called *macroplankton*.

The various phyla of worms are represented in the plankton by only a few forms, of which the chaetognath *Sagitta* or arrow worm and the polychaete *Tomopteris* are often abundant. Many benthic worms, however, produce larvae that are temporarily part of the plankton (*meropelagic*).

Many molluskan and echinoderm species are meropelagic and it is by means of their larvae that heavy, slow moving benthic forms become widely dispersed. Two groups of snails are holopelagic: the heteropods that inhabit tropical and subtropical waters and the pteropods which occur in cold waters and are important food for whalebone whales.

Crustaceans form one of the principal groups of the net plankton, and of these the holopelagic copepods are by far the most abundant (Digby 1954). *Calanus finmarchicus* is one of the most noteworthy species and is the principal food of the commercially important herring fish. Other important crustaceans that enter the plankton either as larvae or adults are ostracods, cumaceans, amphipods, mysidaceans, euphausiaceans, decapod shrimps and prawns, and stomatopods. Many of these forms are also benthic or nektonic during a part of the life cycle.

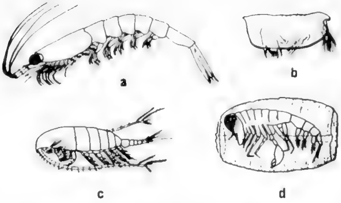


FIG. 28-3 **(C) Crustaceans: a) euphausiid *Euphausia*, b) ostracod *Conchoecia*, c) copepod *Calanus*, d) amphipod, *Phronemia*, in empty mantle of the pelagic tunicate *Salpa*.**

Among the chordates are the remarkable and sometimes abundant tunicates. The eggs and immature stages of many fish are pelagic in that they absorb just enough water shortly after being spawned to have almost precisely the same density as the surrounding water. The eggs of skates and rays, some of the sharks, and some other fishes, such as the herring, however, sink to the bottom where they remain until they hatch.

Flotation mechanisms

The specific gravity of sea water is 1.02 to 1.03, while that of naked cells or protoplasm varies from 1.02 to 1.08. The specific gravity of the entire

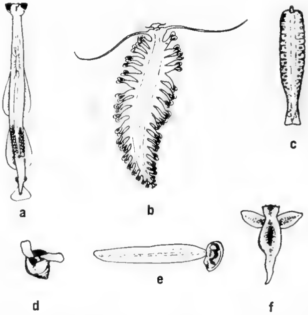


FIG. 28-3 **(D) Miscellaneous: a) arrow worm *Sagitta*, b) annelid *Tomopteris*, c) nemertean *Nectonemertes*, d) pteropod mollusk *Limacina*, e) tunicate *Oikopleura*, f) pteropod mollusk *Clione*.**

organism may be considerably higher if it possesses a skeleton or shell.

Organisms have various devices to remain afloat, aside from swimming: absorption of large amounts of water to form jelly-like tissues or sap, storage of gas or air bubbles within the body, formation of lightweight fat deposits in the body or oil droplets within the cells, increase of surface area in proportion to body mass thereby increasing frictional resistance. Increase in the relative amount of body surface is achieved by decrease in size, flattening, attenuation of body form, extensions of body parts as antennae, spines, tentacles, or cerci, surface hairs or tubercles of various sorts, surface sculpturing, or formation of colonies (Marshall 1954, Davis 1955). These devices result in many strange shapes among plankton organisms. When the organisms die, the protoplasm disintegrates, special flotation mechanisms are usually destroyed, there is a loss of swimming movements, and what is left of the organism sinks to the bottom.

Abundance

The actual abundance of plankton varies greatly from place to place and from one season to the next. Smaller species tend to be more numerous than larger ones. The mean annual abundance of diatoms is commonly in the tens of thousands per liter and for shorter periods during the year algal blooms may increase the population to hundreds of thousands of cells per liter (Ricketts and Calvin 1948). Zooplankton is, however, much less abundant. It has been repeatedly noted that large populations of phyto- and zooplankton do not occur in the same place at the same time. Various explanations have been offered: one, that it is due to the feeding of the zooplankton on the phytoplankton (Harvey 1934), and another, that it is due to the phytoplankton, when abundant, producing conditions that are inimical or toxic to the zooplankton (Hardy and Gunther 1935).

The total net zooplankton per unit volume of water is some 16 times more numerous in the neritic coastal waters off the Atlantic coast of North America than in the Sargasso Sea (Clarke 1940). The abundance of plankton is generally higher in cold than in warm ocean waters, correlated with the greater amount of phosphate present in colder waters (Harvey 1955). Annual productivity is probably less in cold waters, however, because there are fewer generations per year. Cold-water plankton tend to be of larger individual size. There is generally a greater variety of species in most taxonomic groups in warm waters than in cold. Abundance of plankton responds to, and has an effect on, the chemical content of the water.

Yearly cycle

In general, winter is characterized by minimum levels of plankton. Nitrogen and phosphorus salts increase in surface waters because of the decomposition of organisms that have died during the preceding months, to the lesser absorption by phytoplankton, and to the greater mixing of waters from various depths accompanying the loss of thermal stratification. During the spring, as the result of increasing light, reduction of vertical turbulence of the water, and rising temperatures, the phytoplankton increases to a maximum for the year. In temperate and boreal regions the phytoplankton consists largely of diatoms. The zooplankton at this time abounds in immature stages.

By summer, nitrogen and phosphorus become diminished in the surface waters because of their use by phytoplankton and lack of replenishment from greater depths with the re-establishment of thermal stratification. Phytoplankton consequently declines rapidly, lacking nutrients and being consumed by the increasing zooplankton population. Zooplankton reaches its maximum during the summer but as it exhausts its phytoplankton food supply, it also declines. Decomposition of dead plankton in shallow waters and the destruction of the seasonal thermocline with vertical mixing of waters in the open ocean again returns nitrogen and phosphorus to surface in the autumn and this usually allows a second smaller maximum of plankton to develop.

High arctic seas usually have a single maximum of short duration in the summer. In the tropics, on the other hand, there is generally no conspicuous peak, although plankton tends to be more abundant during the winter months (Bogorov 1958). In the Indian Ocean, physical oceanographic changes associated with the monsoons create a seasonal plankton cycle.

Diel movements

Many zooplankters vary in the depth at which they are most highly concentrated at different times during the 24-hour diel cycle. The daily movements to the surface waters at night and to greater depths during the day is especially marked in the copepods (Clarke 1934), and occurs in euphausiaceans, mysidaceans, amphipods, ostracod and decapod larvae, pteropods, chaetognaths, polychaetes, siphonophores, and tintinnids. Even some nektonic animals, such as herring and squid, show vertical diel migrations. Most phytoplankton are confined to the upper lighted zone, although dinoflagellates have been shown to have short, vertical, daily movements in response to light (Hasle 1950). The vertical movements of these organisms and of small fish are probably responsible for the shifts in the position of the deep scattering layer evident in the reverberation of high frequency sound waves sent out from the surface (Eyring *et al.* 1948, Backus and Barnes 1957).

NEKTON

Mollusks, fishes, birds, and mammals make up the nekton of the sea. Mollusks are represented by the squids; fish, by the sharks, flying fish, herrings, mackerels, as well as many others including numerous varieties of small species; and mammals, by the seals, porpoises, dolphins, and whales. The distribution of fish is irregular, but in general they occur more abundantly in neritic waters than in the open ocean. Likewise they are much more numerous in the epipelagic than in lower strata. Most pelagic fish, except sharks, possess a swim-bladder useful for maintaining hydrostatic equilibrium at the depth where they occur; those fish that lack one are commonly bottom forms (Marshall 1954). In Arctic waters, fish are less abundant, and mammals relatively more important, than is the case farther south.

Birds, like many other marine animals, are more numerous in the neritic biochore than in the open ocean. In the oceans far from land occur only penguins, albatrosses, shearwaters, and petrels, and even these species become more common shoreward. Other marine species in neritic waters are tropicbirds, pelicans, gannets, boobies, cormorants, frigatebirds, ducks, gulls, terns, skimmers, auks, and murres. These marine birds may spend many days or weeks feeding and travelling over the water, but all must search out some shore, cliff, or isolated island on which to nest. Here they sometimes concentrate in enormous numbers during the nesting season because of the limited number of suitable nesting locations available.

BENTHOS

Benthos is of much greater variety in marine than in fresh-water habitats. These animals are very abundant in the littoral zone and decrease in numbers with depth until only scattered individuals are found in the deep ocean trenches. Benthos consists of *sessile* forms, the sponges, barnacles, mussels, oysters, crinoids, corals, hydroids, bryozoans, and some worms; *creeping* forms such as crabs, lobsters, certain copepods, amphipods, other crustaceans, many protozoans, snails, echinoderms, some bivalves, and some fishes; and *burrowing* forms including most clams, worms, and some crustaceans. Sessile and creeping forms are often grouped as *epifauna* and the burrowing forms as *infauna*. Epifauna in the littoral zone decreases in variety toward the Poles since it is subjected to cold and ice erosion, but the species composition of infauna remains about the same.

OCEANIC PLANKTON AND NEKTON BIOME

This biome is characterized by the predominance of organisms possessing life-forms adapted to keep them afloat. Plankton and nekton predominate, although the deep-sea benthos may also be considered as belonging to this biome. Seasonal aspection may bring drastic changes in species composition, especially in plankton. Dominance, in the sense used for terrestrial communities, probably does not exist, except possibly in the Sargasso Sea where the floating vegetation establishes the habitat. The ecosystem is self-contained, however, since energy is derived from the sun and nutrient material continues to recirculate with little or no dependence on terrestrial resources.

The *Sargassum* community of the Atlantic Ocean is of special interest. The floating *Sargassum* alga accumulates and is held within a limited area by circular ocean currents. This plant belongs to the intertidal zone of the Caribbean islands but is torn loose in large amounts along with attached animals during the hurricane season. It continues to grow thereafter, but does not reproduce. The fauna that it contains is a truly littoral one, rather than pelagic, but because the alga accumulates in fresh amounts as fast as old plants die, the animals reproduce and maintain a continued existence far from any shore.

Composition and characteristics

The species composition of this biome varies consistently with depth so that a series of overlapping secondary communities may be recognized (Murray and Hjort 1912, Ekman 1953, Marshall 1954, Bruun in Hedgpeth 1957).

The *epipelagic community* or stratal society has the greatest abundance of plankton, nekton, and birds as already described. The aquatic animals are generally colorless, transparent, or of a blue cast.

In the *mesopelagic community* the fishes are usually small, laterally compressed, often silvery or grayish in color, with very large or telescopic eyes, and usually provided with luminescent organs. Some velvety black or brown fishes also occur here. Invertebrates are reduced in number and variety and tend to be reddish in color. Since red rays do not penetrate to the depths where these animals live, they are essentially invisible.

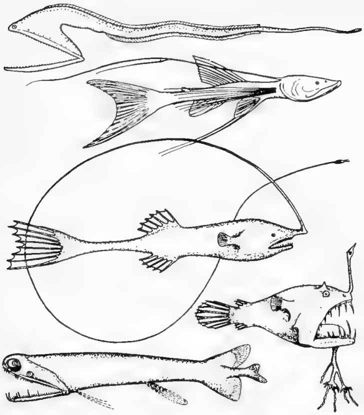


FIG. 28-4 **Representative deep-water fishes (Sverdrup *et al.* 1942).**

The *bathy- and abyssopelagic communities* are considered as one. The fishes are slender and dark-colored. Pelagic invertebrates include a few endemic species of radiolarians, jellyfish, ctenophores, nemertinians, ostracods, copepods, amphipods, euphausiaceans, mysidaceans, shrimps, and squids. Red color is more common than at intermediate depths. Benthic animals commonly have flat bodies, very long legs, or other means of distributing their weight over the loose, flocculent ooze. Many species rise above the ooze on stalks. The fragile glass sponges, long-stemmed crinoids, and long-legged crabs are possible only in very quiet waters that occur at great depths. Skeletons of all animals are fragile because of the difficulty of forming lime at low temeperatures. Abundance decreases with depth, but even at 8300 m in the hadal zone, some twenty species have been found, chiefly holothurians, polychaetes, and sea anemones.

Bioluminescence is exceptionally well developed among deep-sea forms. In some invertebrates, light-producing organs are scattered over the body. In other invertebrates and in pelagic fishes, there are special luminescent organs. It is estimated that two-thirds of the bathypelagic fish species and over 96 per cent of the individuals are luminous. Although several species of organisms occurring in surface waters are luminous, bioluminescence is more highly developed in the twilight zone, between 300 and 800 m, and occurs at still greater depths in the complete absence of natural light. The adaptive significance of bioluminescence is highly speculative. It may serve, in part, for attracting and seeing prey. Luminescent display may also serve for species and sex recognition as does color in many surface animals. Joined with this bioluminescence is often the development of large eyes and special structures to permit vision at the very low light intensities that are produced. Perhaps as compensation for the difficulties of vision is the extensive development of antennae on some crustaceans and the very long rays in the fins of some fish which may serve for contact reception. In those fish where the eyes are small there is a reciprocally large development of olfactory organs.

The benthos and pelagic forms of the greater depths are doubtless derived from intermediate-depth forms, and these in turn from forms occurring on the continental shelf. Species have come to live in the deeper waters only as they became progressively adapted to this rigorous habitat. Relatively few forms have reached the hadal zone.

The deep-sea habitat has existed relatively unchanged since very early geological time except for the increasing deposition of bottom sediments and for some fluctuations in temperature. This uniform habitat has allowed some very ancient forms to persist to the present time. The recently discovered coelacanth fish *Latimeria,* the mollusk *Neopilina,* and certain crustaceans belong to taxonomic groups that supposedly became extinct many millions of years ago. The examination of deep-sea bottom cores will doubtless give us information as to what kinds of animals were present in past ages. Determination of ratios of different oxygen isotopes and of different minerals in the composition of the fossil skeletons in these cores may make possible the determination of water temperatures and salinities at the time these fossil organisms were living (Ladd 1959).

Food chains

As in aquatic and terrestrial communities, bacteria in the sea are largely responsible for the final decomposition of excreta and dead bodies to make their essential nutrients available for reabsorption by the green phytoplankton (Ketchum 1947, Harvey 1955).

Nitrogen and phosphorus are least concentrated near the surface of the ocean, since this is the stratum in which they are most rapidly absorbed by the photoplankton. Excreta and dead organisms sink during the process of decomposition, so nitrogen regeneration is most evident at depths of 500 to 1500 m.

The organic matter that remains undissolved accumulates on the sea bottom. Numerous species of invertebrates depend on it for food and on the bacteria that it contains (ZoBell 1952). The deep-sea fishes feed on these invertebrates or are carnivorous on other fish. Many of them have very wide mouths, distensible stomachs, and formidable teeth. In addition to these food coactions, it is also likely that many deep-sea fish and larger invertebrates undergo vertical migrations so that they obtain food by preying on living organisms at more moderate depths. Much that is known about the life histories of these deep benthic species has been summarized by Marshall (1954).

Especially fertile regions of the open ocean occur when there is deep mixing of waters by *turbulence* and *upwelling*. Vertical water currents bring nutrients up to the surface from intermediate depths where they had accumulated. Prominent regions of upwelling occur around the Antarctic continent, off the coasts of California, Peru, and Somali, and off the west coasts of both north and south Africa.

The net zooplankton feed predominantly on the nannoplankton, probably including bacteria, and on the phytoplankton (Clarke 1934). Particulate organic matter, only partially decomposed, may also be important. Most animals depending on these small organisms and organic detritus have various filter-feeding mechanisms for straining food out of the water. They do not actively search and catch individual items through directed actions. Invertebrate animals may also be able to absorb some essential salts and dissolved organic compounds to build their skeletal structures and for general metabolism, but there is considerable controversy on this point (Collier 1953).

The baleen or whalebone whales (Mysticeti) are toothless but possess large plates in their mouths that strain out the plankton (especially copepods, euphausiaceans, mysidaceans) that they use as food. Only occasionally are small fish or other invertebrates ingested. Some whales reach tremendous proportions, and the differential in size between these animals and their food is one of the most remarkable in the animal kingdom. Much more common is the feeding on plankton by squids, the young stages of most fishes and such adult fishes as sardine, anchovy, menhaden, herring, and mackerel. The menhaden is unique in having such fine-mesh gill-rakers that it can feed extensively on diatoms, which because of their smaller size cannot be readily secured by other large marine animals (Clarke 1954).

Small nektonic species are in turn preyed on by larger species. Sharks commonly hold the last link in the food chain. The pelagic birds are also fish-eaters or depend on floating carrion for their food.

Productivity

Most studies of plankton productivity have been conducted in the neritic zone. In the English Channel, the mean annual standing crops of phytoplankton, zooplankton, and pelagic fish in dry weight of organic matter are 0.4, 1.5, and 1.8 g/m^2. This is unusual in giving a larger biomass of herbivores and carnivores than of photosynthetic plant material. However, the daily productivity of phytoplankton makes up for this because it is over 100 per cent, while that of zooplankton is only 10 per cent and that of fish 0.09 per cent. The productivity ratio of phytoplankton : zooplankton : fish is approximately 280:100:1 (Harvey 1950).

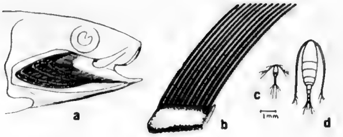


FIG. 28-5 **The filter feeding apparatus of the California sardine: a) gill cover and gills removed to show one side of branchial sieve formed by gill rakers; b) enlarged drawing of a section of the branchial sieve; c) a small copepod, *Oithona plumifera*, drawn to the same scale as b); d) a medium-sized copepod, *Calanus finmarchicus*, drawn to the same scale as b) (Sverdrup *et al.* 1942).**

The daily net productivity of phytoplankton in the upper 20 m of Block Island Sound near the eastern end of Long Island has been estimated at 26 per cent of the standing crop in excess of that consumed by zooplankton and bacteria in the surface layer. The zooplankton consumes not more than 4 per cent of the phytoplankton per day. Most of the excess daily production (19 per cent) in the surface waters settles downward and is used by animals and bacteria on or near the bottom, with the rest (7 per cent) becoming laterally dispersed into adjacent areas (Riley 1952). The daily productivity of zooplankton in this same area was calculated at 17 per cent of the standing crop (Deevey 1952).

Phytoplankton productivity varies with the time of the year. Near Kiel, Germany, in August there is a surplus of phytoplankton production over the amount consumed by animals; the productivity amounts to 350 mm^3/m^3/day while animal consumption is 60 mm^3/m^3/day. During February, the productivity of plankton is only 10 mm^3/m^3/day while the food requirements of animals is 18 mm^3/m^3/day. This deficiency in food production is correlated with the decrease at that time in the standing crop of both plants and animals (Sverdrup *et al.* 1942).

The average net phytoplankton of the Sargasso Sea is only one-quarter to one-third what it is in the more productive temperate waters (Riley 1957). Productivity is especially high in those parts of the ocean where there is upwelling. It is in these areas

Table 28-1 Vertical zonation of mollusks on a rocky shore at Cape Ann, Massachusetts. Numbers given represent the density of individuals per square meter (after Dexter 1945).

Zone	*Littorina saxatilis*	*Littorina littorea*	*Mytilus edulis*	*Mya arenaria* (seed)	*Littorina obtusata*	*Thais lapillus*	*Acmaea testudinalis*	*Anomia aculeata*	*Crepidula fornicata*
High tide level	4	4							
105 cm lower	23	112							
115 cm lower	248	2,225	23	77					
131 cm lower	58	1,339	116	81	248	35			
140 cm lower	31	387	132	0	151	8			
156 cm lower		704	31	8	341	15			
174 cm lower		1,300		0	163	70	8		
184 cm lower		813		0	77	15	15	15	8
199 cm lower (near Spring low-tide level)		387		15					45

that the yield of commercial fish of economic interest to man is the greatest.

BALANOID-GASTROPOD-THALLOPHYTE BIOME

This community extends from high to below low tide levels on rocky shores. Benthic animals and attached algal plants are conspicuous and important. The benthos is mostly epifauna as the substratum is too hard to permit development of extensive infauna. When the tide is out, the organisms are subjected to drying, the occasional inflow of fresh water, higher temperatures, and greater light intensities. Organisms avoid desiccation when the tide is out by variously crawling under stones or thick algal growths, closing thick shells or operculae, retreating into crevices, or secreting a mucous seal. Most organisms are also faced with the pounding action of waves. Various holdfast or anchoring devices have developed, and many species protect their more delicate structures with a hard shell. The adaptations for life on the seashore are many and varied (Yonge 1949). The plankton and nekton associated with the benthos include many species not common to the oceanic biome.

Zonation

Vertical zonation of species on rocky shores is usually conspicuous (Table 28-1), although individual species may extend widely into adjacent areas (Hewatt 1937, Yonge 1949, Stephenson 1949, Southward 1958).

Beginning on the landward side there is a *supralittoral zone* mostly above the action of tides and inhabited as much by land as by marine animals. This is followed seaward by a *supralittoral* or *Littorina fringe* which is wetted by the highest tides and by the splashing of waves. Because of the presence of either Myxophyceae or lichens, this zone is often discolored; commonly, black. The fringe is especially characterized by large numbers of small snails and sometimes isopods.

Next below this fringe is the *midlittoral* or *balanoid* zone. It is strictly inter-tidal, being covered and uncovered every day, and is occupied characteristically by acorn barnacles. This zone is often divided into subzones with the barnacles predominant in the upper portion, while polychaets, colonial hydroids, or other forms are relatively more important in the lower part. The subzonation of algae is often also well marked.

The lowest zone ever exposed, and then only at extreme low tides, is called the *infralittoral fringe*. It is a transition area. The entire area between extreme high and low tides, including the midlittoral zone and its supralittoral and infralittoral fringes, when considered as a unit, may be referred to as the *littoral, eulittoral,* or *tidal zone* to distinguish it from the *infralittoral* or *sublittoral* zone that extends from the lowest of low tides to the edge of the continental shelf.

Zonation is brought about in large part by differences between species in tolerance to length of exposure and submergence. Animals get into the proper zones by one of several ways (McDougall 1943). Motile species move in and out of favorable areas in direct response to stimuli. In sessile forms, however, it is the motile larvae which are dispersed uniformly, but die off in unfavorable microhabitats. In some forms the larvae become aggregated into a certain area before settling because of response to environmental factors, but the exact nature of the factors responsible for the aggregation of these pelagic larvae remains obscure. The presence of organisms already there may exert an influence on

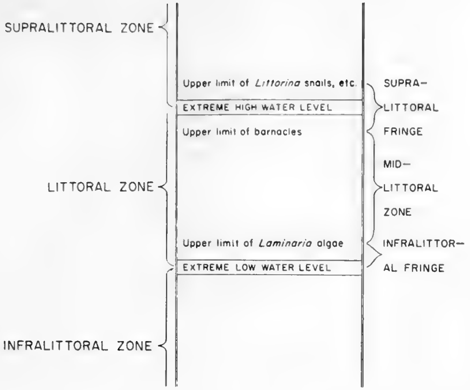


FIG. 28-6 **Diagram illustrating terminology of zonation on rocky coasts (Stephenson 1949).**

the species of larvae which will settle, but this needs more study. Young periwinkles are transported by wave action to the lower margin of stony beaches, and further shoreward movement is mainly locomotive. They achieve their proper zonation by the end of the first year of life (Smith and Newell 1955).

Littoral zone

Brown algae form thick masses and give protection to those animals that find shelter in or under them. A fauna of copepods, ostracods, water mites and young littorinids inhabit these seaweeds. In England, the numbers of individuals per 100 g of seaweed vary from about 44 on brown algae to over 13,000 on lichens (Colman 1940).

The animal life on rocky shores is varied and luxuriant. Several species of acorn barnacles, snails, marine limpets, marine mussels, goose barnacles, sea anemones, chitons, sponges, hydroids, bryozoans, flatworms, annelids, amphipods, isopods, crabs, sea urchins, starfishes, tunicates, and insects are present. Total abundance of animals may run into tens of thousands of individuals per square meter (Allee 1923, Newcombe 1935, Dexter 1947, Yonge 1949, Stephenson 1950, 1952, 1954, Shelford *et al.* 1935, Hewatt 1937, Ricketts and Calvin 1948).

Sublittoral zone

This community is not subjected to exposure by tides or to the pounding of surf, but is affected considerably by wave action and the complete circulation of water. Animals move around somewhat more freely and there is less need for strong holdfast structures. Most organisms lack physiological tolerance for long exposure to the air and hence differ fundamentally in structure and mores from the community described above.

Laminarias or kelps are the largest of the brown algae and occur commonly in this community. They have root-like holdfasts attached to the bottom and their stalks, which are often several meters long, bear leaf-like branches that float at the surface in the larger species. A long list of animals find shelter and food in the kelp beds and especially in the protection of the holdfasts (Andrews 1945). Polychaete worms are particularly abundant in these holdfasts (Colman 1940). Filamentous red algae (Rhodophyceae) are also prominent.

Abundant characteristic animals on the Pacific coast are sea urchins, sea cucumbers, starfishes, snails, rock oyster, chitons, limpets, scallops, mussels, nudibranchs, barnacles, crabs, hermit crabs, hydroids, tunicates, shrimps, and various fish. Distribution of fish species correlates strongly with the type of bottom or benthos that is present (Popov 1931).

The variety of animals in this community is great, both in genera and species, but the density of any one benthic species is seldom greater than $10/m^2$ on the Pacific coast of North America (Shelford *et al.* 1935), in contrast with the littoral zone. Off the coast of California, the average fresh weight of the standing crop of plants decreases at depths of 1.5 to 22 m from 4667 to 606 g/m^2, while animals increase from 125 to 377 g/m^2 (Aleem 1956).

Tidal pools

Sea-water is often retained in depressions or pools in the littoral zone and hence organisms here are never completely exposed to the air. They are, however, subject to high light intensity and increases in the temperature between tides (Klugh 1924). Tidal pools are usually rich in both plant and animal life, and some species are largely restricted to them. Red algae and kelps prefer the more shaded, cooler pools; the green algae and some of the smaller brown algae predominate in the well-insolated pools. Animals of both the sublittoral and littoral zones are found here.

Food chains

The basic food elements in these rocky shore communities are the free-floating plankton and detritus in the water, the algae, and the organic debris adhering to the rock surfaces (Dexter 1947). Many organisms have straining mechanisms that automatically collect food materials out of the large volume of water with which they have contact. Snails crawl over the rocks and seaweeds, scraping away at the algae and plant tissue and eroding the rock surfaces. Crabs and fish have a wealth of invertebrates upon which to feed, and are generally at the top of food chains along with birds that feed along the shore.

Marine shore animals have developed many devices to protect them from predators (Flattely and Walton 1922). Some crabs are concealed by seaweeds, hydroids, or other organisms growing on their carapaces. Hermit crabs take refuge in the shells of snails. Protective and warning coloration is common. Protective armor occurs in the form of shells, chitinous exoskeletons, spicules, spines, setae, bristles, and constructed tubes. Various forms of weapons have evolved, some of them poisonous, as the nematocysts of coelenterates, stylets of some gastropods, spines of the king crab, and chelae of crustaceans. Autotomy, or the ability to throw off an appendage grasped by an enemy, is highly developed in crabs, lobsters, and echinoderms. Well developed powers of regeneration of lost parts occur in these forms, while in worms, sponges, hydroids, and other groups, regeneration of entire new bodies from small fragments is often possible.

Dominance and succession

Dominance is exerted by those organisms that compete most successfully for the space that is available. When they become established, they largely control the presence of other species. This is true both with the seaweeds and with the more abundant and successful animals. In describing competition on wharf pilings at Beaufort, North Carolina, McDougall (1943: 367) states: *So many barnacle larvae, for example, may settle on a small area of clean surface that only a fraction of one per cent of their number will ultimately find space to grow to full size. Incrusting bryozoans, such as* Schizoporella, *spread over and smother barnacles and other low-growing species in their vicinity. Colonial hydroids, sponges, and ascidians often form densely matted tangles which accumulate quantities of sediment and effectively smother barnacles, oysters, bryozoans, and other species less luxuriant than themselves.* The colonial hydroid *Tubularia crocea* dominates the pilings in April and May but during June, with water temperatures becoming higher, the animals die and slough off, taking with them many associated species. In the bare areas thus exposed, various other sessile species become established. By the end of August, two other colonial hydroids, *Pennaria tiarella* and *Eudendrium carneum,* and a colonial bryozoan, *Bugula neritina,* become dominant. In late October, as water temperatures fall, these summer species die and *Tubularia* again becomes active and reproduces abundantly. Low winter temperatures temporarily curtail its activities. It is apparent that true succession actually occurs but is passed through quickly and may be obscured by seasonal changes in the species composition of the biota (Redfield and Deevey 1952).

PELECYPOD-ANNELID BIOME

Habitat

This biome develops on depositing sand and mud bottoms in contrast to the biome just described that occurs on eroding rocky shores. There is still a good deal of wave action over sandy bottoms. Fine sand particles shift about almost continuously, and animals have difficulty in preventing their burrows from collapsing. In general, the water over muddy shores is shallower, quieter, and warmer. The mud forms a soft, compact bottom, but is also easily moved or shifted around by storms and wave action. Animal burrows in mud are more permanent. Species tend to segregate depending on the fineness of the soil particles and on the amount of organic matter present. Shores of high mud content may be low in oxygen because of decaying organic matter, so animal populations tend to be largest and most varied in a mixture of mud and sand. Tidal currents are weaker, and change in the level of water less pronounced on sand and muddy shores than on rocky ones.

Composition and characteristics

Important plants in this biome are the marine eelgrass which is a seed plant, and green algae, particularly the sea-lettuce, which grows in sheets either attached to the substratum or lying fragmented over large areas, and *Enteromorpha,* which grows in tufts or tangles. Occurring on eelgrass and sea-lettuce may be several kinds of epiphytic algae. These plants form extensive stands and are important to animals for attachment, shelter, and food. Eelgrass was almost eliminated from the Atlantic coast in 1931–32, possibly because of a protozoan disease. This disturbance had a profoundly deleterious effect on the abundance of many animals, including the brant, a bird that depended on it almost exclusively for food, and on scallop and other coastal fisheries. Twenty years later there was evidence that eelgrass was recovering much of its former abundance (Cottam and Munro 1954).

Predominant animals are pelecypods, polychaete worms, particularly *Arenicola* and *Nereis;* starfishes, brittle-stars, sea cucumbers, crabs, amphipods, and snails. Populations may run to several thousands of individuals per square meter. A variety of small fish occur here. Birds include sandpipers, plovers, and herons.

The biome is world-wide in distribution, but the characteristic life-forms are represented by different species locally. Thus a number of secondary communities (biociations) may be recognized (Petersen 1914, Jones 1950, Thorson in Hedgpeth 1957).

Many of the animal constituents in this biome are burrowing forms. The substratum of mud and sand holds considerable water and when the tide is out on exposed flats, pelecypods, worms, and other animal constituents retract their fleshy organs into their burrows or shells and remain in a water saturated environment (Hesse, Allee, and Schmidt 1951). They are thus never rhythmically exposed to the atmosphere with changes in the tide even on the shore. Furthermore, most forms are generally tolerant of low oxygen and high carbon dioxide concentrations. In order to maintain respiration when retracted in their underground burrows these animals have long siphons, sometimes longer than their bodies, or long tubes or canals that extend to the surface. Through these they maintain a circulation of water, often by means of special pumping organs.

Burrowing crustaceans have setose appendages, modified for digging, and small eyes. Those that remain near the surface have long antennae and robust bodies; those that live in deep burrows have short antennae and slender bodies. For the same reason, burrowing clams that remain near the surface have heavy shells while those that burrow deeper have more fragile shells. These clams either have wide, slimy feet and small shells and crawl with ease through the sand, or have a slender foot that can expand at the end to give enough anchorage so that the animal can pull itself downward into the sand or mud (Pearse *et al.* 1942).

The infauna also includes many microscopic forms, such as nematodes, flatworms, copepods, ostracods, foraminiferans, and other protozoans. These small organisms may be enormously abundant in number of individuals. In respect to the ciliated protozoans, some species are ubiquitous, but other species are characteristic of this habitat (Fauré-Fremiet 1950). Some species of ciliates occur in the intergranular spaces of the sand and mud, other species are associated with the surface film of diatoms (Webb 1956).

In contrast to the great variety of infauna in this biome, the epifauna is more restricted, although some species are abundant. The fiddler crab browses in great armies on beaches left exposed by the tide, but retreats into its burrow and plugs up the opening when the tide comes in. The characteristic ghost crab of sandy beaches of middle latitudes spends most of its time above high tide level but must return occasionally to water to dampen its gill chamber.

Zonation

Zonation is less conspicuous than on rocky shores because of the prevalence of burrowing forms and of running and swimming species that move up and down with the tides (Brady 1943). Some evidence for zonation occurs on sandy beaches with crustaceans (Dahl 1953) and with pelecypods and annelids (Stephen 1953). A more pronounced change in species composition occurs in the sublittoral zone; in the North Pacific this change comes at a depth of 3 m (Shelford *et al.* 1935). Pelecypods and annelids still predominate (Holme 1953, Sanders 1956).

Food coactions and productivity

Bacteria are more abundant on mud bottoms than in the open sea (ZoBell 1946). On mud flats they may average 10 million cells/per cc of mud, or with a biomass of nearly 40 g/m^3. Bacteria are, of course, vital for the decomposition of organic debris, dead organisms, and wastes, but may also be used directly as food. Assuming that the bacteria divide rapidly enough to increase their biomass 10 times per day, this gives a 24-hour production of 400 g/m^3, mostly concentrated in the 5 cm beneath the surface.

Many protozoans and zooplankters feed on bacteria and detritus, and a large number of mud and sand dwelling invertebrates of larger size, such as pelecypods, annelids, and crustaceans, are deposit-feeders, or have special straining devices in the form of sieves, brushes, and hairy or mucous nets for collecting bacteria, organic particles, and small plankton organisms suspended in the water (Blegvad 1914, Yonge 1953). Deposit-feeders tend to predominate where the bottom is composed of fine sediments, while suspension-feeders predominate where the bottom is made of coarser materials (Sanders 1956). Snails, amphipods, and others feed on the plant tissues of eelgrass, sea lettuce, and algae. Crabs, echinoderms, and fish feed partly on organic debris and partly on the smaller invertebrates. Fish feed on the invertebrates and larger fish feed on smaller ones. On sand and mud flats on the coast of California, only 5 per cent of all animal species are strictly carnivorous. Only a few species of animals feed directly on plants, but plant tissue becomes more available after its death and partial decomposition. The principal food chain is plants: detritus and bacteria: detritus and bacteria feeders: animal feeders: birds (MacGinitie 1935).

At low tide, feeding and other activities are at a minimum as the bottom forms retract into their burrows and motile forms retreat seaward. However, some of the snails continue to feed on plants, and insects and birds come into the exposed area in search of debris and small animals for food. As the tide returns, the insects and birds retreat landward, but pelecypods extend their siphons, annelids rise from their burrows, shrimps, crabs, and fish move about over the surface, and the whole community becomes a scene of bustling activity.

Petersen (1918) and Jensen (1919) of Denmark were concerned with measuring the productivity of invertebrates in the sea, especially benthos, as a source of food for commercially important fish. More accurate calculations in the English Channel (Harvey 1950) give the ratio between the mean annual dry organic weight of bottom invertebrates and the bottom-dwelling fish as 15:1. Annual productivity of the invertebrate fauna is twice as great as that of the fish, so the productivity ratio between the two groups is 30:1.

Dominance

In contrast to rock-bottom communities, competition for space is not an important factor in mud- and sand-bottom communities. Actual evidence purporting dominance to exist is not convincing (MacGinitie 1939). Eelgrass and algae do not appreciably react on the physical characteristics of the habitat except to increase the supply of oxygen.

Starfishes and brittle-stars may exert control to a limited extent where they are numerous by feeding on and preventing pelecypods from becoming established in the community (Clements and Shelford 1939). It is possible that fishes may at times modify the species composition of an area, but for the most part it appears that the presence and distribution of species is controlled directly by the physical conditions of the habitat (Jones 1950) and that only population size is modified by predation and competition.

CORAL REEF BIOME

Coral reefs are formed by the accumulation of the calcareous skeletons of myriads of organisms. They extend from the sea bottom at depths of 46 m, or rarely 74 m, to slightly above low tide level. The best formation of coral reefs is confined to warm waters above 18°C, although individual species may extend into colder regions (Vaughan 1919, Wells in Hedgpeth 1957).

Predominant organisms involved are commonly the anthozoan stony corals and organ corals and the hydrozoan milliporids. Some reefs, however, are formed principally by Foraminifera and still others by calcareous algae. All massive coral structures employ calcareous algae as cement. These algae not only thrive in the pounding surf on the windward side of the reef, but by their growth are able to repair damage to the reef caused by storms. Most typical reef-building animals are colonial and of shapes varying from closely compact, globose, or encrusting, to loosely branched or dendritic, depending in part on their exposure to wave action. Each polyp in a colony secretes its own calcareous skeleton and when it dies the next generation builds on top of the old so that the accumulation of a lime structure is fairly rapid.

The bright yellow or red colors of corals near enough to the water's surface for adequate light penetration are the result of algae, the zooxanthellae, which are either embedded in the body wall or free in the internal cavities. In addition, there are bands of green filamentous algae growing to a depth of 2 or 3 cm in the pores of the inert coral skeleton that may have a biomass sixteen times that of the zooxanthellae. In their photosynthesis, these algae probably absorb carbon dioxide and nutrients from the animal tissues of the coral and liberate oxygen and provide nourishment of value to the animals (Odum and Odum 1955), although this has been disputed. Perhaps because of this symbiotic relationship which requires solar radiation, living corals are largely confined to the upper, shallower waters. Coral animals actively ingest zooplankton, but apparently not phytoplankton, from the surrounding water (Hand 1956, Yonge 1958).

Reefs may be either fringing, barrier, or atoll

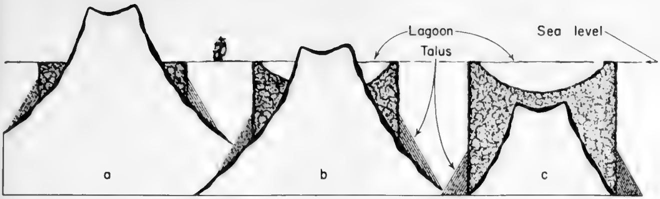


FIG. 28-7 **Three types of coral reefs and their possible manner of origin, according to Charles Darwin: a) fringing reef, b) barrier reef, c) atoll.**

(Fig. 28-7). Fringing reefs are in direct contact with the shore; barrier reefs are separated from the shore by a lagoon of varying width; atolls are annular or horseshoe-shape, surrounding a lagoon that does not contain any central land mass. The Great Barrier Reef that extends for great distances off the east coast of Australia is a good example of the second type of reef, and atolls are numerous in the South Pacific. According to a theory first proposed by Darwin, barrier and atoll reefs form from fringing reefs either as the land subsides or the water level rises (Vaughan 1919). Atoll islands are formed either when the water level falls or when waves break off and pile up chunks of coral limestone to build the reefs a few feet above the high tide level. As the stone dissolves or becomes pulverized, it forms a soil on which plants can grow and terrestrial communities of animals invade. Reefs are often not continuous because the organisms are intolerant of fresh-water brought down by streams, and because they are very sensitive to smothering by mud or sand. On the exposed ocean side there is generally a zonation of different species from the shore outward. (Odum and Odum 1955, Goreau 1959, Wells in Hedgpeth 1957).

The coral organisms, particularly the algae and the coelenterates, are true dominants in this biome since they build the substratum that makes possible the development of the community and the occurrence of other organisms. Competition for space, light, and protection from wave action is keen.

There is a great variety of secondary species associated with the corals. These include many kinds of alcyonarians; numerous brittle stars, crinoids, and holothurians; a great variety of chaetopod, echiurid, and sipunculid worms; crustaceans, including hermit crabs; mollusks; and large numbers of brilliantly colored, strikingly-marked fish. The many crevices, holes, and cavities in and between the coral provide excellent hiding places and refuge from predators so that the impressive development of color among the fishes may be due, in part, to lack of predation pressure. The fishes have a variety of food habits and are represented in all consumer trophic levels (Hiatt and Strasburg 1960).

At the Eniwetok atoll in the South Pacific, the average dry weight biomass of the living photosynthetic plant material is estimated at 703 g/m^2, that of the herbivorous and carnivorous animals at 132 g and 11 g, respectively. These weights exclude the dead skeletal materials associated with the protoplasm. The ratio between plants and herbivores is 5.3:1, between herbivores and carnivores 11:1, or a composite ration of 64:12:1. The total primary productivity per year as the result of photosynthesis was estimated at 12.5 times the biomass of the standing crop. This is sufficient to balance approximately the total plant and animal energy needs of the reef and thus render the coral reef a self-contained steady-state ecosystem (Odum and Odum 1955).

SUCCESSION TO LAND

The three great biocycles—ocean, freshwater, and land—come into contact with each other around the margins of the seas. The change in the physical nature of the habitat from salt water to freshwater is a drastic one, but not more drastic than the change from salt water to land. The transition of animal and plant life is abrupt, and a zonation or physiographic succession of communities can be recognized. This transition from the ocean to freshwater and from the ocean to land as we see it today is of special interest since it parallels the probable evolution and dispersal of life in past ages.

Life is generally believed to have originated in the littoral region. Apparently no great groups [phyla] of animals originated except in the ocean. The routes by which animals probably left the ocean and reached fresh-water and land have been various. Some animals probably migrated directly across sea beaches; others probably ascended rivers, passed through marshes and swamps, or burrowed through *soil. Some animals were transferred from the ocean by land elevations which isolated them in bodies of water which gradually became fresh. . . . Emigration from the sea did not take place at any one time. It has occurred many times in the past and is slowly progressing on many shores today. . . . The most successful animal colonizers of the land have been: (1) the arthropods, which have in many cases developed book-lungs or tracheae for breathing air; (2) the vertebrates, with lungs and dry skins; and (3) the snails, with slime and spirally coiled shells to prevent desiccation. . . . There are at present many examples of animals which are in the midst of their transformation from marine to fresh-water animals, or from marine or fresh-water into land animals. Not only have plants and animals emigrated from sea to land, but there are countless instances when migrations have taken, and are taking place in the opposite direction. Grasses, insects, reptiles, birds, and mammals have left the land for the sea. . . . Fishes began in fresh-water, but now range through the ocean at all depths* (Pearse 1950: pp. 9–10, 14).

On rocky shores and cliffs there is a splash or supralittoral zone above high tide level. Green algae occur here and scattered individuals of marine snails, acorn barnacles, limpets, amphipod sandfleas, and flatworms, as well as insects, especially Diptera and other forms that come from the land. Above the influence of splashing, the rocks may be covered with lichens and mosses, representing the initial stages in the terrestrial rock sere. However, salt spray is often blown inland a considerable distance to affect conspicuously the development of normal terrestrial vegetation and its accompanying animal life. Cliffs along the ocean, as well as sandy beaches and islands, are favorite nesting places for large numbers of pelagic birds.

Above water action on sandy shores, the wind may blow the sand into dunes with the consequent development of the dune sere. On muddy flats there is typically a development of salt marshes, particularly in protected embayments or along the margins of outflowing rivers. The high marshes are flooded completely only during the spring tides, but the ground water is more or less continuously saline. As sediment accumulates the marsh eventually becomes dry land (Steers 1959).

The seashore snails (*Littorina*), the marsh snail (*Melampus*), mussels (*Brachidontes, Mytilus*), crabs (*Carcinides, Cancer*), amphipods (*Gammarus, Orchestia*), and isopods (*Philoscia*) occur through the extensive salt marshes on the Atlantic Coast of North America and there are numerous flies and mosquitoes. Killifishes are abundant and devour many mosquito larvae. Herons, plovers, sandpipers, ducks, rails, bitterns, redwinged blackbirds, marsh wrens, and sharp-tailed sparrows feed or nest. Muskrats and meadow voles, as well as other species of mammals, occur in salt marshes but are not particularly characteristic of them (McAtee 1939).

In tropical regions mangroves may develop instead of marshes on mucky, poorly aerated bottoms. The red mangrove has an extensive prop root system and grows in deep water not ordinarily exposed even at low tide. The mangroves protect the shore from erosion and aid in the accumulation of deposits of peat and mud that build up the shore and form islands. The black mangrove at higher levels usually produces erect roots that stick up through the mud and serve as pneumatophores. Mangroves are usually heavily populated beneath by crabs and other marine species.

SUCCESSION TO FRESH WATER

Where rivers flow into the ocean on low coastal plains and there are extensive embayments or estuaries, as along the Atlantic Coast, there is a very gradual change from salt water to brackish water (salinity: 0.5–30°/00) to entirely fresh water. This habitat gradient fluctuates back and forth with the tides. Since fresh water is less dense and often warmer, it flows over the top of the salt water with the result that strata with different physical characteristics are formed and these different strata are inhabited by different kinds of fish and other organisms.

Species of marine organisms extend towards fresh water as far as permitted by their tolerance of reduced salinity. Since this tolerance varies between species, the marine flora and fauna become impoverished as the fresh-water flora and fauna become enriched. There are, however, many more marine species than fresh-water species in estuaries, although productivity in brackish water is considerably less than in the sea. A few species find optimum environmental conditions in brackish waters and decrease in abundance both toward fresh water and towards the open sea. Economically important brackish and shallow water species on the Atlantic coast are the blue crab, lobster, American oyster, scallops, hard-shell clam, soft-shell clam, and such fishes as the Atlantic croaker, striped bass, American shad, scup, weakfish, and others.

Of special interest are fish that perform long migrations between fresh and salt water for spawning purposes. *Anadromous* fish, principally salmon, shad, striped bass, and some trout, come from the ocean into fresh-water streams; *catadromous* fishes, like the fresh-water eels, reverse the process. The chum salmon spends several years in the sea until it becomes sexually mature, then it ascends fresh-water streams to their cool, gravelly-bottom headwaters to

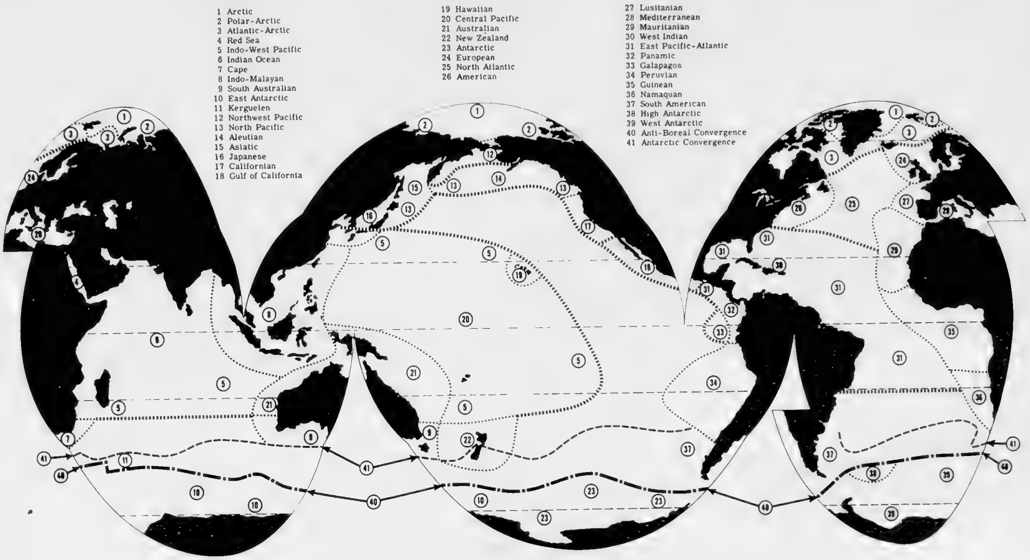


FIG. 28-8 Regions and subregions in the faunal distribution on the continental shelf. The Anti-boreal and Antarctic Convergences represent areas where warm surface waters sink, because of their greater salt content, below the cold surface waters of the Antarctics. Prepared from information given by Ekman 1953.

spawn, after which it dies. The Atlantic salmon, however, has a shorter developmental period and may spawn more than once. Tagged salmon and shad are commonly known to ascend the same streams in which they were hatched, and recent studies indicate that they recognize their home waters by chemical stimuli (smell), memory of which is retained from very young stages (Hasler 1954). Apparently salmon eggs must be laid in fresh water as otherwise the outer membranes do not harden and the number hatching is reduced (Black 1951). Furthermore, young salmon cannot tolerate sea water until they have developed chloride-secreting cells in the gills.

The adult female eel spends 5 to 20 years in the fresh-water streams that drain into the Atlantic Ocean in both the Western Hemisphere and in Europe. They often ascend these streams far into the interior of the continents. The male, however, remains in the brackish water of the bays and estuaries. It is here that mating takes place as the female returns to the sea to spawn. The journeys of the females have been difficult to follow but apparently both the American and European species spawn in the depths of the tropical sea northeast of the West Indies. The females then die. It is here that the smallest immature forms occur in mixed populations in the open sea. It is still a mystery how the young of the two species become separated and get to their respective continents.

ZOOGEOGRAPHY

There have been several attempts to recognize taxonomic and geographic divisions in marine communities, beginning with Petersen (1914), but probably the best and most complete is that of Ekman (1953). Ekman divides marine life first of all into *faunas,* based partly on temperature and partly on geography, then into *regions* and *subregions* (Fig. 28-8). Subregions may be still further divided into *provinces* (Stephenson 1954). Families and genera that are endemic or restricted in their distribution have been most useful for distinguishing the major geographic divisions. These divisions are faunistic ones and each division may contain two or more of the biomes that we have just described.

Pelagic biome

There is enough interchange of water between the different oceans to give considerable uniformity in the taxonomic composition of pelagic organisms. Ubiquitous species found in all oceans and in both equatorial and polar regions include species of siphonophores, ctenophores, polychaetes, copepods, chaetognaths, and amphipods.

The principal division of the epipelagic community is into a warm-water fauna lying between summer isotherms of 14°–15°C north and south of the equator and into Arctic and Antarctic faunas. A large number of species in the warm-water fauna are worldwide. In general, the fauna of the Indian and Pacific Oceans is richer in species than that of the Atlantic Ocean.

The arctic and antarctic faunas contain several characteristic and endemic species, some of which may at times become very numerous. The blue and fin whales of the antarctic have long been sought by man for their oil.

There is essentially only one region of abyssal-benthos with many genera of animals widely distributed. Doubtless this is due to the considerable uniformity of environmental conditions in the various ocean bottoms. Subregions can be recognized, however, on the basis of relative proportions of endemic species.

Biomes of the continental shelf and coral reefs

The shelf fauna, made up of benthos and associated organisms, is divisible into warm-water, temperate, Arctic, and Antarctic faunas. The poleward limits of the warm-water fauna are correlated with minimum yearly temperatures of 16°–18°C. This fauna may be further divided into tropical and subtropical sub-faunas along an isotherm of 20°C. The Arctic and Antarctic faunas are limited towards the equator by summer isotherms of 4°–7°C. Temperate faunas lie between the warm- and cold-water faunas and in turn are sometimes divided into warm and cold temperate sub-faunas.

The tropical sub-fauna is by far the richest in species and contains numerous endemic elements which do not penetrate extensively even into the subtropical zone. Coral reefs are found only in the tropics. The variety of forms making up each fauna becomes progressively less poleward. The tropics have been the center of origin, differentiation, and dispersal of these cold-blooded organisms, and species have invaded colder waters only as they have been able to acclimatize to them.

Many tropical genera and families are circumtropical in distribution; that is, they are found in the Indian, Pacific, and Atlantic Oceans, although represented by different species in each area. There are, however, a few species that are also circumtropical, including the brittle-star (*Amphipholis squamata*), certain crabs (*Grapsus grapsus, Planes minutus, Plagusia depressa*), the hammerhead shark (*Zygaena malleus*), the porcupinefish (*Diodon hystrix*), and nearly all the marine turtles.

It is not possible here to describe the fauna found in the various regions and subregions nor to analyze the interesting paleo-ecological history of each region. In general the *Indo-West Pacific region* and specifically the Indo-Malayan subregion have the greatest abundance, variety, and distinctness of animal life. This is expressed in many different taxonomic groups with significant percentages of families, genera, and species being exclusive to the region or subregion. This may represent the ancient profusion of forms that during the early Tertiary extended more or less around the world. This ancient fauna persisted here because the region was not subjected to the cooling of the climate and waters that occurred elsewhere during late Tertiary and the Quaternary and which brought impoverishment of the fauna.

The West Indian subregion of the *Atlanto-East Pacific region* ranks next to the Indo-Malayan subregion in size and richness of fauna. The shelf fauna of the *North Pacific region* and adjacent Polar-Arctic, especially on the American side of the Pacific Ocean, is much richer than that of the *North Atlantic region*. Both the *Arctic* and *Antarctic regions* have a number of endemic forms, but in general the Antarctic fauna, especially of invertebrates, is much richer in species. There are a few species of crabs, *Cancer,* a starfish, *Ctendiscus crispatus,* and some other organisms that occur in both polar regions with continuous intermediate distribution. However, the species occur in shallow waters in the polar regions and only in the deeper cooler waters of the tropics. Various other species or related forms are found in the two opposite polar or temperate regions only, with presumably the interconnecting tropical linkage having become broken sometime during past geological time.

APPLIED ECOLOGY

Although 71 per cent of the earth's surface is occupied by oceans and only 29 per cent by land, nearly all of the food and raw materials used by man is derived from the latter. This is in spite of the fact that agricultural soil is only a few inches thick and must be cultivated, protected from erosion, and fertilized, while the ocean with its chemical fertility, its photosynthetic production of basic plant food, and its fisheries appears almost inexhaustible.

Because of its high productivity, the plankton of the sea represents an important potential food supply for man (Davis 1955). Its energy value is approximately 4 Cal/g dry weight, and it is more or less palatable (Clarke and Bishop 1948). However, there are difficulties involved in securing significant amounts, poisonous species sometimes occur, it is not easily digested and assimilated, and consequently it has not as yet proved to be a feasible diet. The energy value of the plankton is used by man at the present time primarily as it is transferred into higher links of the food chain. Aside from the fishes, the chief marine organisms used as food are the oysters and other mollusks, shrimp, crabs, lobsters, and sea turtles. These are mostly animals of the continental shelf and estuaries.

There are a number of problems in the use and conservation of marine organisms. Natural beds of American oysters on the Atlantic coast have nearly all been exhausted through over-fishing and pollution. Because of heavy erosion of the land, silt deposition has become excessive in most of the bays and estuaries and there is increasing difficulty for oyster spat to find clean hard surfaces on which to set. Surfaces that are loose or covered with silt are not suitable since the spat is very small and easily smothered. A common practice is to return to suitable areas all shells of mollusks removed or to introduce other suitable hard objects to furnish the necessary substratum for oyster setting. Control of erosion over the watershed would greatly alleviate the problem. The trend is increasing to lease suitable areas of water and to farm oysters in the manner of an agricultural crop (Korringa 1952).

In spite of their position at or near the top of the food chain, the greatest utilizable food resource of the sea is its fin fishes. The service of transferring the basic fertility of the sea through successive stages in the food cycle to fishes is performed by nature, and man needs only to harvest the final crop. The great bulk of commercial fish is in the families of herrings, codfish, salmons, flounders, and mackerels. Probably most kinds of fish are potentially useful, although some species that occur in coral reefs are inedible or poisonous. Tunas were not widely eaten in the United States until 1928; swordfish, once anathema to fishermen, are now as expensive as steak. Sharks were not used until a few years ago, but are now a major source of vitamins. The loss of elements from the ecosystem with the removal of fish is replaced by the continued inflow of nutrients from the land by way of the rivers. A fishery, temporarily exhausted, will usually become replenished by natural processes if left alone for a period of time. When one realizes that with the same expenditure of effort a man in a year's time can harvest two and one-half times as much edible fish as he can pork in pigs, it would appear that the ocean community is one that should be more extensively utilized (Taylor 1951, Walford 1958).

The situation is different with whales and seals. Whales have been pursued so vigorously for their oils that certain species are in danger of extinction. Seals have been taken extensively for their fur. International regulations have now been set up to limit the take of both groups of species.

The applied ecologist is also concerned in the fouling of ship bottoms by growth of organisms, particularly those belonging to the balanoid-gastropod-thallophyte biome. This is of major economic importance because of reduction of speed and the greater fuel consumption imposed on fouled ships. The problem has stimulated intensive studies of the behavior of the organisms concerned and the searching for chemicals or methods of treatment of ship bottoms to prevent their setting (Iselin 1952).

SUMMARY

Geographic distribution of marine organisms depends on their responses to current, temperature, and physical barriers; their local distribution is affected by waves and tides, type of bottom, salinity, and depth. Major divisions of the marine biocycle are pelagic (open water) and benthic (bottom). Major communities recognized are the oceanic plankton and nekton biome in the open sea, the balanoid-gastropod-thallophyte biome on rocky shores, the pelecypod-annelid biome on sand and mud bottoms, and the coral reef biome.

Organisms making up the oceanic biome are widely distributed around the world but may be divided into warm-water and Arctic and Antarctic faunas. Coral reefs are found only in the Tropics. The two biomes on the continental shelf subdivide into warm-water, temperate, Arctic, and Antarctic faunas and into more restricted regions and subregions. The warm-water faunas are richest in species, especially in the Indo-Malayan and West Indian subregions.

Marine plankton include a greater variety of forms than does fresh-water plankton, although rotifers are nearly absent; cladocerans, less important. They possess various unique mechanisms for flotation. Although abundance varies greatly from place to place and from season to season, plankton is generally much more numerous in neritic coastal waters than in the open sea. Diel movements between the surface at night and greater depths during the day are pronounced.

Mollusks (squids), fishes, birds, and mammals constitute the nekton. The taxonomic composition of the fish fauna varies with depth. Bioluminescence is exceptionally well developed among deep-sea nekton and benthos.

Benthos includes a great variety of sessile, creeping, and burrowing forms. It is very abundant in the littoral zone, and decreases in numbers with depth until only scattered individuals are found in the deep ocean trenches. There is considerable difference in the life-form and species composition of benthos occurring on rocky shores and on sand and muddy ones. Zonation of species is more prominent on rocky than on depositing shores. Succession and dominance occurs in some situations, but is less important than in terrestrial communities. Coral reefs have many special features.

Food chains in the sea are similar to those in fresh water but different species make up the various links in the different communities. Productivity is especially high in regions where upwelling and turbulence bring nutrients from deeper levels up to the surface.

The three great biocycles of ocean, fresh-water, and land come into contact around the margins of the seas. The succession from the ocean to land is abrupt and from the ocean to fresh-water only slightly less so.

Because of its high productivity and occurrence over 71 per cent of the earth's surface, the plankton of the sea represents an important potential food supply for man. However, the energy value of this plankton is used by man at the present time only as it is transferred with considerable loss into the higher food-chain links of mollusks, larger arthropods, fishes, and to a certain extent, sea turtles. The conservation and development of marine resources represent a major challenge to the applied ecologist.

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