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Ecology: The Experimental Analysis of Distribution and Abundance

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Sixth Edition

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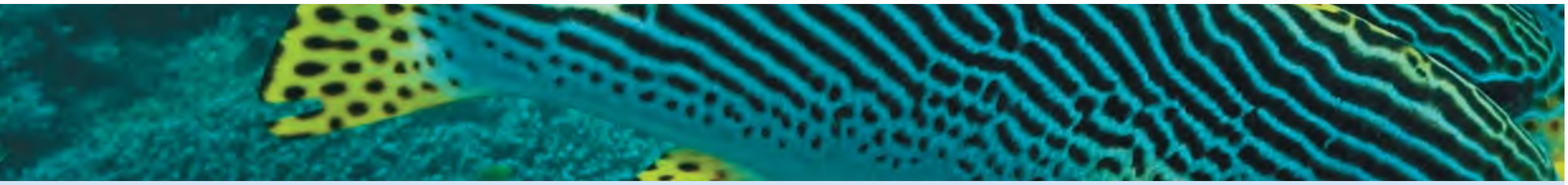
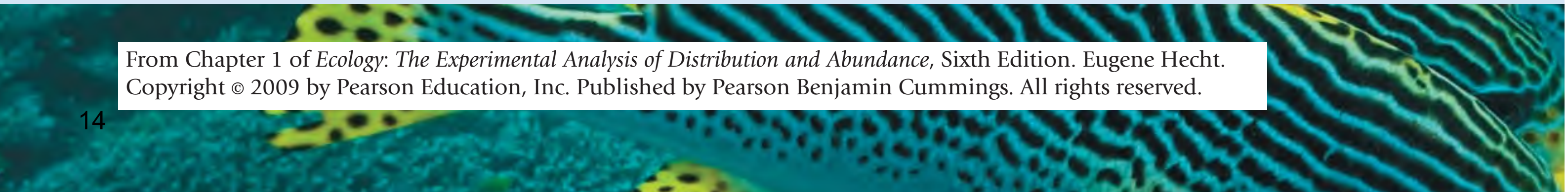


Introduction to the Science of Ecology

Key Concepts

- Ecology is the scientific study of the interactions that determine the distribution and abundance of organisms.
- Descriptive ecology forms the essential foundation for functional ecology, which asks *how* systems work, and for evolutionary ecology, which asks *why* natural selection has favored this particular solution.
- Ecological problems can be analyzed using a theoretical approach, a laboratory approach, or a field approach.
- Like other scientists, ecologists observe problems, make hypotheses, and test the predictions of each hypothesis by field or laboratory observations.
- Ecological systems are complex, and simple cause–effect relationships are rare.



From Chapter 1 of *Ecology: The Experimental Analysis of Distribution and Abundance*, Sixth Edition. Eugene Hecht.

KEY TERMS

experiment Test of a hypothesis. It can be observational (observe the system) or manipulative (perturb the system). The experimental method is the scientific method.

hypothesis Universal proposition that suggests explanations for some observed ecological situation. Ecology abounds with hypotheses.

model Verbal or mathematical statement of a hypothesis.

principle Universal statement that we all accept because they are mostly definitions, or are ecological translations of physical–chemical laws.

scientific law Universal statement that is deterministic and so well corroborated that everyone accepts it as part of the scientific background of knowledge. There are laws in physics, chemistry, and genetics, but not yet in ecology.

theory An integrated and hierarchical set of empirical hypotheses that together explain a significant fraction of scientific observations. The theory of evolution is perhaps the most frequently used theory in ecology.

Introduction to the Science of Ecology

You are embarking on a study of ecology, the most integrative discipline in the biological sciences. The purpose of this chapter is to get you started by defining the subject, providing a small amount of background history, and introducing the broad concepts that will serve as a road map for the details to come.

Definition of Ecology

The word *ecology* came into use in the second half of the nineteenth century. Ernst Haeckel in 1869 defined ecology as the total relations of the animal to both its organic and its inorganic environment. This very broad definition has provoked some authors to point out that if this is ecology, there is very little that is *not* ecology. Four biological disciplines are closely related to ecology—genetics, evolution, physiology, and behavior (**Figure 1**). Broadly interpreted, ecology overlaps each of these four subjects; hence, we need a more restrictive definition.

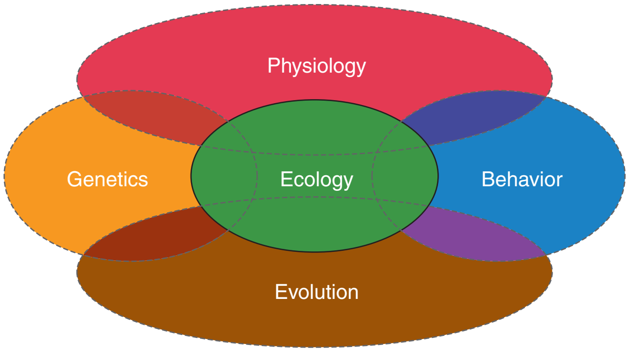


Figure 1 The four biological disciplines closely related to ecology.

Charles Elton in his pioneering book *Animal Ecology* (1927) defined ecology as scientific natural history. Although this definition points out the origin of many of our ecological problems, it is again uncomfortably vague. In 1963 Eugene Odum defined ecology as the study of the structure and function of nature. This statement emphasizes the form-and-function idea that permeates biology, but it is still not a completely clear definition. A clear but restrictive definition of ecology is this: Ecology is the scientific study of the distribution and abundance of organisms (Andrewartha 1961). This definition is static and leaves out the important idea of relationships. Because ecology is about relationships, we can modify Andrewartha's definition to make a precise definition of **ecology**: *Ecology is the scientific study of the interactions that determine the distribution and abundance of organisms*.

This definition of ecology appropriately constrains the scope of our quest, and is the meaning that will be adopted in this chapter. To better understand what ecology is, we need to know what is special about scientific studies, and what is meant by distribution and abundance. **Distribution**—where organisms are found—and **abundance**—how many organisms are found in a given area—are key facts that must be determined before we can address the most difficult question: *Why* this particular distribution, *why* this abundance? We seek the cause-and-effect relationships that govern distribution and abundance.

History of Ecology

The historical roots of ecology are varied, and in this section we will explore briefly some of the origins of ecological ideas. We are not the first humans to think about ecological problems. The roots of ecology lie in natural history. Primitive tribes, for example—who depended on hunting, fishing, and food gathering—needed detailed knowledge of where and when their quarry might be found. The establishment of agriculture also increased the need to learn about the ecology of plants and domestic animals. Agriculture today is a special form of applied ecology.

Outbreaks of pests such as locusts in the Middle East and North Africa or rats in rice crops in Asia are not new problems in agriculture. Spectacular plagues of animals attracted the attention of the earliest writers. The Egyptians and Babylonians feared locust plagues (**Figure 2**), often attributing them to supernatural powers (Exodus 7:14–12:30). In the fourth century B.C., Aristotle tried to explain plagues of field mice and locusts in *Historia Animalium*. He pointed out that the high reproductive rate of field mice could produce more mice than could be reduced by their natural predators, such as foxes and ferrets, or by the control efforts of humans. Nothing succeeded in reducing these mouse plagues, Aristotle stated, except the rain, and after heavy rains the mice disappeared rapidly. And even today, Australian wheat farmers face plagues of house mice, and ask the same question: How can we get rid of these pests?

Pests are a problem for people because they violate our feeling of harmony or balance in the environment. Ecological harmony was a guiding principle basic to the Greeks' understanding of nature. The historian Frank Egerton (1968a) has traced this concept from ancient times to the modern term *balance of nature*. The concept of *providential ecology*, in which nature is designed to benefit and preserve each species, was implicit in the writings of Herodotus and Plato. A major assumption of this concept was that the number of every species remained essentially constant. Outbreaks of some populations were acknowledged, but were usually attributed to divine punishment. And since each species had a special place in nature, extinction could not occur because it would disrupt the balance and harmony in nature.

Figure 2 A young girl looks at a dense swarm of the desert locust in North Africa.

How did we get from these early Greek and Roman ideas about harmony to our modern understanding? A combination of mathematics and natural history paved the way. By the seventeenth century students of natural history and human ecology began to focus on population ecology and to construct a quantitative framework. Graunt, who in 1662 described human population change in quantitative terms, can be called the "father of demography"[1] (Cole 1958). He recognized the importance of measuring birth rates, death rates, and age structure of human populations, and he complained about the inadequate census data available in England in the seventeenth century. Graunt estimated the potential rate of population growth for London, and concluded that even without immigration, London's population would double in 64 years.

Today, human population growth is an increasing concern, but population growth was not always measured quantitatively for animals and plants. Leeuwenhoek made one of the first attempts to calculate theoretical rates of increase for an animal species (Egerton 1968b). He studied the reproductive rate of grain beetles, carrion flies, and human lice, counting the number of eggs laid by female carrion flies and calculating that one pair of flies could produce 746,496 flies in three months.

By the eighteenth century, natural history had become an important cultural occupation. Buffon, who authored *Natural History* (1756), touched on many of our modern ecological problems and recognized that populations of humans, other animals, and plants are subjected to the same processes. Buffon discussed, for example, how the great fertility of every species was counterbalanced by innumerable agents of destruction. He believed that plague populations of field mice were checked partly by diseases and scarcity of food. Buffon did not accept Aristotle's idea that heavy rains caused the decline of dense mouse populations, but thought instead that control was achieved by biological agents. Rabbits, he stated, would reduce the countryside to a desert if it were not for their predators. If the Australians had listened to Buffon before they introduced rabbits to their environment in 1859, they could have saved their rangelands from destruction (**Figure 3**). Buffon in 1756 was dealing with problems of population regulation that are still unsolved today.

Malthus, the most famous of the early demographers, published one of the earliest controversial books on demography, *Essay on Population* (1798). He calculated that although the number of organisms can increase geometrically (1, 2, 4, 8, 16,. . .), food supply can

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[1] Demography originated as the study of human population growth and decline. It is now used as a more general term that includes plant and animal population changes.

Figure 3 European rabbit overpopulation in eastern Australia. Rabbits were introduced to Australia in 1859 and have become a serious pest because of their abundance. Their burrowing increased soil erosion, and they competed with sheep and cattle for forage.

never increase faster than arithmetically (1, 2, 3, 4,. . .). The arithmetic rate of increase in food production seems to be somewhat arbitrary. The great disproportion between these two powers of increase led Malthus to infer that reproduction must eventually be checked by food production. What prevents populations from reaching the point at which they deplete their food supply? What checks operate against the tendency toward a geometric rate of increase? Two centuries later we still ask these questions. These ideas were not new; Machiavelli had said much the same thing around 1525, as did Buffon in 1751, and several others had anticipated Malthus. It was Malthus, however, who brought these ideas to general attention. Darwin used the reasoning of Malthus as one of the bases for his theory of natural selection. The struggle for existence results from the high reproductive output of species.

Other workers questioned the ideas of Malthus and made different predictions for human populations. For example, in 1841 Doubleday put forward the True Law of Population. He believed that whenever a species was threatened, nature made a corresponding effort to preserve it by increasing the fertility of its members. Human populations that were undernourished had the highest fertility; those that were well fed had the lowest fertility. You can make the same observations by looking around the world today (**Table 1**). Doubleday explained these effects by the oversupply of mineral nutrients in well-fed populations. Doubleday observed a basic fact that we recognize today: low birth rates occur in wealthy countries—although his explanations were completely wrong.

Table 1 Total fertility rate of human populations and gross national income per person in selected countries of the globe in 2007.

Country	Total fertility rate	Gross national income per person
Sudan	4.5	2160
Gambia	5.1	1970
Niger	7.1	830
Tanzania	5.4	740
Botswana	3.1	12,240
South Africa	2.7	11,710
Canada	1.5	34,610
United States	2.1	44,260
Costa Rica	1.9	10,770
Mexico	2.4	11,330
Haiti	4.0	1490
Brazil	2.3	8800
Peru	2.5	6070
Turkey	2.2	9060
India	2.9	3800
Pakistan	4.1	2500
Indonesia	2.4	3950
China	1.6	7730
Japan	1.3	33,730
Sweden	1.9	34,780
Switzerland	1.4	40,630
Russia	1.3	11,620
Italy	1.4	29,840
Solomon Islands	4.5	2170

The total fertility rate is the average number of children a woman would have, assuming no change in birth rates. The gross national income (GNI) is in U.S. dollars per person. (Data from 2007 World Population Data Sheet.)

Interest in the mathematical aspects of demography increased after Malthus. Can we describe a mathematical law of population growth? Quetelet, a Belgian statistician, suggested in 1835 that the growth of a population was checked by factors opposing population growth. In 1838 his student Pierre-François Verhulst derived an equation describing the initial rapid growth and eventual leveling off of a population over time. This S-shaped curve he called the logistic curve. His work was overlooked until modern times, but it is fundamentally important, and we will return to it later in detail.

Until the nineteenth century, philosophical thinking had not changed from the idea of Plato's day that there was harmony in nature. Providential design was still the guiding light. In the late eighteenth and early nineteenth centuries, two ideas that undermined the idea of the balance of nature gradually gained support: (1) that many species had become extinct and (2) that resources are limited and competition caused by population pressure is important in nature. The consequences of these two ideas became clear with the work of Malthus, Lyell, Spencer, and Darwin in the nineteenth century. Providential ecology and the balance of nature were replaced by natural selection and the struggle for existence (Egerton 1968c).

The balance of nature idea, redefined after Darwin, has continued to persist in modern ecology (Pimm 1991). The idea that natural systems are stable and in equilibrium with their environments unless humans disturb them is still accepted by many ecologists and theoreticians.

Humans must eat, and many of the early developments in ecology came from the applied fields of agriculture and fisheries. Insect pests of crops have been one focus of work. Before the advent of modern chemistry, biological control was the only feasible approach. In 1762 the mynah bird was introduced from India to the island of Mauritius to control the red locust; by 1770 the locust threat was a negligible problem (Moutia and Mamet 1946). Forskål wrote in 1775 about the introduction of predatory ants from nearby mountains into date-palm orchards to control other species of ants feeding on the palms in southwestern Arabia. In subsequent years, an increasing knowledge of insect parasitism and predation led to many such introductions all over the world in the hope of controlling nonnative and native agricultural pests (De Bach 1974).

Medical work on infectious diseases such as malaria in the late 1800s gave rise to the study of epidemiology and interest in the spread of disease through a population. Malaria is still one of the great scourges of humans. In 1900 no one even knew the cause of the disease. Once mosquitoes were pinpointed as the vectors, medical workers realized that it was necessary to know in detail the ecology of mosquitoes. The pioneering work of Robert Ross (1911) attempted to describe in mathematical terms the propagation of malaria, which is transmitted by mosquitoes. In an infected area, the propagation of malaria is determined by two continuous and simultaneous processes: (1) The number of new infections among people depends on the number and infectivity of mosquitoes, and (2) the infectivity of mosquitoes depends on the number of people in the locality and the frequency of malaria among them. Ross could write these two processes as two simultaneous differential equations:

$$\left(\begin{array}{l}\text{Rate of increase of}\\ \text{infected humans}\end{array}\right) = \underset{\substack{\downarrow\\ \text{(Depends on number of infected mosquitoes)}}}{\left(\begin{array}{l}\text{New infections}\\ \text{per unit time}\end{array}\right)} - \left(\begin{array}{l}\text{Recoveries per}\\ \text{unit time}\end{array}\right)$$

$$\left(\begin{array}{l}\text{Rate of increase of}\\ \text{infected mosquitoes}\end{array}\right) = \underset{\substack{\downarrow\\ \text{(Depends on number of infected humans)}}}{\left(\begin{array}{l}\text{New infections}\\ \text{per unit time}\end{array}\right)} - \left(\begin{array}{l}\text{Death of infected}\\ \text{per unit time}\end{array}\right)$$

Ross had described an ecological process with a mathematical model, and his work represents a pioneering parasite–host model of species interactions. Such models can help us to clarify the problem—we can analyze the components of the model—and predict the spread of malaria or other diseases.

Production ecology, the study of the harvestable yields of plants and animals, had its beginnings in agriculture, and Egerton (1969) traced this back to the eighteenth-century botanist Richard Bradley. Bradley recognized the fundamental similarities of animal and plant production, and he proposed methods of maximizing agricultural yields (and hence profits) for wine grapes, trees, poultry, rabbits, and fish. The conceptual framework that Bradley used—monetary investment versus profit—is now called the "optimum-yield problem" and is a central issue in applied ecology.

Individual species do not exist in a vacuum, but instead in a matrix of other species with which they interact. Recognition of communities of living organisms in nature is very old, but specific recognition of the interrelations of the organisms in a community is relatively recent. Edward Forbes in 1844 described the distribution of animals in British coastal waters and part of the Mediterranean Sea, and he wrote of zones of differing depths that were distinguished by the associations of species they contained. Forbes noted that some species are found only in one zone, and that other species have a maximum of development in one zone but occur sparsely in other adjacent zones. Mingled in are stragglers that do not fit the zonation pattern. Forbes recognized the dynamic aspect of the interrelations between these organisms and their environment. As the environment changed, one species might die out, and another might increase in abundance. Karl Möbius expressed similar ideas in 1877 in a classic essay on the oyster-bed community as a unified collection of species.

Studies of communities were greatly influenced by the Danish botanist J. E. B. Warming (1895, 1909), one of the fathers of plant ecology. Warming was the first plant ecologist to ask questions about the composition of plant communities and the associations of species that made up these communities. The dynamics of vegetation change was emphasized first by North American plant ecologists. In 1899 H. C. Cowles described plant succession on the sand dunes at the southern end of

Lake Michigan. The development of vegetation was analyzed by the American ecologist Frederick Clements (1916) in a classic book that began a long controversy about the nature of the community.

With the recognition of the broad problems of populations and communities, ecology was by 1900 on the road to becoming a science. Its roots lay in natural history, human demography, biometry (statistical approach), and applied problems of agriculture and medicine.

The development of ecology during the twentieth century followed the lines developed by naturalists during the nineteenth century. The struggle to understand how nature works has been carried on by a collection of colorful characters quite unlike the mythical stereotypes of scientists. From Alfred Lotka, who worked for the Metropolitan Life Insurance Company in New York while laying the groundwork of mathematical ecology (Kingsland 1995), to Charles Elton, the British ecologist who wrote the first animal ecology textbook in 1927 and founded the Bureau of Animal Population at Oxford (Crowcroft 1991), ecology has blossomed with an increasing understanding of our world and how we humans affect its ecological systems (McIntosh 1985).

Until the 1970s ecology was not considered by society to be an important science. The continuing increase of the human population and the associated destruction of natural environments with pesticides and pollutants awakened the public to the world of ecology. Much of this recent interest centers on the human environment and human ecology, and is called environmentalism. Unfortunately, the word *ecology* became identified in the public mind with the much narrower problems of the human environment, and came to mean everything and anything about the environment, especially human impact on the environment and its social ramifications. It is important to distinguish ecology from environmental studies.

Ecology is focused on the natural world of animals and plants, and includes humans as a very significant species by virtue of its impact. **Environmental studies** is the analysis of human impact on the environment of the Earth—physical, chemical, and biological. Environmental studies as a discipline is much broader than ecology because it deals with many natural sciences—including ecology, geology, and climatology—as well as with social sciences, such as sociology, economics, anthropology, political science, and philosophy. The science of ecology is not solely concerned with human impact on the environment but with the interrelations of all plants and animals. As such, ecology has much to contribute to some of the broad questions about humans and their environment that are an important scientific component of environmental studies.

Environmental studies have led to "environmentalism" and "deep ecology," social movements with an important agenda for political and social change intended to minimize human impact on the Earth. These social and political movements are indeed important and are supported by many ecologists, but they are not the science of ecology. Ecology should be to environmental science as physics is to engineering. Just as we humans are constrained by the laws of physics when we build airplanes and bridges, so also are we constrained by the principles of ecology when altering the environment.

Ecological research can shed light on what will happen when global temperatures increase as a result of increasing CO_2 emissions, but it will not tell us what we *ought* to do about these emissions, or whether increased global temperature is good or bad. Ecological scientists are not policy makers or moral authorities, and should not as scientists make ethical or political recommendations. However, on a personal level, most ecologists are concerned about the extinction of species and would like to prevent extinctions. Many ecologists work hard in the political arena to achieve the social goals of environmentalism.

Basic Problems and Approaches to Ecology

We can approach the study of ecology from three points of view: descriptive, functional, or evolutionary. The descriptive point of view is mainly natural history and describes the vegetation groups of the world—such as the temperate deciduous forests, tropical rain forests, grasslands, and tundra—and the animals and plants and their interactions within each of these ecosystems. The descriptive approach is the foundation of all of ecological science, and while much of the world has been reasonably described in terms of its vegetation and animal life, some areas are still poorly studied and poorly described. The functional point of view, on the other hand, is oriented more toward dynamics and relationships, and seeks to identify and analyze general problems common to most or all of the different ecosystems. Functional studies deal with populations and communities as they exist and can be measured now. Functional ecology studies **proximate causes**—the dynamic responses of populations and communities to immediate factors of the environment. Evolutionary ecology studies **ultimate causes**—the historical reasons why natural selection has favored the particular adaptations we now see. The evolutionary point of view considers organisms and relationships between organisms as historical products of evolution. Functional ecologists ask *how:* How does the system operate? Evolutionary ecologists ask *why:* Why does natural selection favor this particular ecological solution? Since evolution not only has occurred in the past but is also going on in the present, the evolutionary ecologist must work closely with the functional ecologist to understand ecological systems (Pianka 1994). Because the environment of an organism contains all the selective forces

ESSAY

Science and Values in Ecology

Science is thought by many people to be value free, but this is certainly not the case. Values are woven all through the tapestry of science. All applied science is done because of value judgments. Medical research is a good example of basic research applied to human health that virtually everyone supports. Weapons research is carried out because countries wish to be able to defend themselves against military aggression.

In ecology the strongest discussions about values have involved conservation biology. Should conservation biologists be objective scientists studying biodiversity, or should they be public advocates for preserving biodiversity? The preservation of biodiversity is a value that often conflicts with other values—for example, clear-cut logging that produces jobs and wood products. The pages of the journal *Conservation Biology* are peppered with this discussion about advocacy (see, for example, *Conservation Biology* February 2007 issue, Brussard and Tull 2007, Scott et al. 2007).

> *There will always be a healthy tension between scientific knowledge and public policy in environmental matters . . .*

Scientists in fact have a dual role. First, they carry out objective science that both obtains data and tests hypotheses about ecological systems. They can also be advocates for particular policies that attempt to change society, such as the use of electric cars to reduce air pollution. But it is crucial to separate these two kinds of activities.

Science is a way of knowing, a method for determining the principles by which systems like ecological systems operate. The key scientific virtues are honesty and objectivity in the search for truth. Scientists assume that once we know these scientific principles we can devise effective policies to achieve social goals. All members of society collectively decide on what social goals we will pursue, and civic responsibility is part of the job of everyone, scientists included. There will always be a healthy tension between scientific knowledge and public policy in environmental matters because there are always several ways of reaching a particular policy goal. The debates over public policy in research funding and environmental matters will continue, so please join in.

that shape its evolution, ecology and evolution are two viewpoints of the same reality.

All three approaches to ecology have their strengths, but the important point is that we need all three to produce good science. The descriptive approach is absolutely fundamental because unless we have a good description of nature, we cannot construct good theories or good explanations. The descriptive approach provides us maps of geographical distributions and estimates of relative abundances of different species. With the functional approach, we need the detailed biological knowledge that natural history brings if we are to discover how ecological systems operate. The evolutionary approach needs good natural history and good functional ecology to speculate about past events and to suggest hypotheses that can be tested in the real world. No single approach can encompass all ecological questions. This chapter uses a mixture of all three approaches and emphasizes the general problems ecologists try to understand.

The basic problem of ecology is to determine the causes of the distribution and abundance of organisms. Every organism lives in a matrix of space and time. Consequently, the concepts of distribution and abundance are closely related, although at first glance they may seem quite distinct. What we observe for many species is that the numbers of individuals in an area vary in space, so if we make a contour map of a species' geographical distribution, we might get something similar to **Figure 4**.

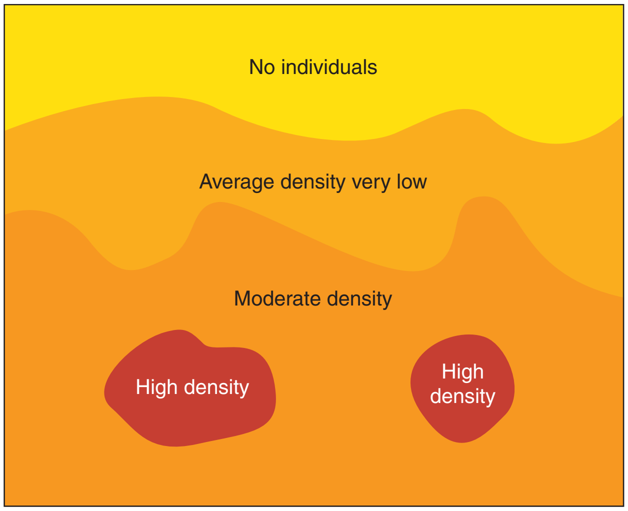

Figure 4 Schematic contour map of the abundance of a plant or animal species.

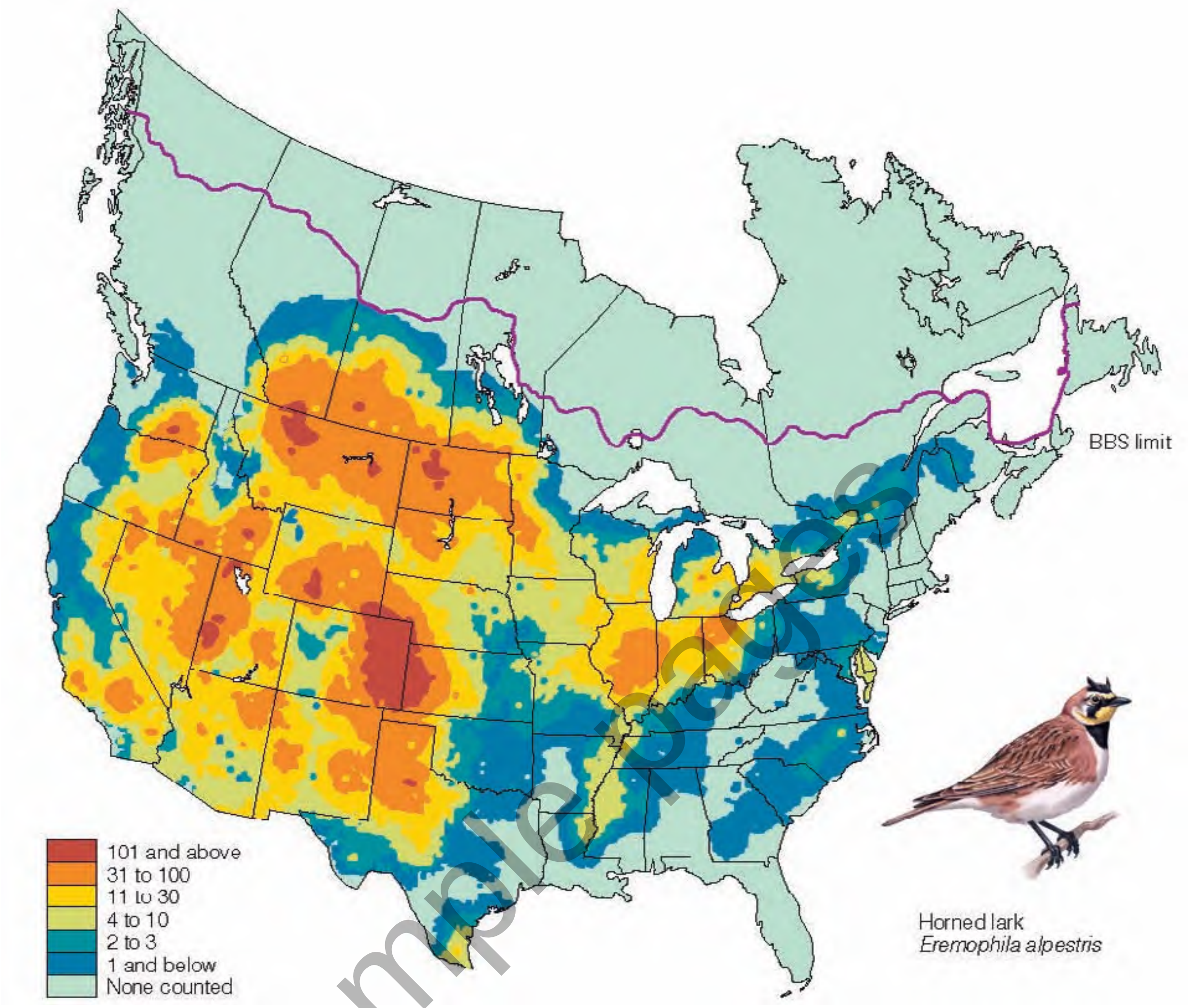

Figure 5 Abundance of the horned lark in North America from 1994 to 2003. Data are from the Breeding Bird Survey (BBS). Maximal abundance of this bird is reached in the short grass prairie of western Kansas and Nebraska and eastern Colorado. (From Sauer et al. 2005.)

Figure 5 illustrates this idea for the horned lark of North America. Horned larks are most common in the prairies of eastern Colorado and in western Kansas and Nebraska, and are absent altogether in Florida. Why should these patterns of abundance occur? Why does abundance decline as one approaches the edge of a species' geographic range? What limits the eastern and northern extension of the horned lark's range? These are examples of the fundamental questions an ecologist must ask of nature.

Similarly, the red kangaroo occurs throughout the arid zone of Australia (**Figure 6**). It is absent from the tropical areas of northern Australia and most common in western New South Wales and central Queensland. Why are there no red kangaroos in tropical Australia? Why is this species absent from Victoria in southern Australia and from Tasmania? We can view the average density of any species as a contour map, with the provision that the contour map may change with time. Throughout the area of distribution, the abundance of an organism must be greater than zero, and the limit of distribution equals the contour of zero abundance. Distribution may be considered a facet of abundance, and distribution and abundance may be said to be reverse sides of the same coin (Andrewartha and Birch 1954). The factors that affect the distribution of a species may also affect its abundance.

The problems of distribution and abundance can be analyzed at the level of the population of a single

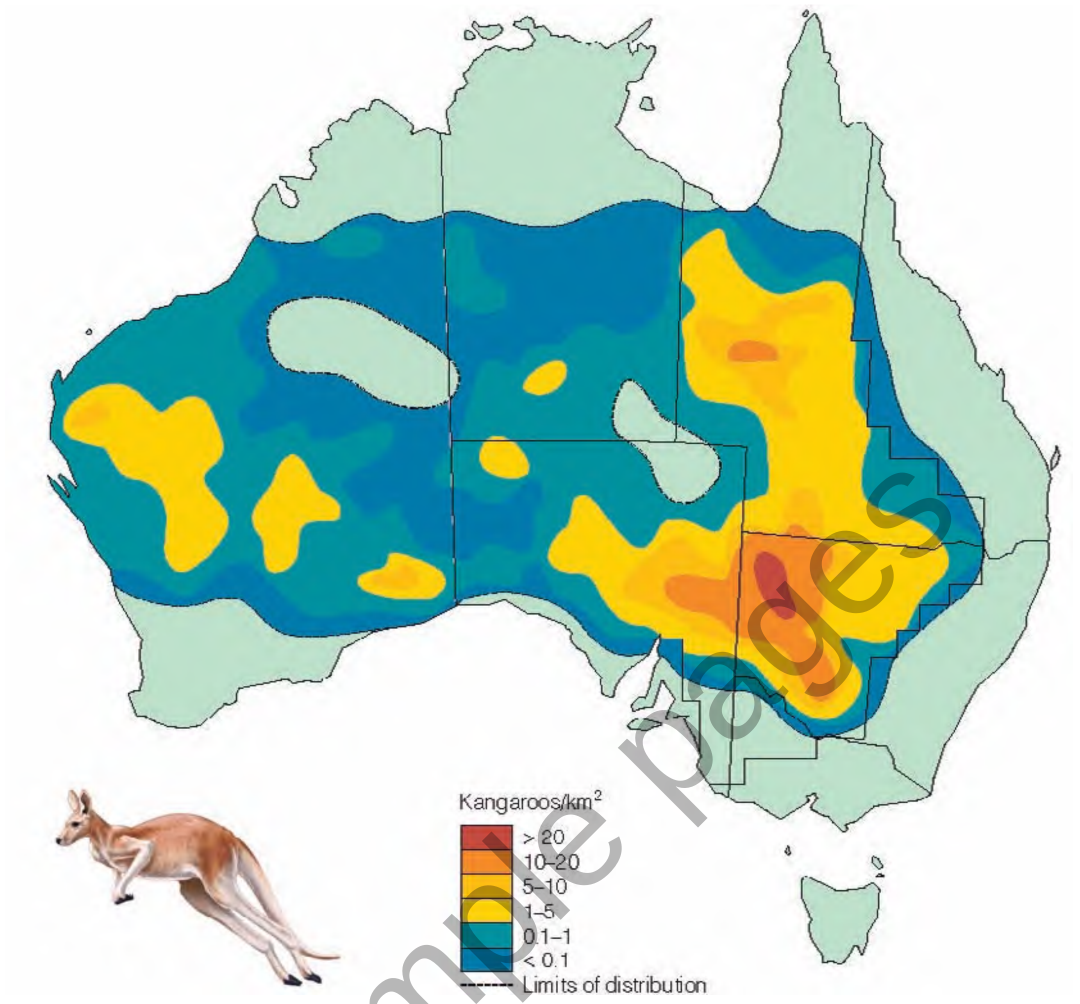

Figure 6 Distribution and abundance of the red kangaroo in Australia. Data from aerial surveys, 1980–1982. (From Caughley et al. 1987.)

species or at the level of a community, which contains many species. The complexity of the analysis may increase as more and more species are considered in a community; consequently, we will first consider the simpler problems involving single-species populations.

Considerable overlap exists between ecology and its related disciplines. Environmental physiology has developed a wealth of information that is needed to analyze problems of distribution and abundance. Population genetics and ecological genetics are two additional foci of interest that we touch on only peripherally. Behavioral ecology is another interdisciplinary area that has implications for the study of distribution and abundance. Evolutionary ecology is an important focus for problems of adaptation and studies of natural selection in populations. Each of these disciplines can become an area of study entirely on its own.

Levels of Integration

In ecology we are dealing primarily with the five starred (*) levels of integration, as shown in **Figure 7**. At one end of the spectrum, ecology overlaps with environmental physiology and behavioral studies of individual organisms, and at the other end, ecology merges into meteorology, geology, and geochemistry as we consider landscapes. Landscapes can be aggregated to include the whole-Earth ecosystem, which is called the **ecosphere** or the **biosphere**. The important message is that the boundaries of the sciences are not sharp but diffuse, and nature does not come in discrete packages.

Each level of integration involves a separate and distinct series of attributes and problems. For example, a population has a density (e.g., number of deer per square kilometer), a property that cannot be attributed

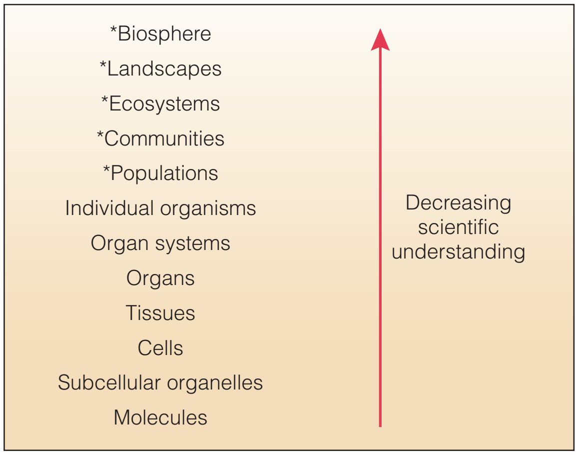

Figure 7 **Levels of integration studied in biology.**

to an individual organism. A community has biodiversity (or species richness), an attribute without meaning at the population level. In general, a scientist dealing with a particular level of integration seeks explanatory mechanisms from lower levels of integration and biological significance from higher levels. For example, to understand mechanisms of changes in a population, an ecologist might study mechanisms that operate on the behavior and physiology of individual organisms, and might try to view the significance of these population events within a community and ecosystem framework.

Much of modern biology is highly reductionistic, as it attempts to work out the physical–chemical basis of life. A good example is the Human Genome Project, an expensive and highly targeted research program to sequence all the genes on human chromosomes. The Human Genome Project is now completed, yet we do not know how many species of beetles live on the Earth, or how many species of trees there are in the Amazon basin. It should not surprise you that the amount of scientific understanding varies with the level of integration. We know an enormous amount about the molecular and cellular levels of organisms, organs and organ systems, and whole organisms, but we know relatively little about populations and even less about communities and ecosystems. This point is illustrated by looking at the levels of integration: Ecology constitutes more than one-third of the levels of biology, but no biology curriculum can be one-third ecology and do justice to current biological knowledge. The reasons for this are not hard to find; they include the increasing complexity of these higher levels and the difficulties involved in dealing with them in the laboratory.

This decrease in understanding at the higher levels has serious implications. You will not find in ecology the strong theoretical framework that you find in physics, chemistry, molecular biology, or genetics. It is not always easy to see where the pieces fit in ecology, and we will encounter many isolated parts of ecology that are well developed theoretically but are not clearly connected to anything else. This is typical of a young science. Many students unfortunately think of science as a monumental pile of facts that must be memorized. But science is more than a pile of precise facts; it is a search for systematic relations, for explanations to problems in the physical world, and for unifying concepts. This is the growing end of science, so evident in a young science like ecology. It involves many unanswered questions and much more controversy.

The theoretical framework of ecology may be weaker than we would like at the present time, but this must not be interpreted as a terminal condition. Chemistry in the eighteenth century was perhaps in a comparable state of theoretical development as ecology at the present time. Sciences are not static, and ecology is in a strong growth phase.

Methods of Approach to Ecology

Ecology has been approached on three broad fronts: the theoretical, the laboratory, and the field. These three approaches are interrelated, but some problems have arisen when the results of one approach fail to verify those of another. For example, theoretical predictions may not be borne out by field data. We are primarily interested in understanding the distribution and abundance of organisms in nature—that is, in the field. Consequently, the descriptive ecology of populations, communities, and ecosystems will always be our basis for comparison, our basic standard.

Plant and animal ecology have tended to develop along separate paths. Historically, plant ecology got off to a faster start than animal ecology, despite the early interest in human demography. Because animals are highly dependent on plants, many of the concepts of animal ecology are patterned on those of plant ecology. Succession is one example. Also, since plants are the source of energy for many animals, to understand animal ecology we must also know a good deal of plant ecology. This is illustrated particularly well in the study of community relationships.

Some important differences, however, separate plant and animal ecology. First, because animals tend to be highly mobile whereas plants are stationary, a whole series of new techniques and ideas must be applied to animals—for example, to determine population density. Second, animals fulfill a greater variety of functional roles in nature—some are herbivores, some are carnivores, some are parasites. This distinction is not complete because there are carnivorous plants and parasitic plants, but the possible interactions are on average more numerous for animals than for plants.

During the 1960s population ecology was stimulated by the experimental field approach in which natural populations were manipulated to test specific predictions arising from controversial ecological theory. During these years ecology was transformed from a static, descriptive science to a dynamic, experimental one in which theoretical predictions and field experiments were linked. At the same time, ecologists realized that populations were only parts of larger ecosystems, and that we needed to study communities and ecosystems in the same experimental way as populations. To study a complex ecosystem, teams of ecologists had to be organized and integrated, which was first attempted during the late 1960s and the 1970s.

Modern ecology is advancing particularly strongly in three major areas. First, communities and ecosystems are being studied with experimental techniques and analyzed as systems of interacting species that process nutrients and energy. Insights into ecosystems have been provided by the comparative studies of communities on different continents. Second, modern evolutionary thinking is being combined with ecological studies to provide an explanation of how evolution by natural selection has molded the ecological patterns we observe today. Behavioral ecology is a particularly strong and expanding area combining evolutionary insights with the ecology of individual animals. Third, conservation biology is becoming a dominant theme in scientific and political arenas, and this has increased the need for ecological input in habitat management. All of these developments are providing excitement for students of ecology in this century.

Application of the Scientific Method to Ecology

The essential features of the scientific method are the same in ecology as in other sciences (**Figure 8**). An ecologist begins with a problem, often based on natural history observations. For example, pine tree seedlings do not occur in mature hardwood forests on the Piedmont of North Carolina. If the problem is not based on correct observations, all subsequent stages will be useless; thus, accurate natural history is a prerequisite for all ecological studies. Given a problem, an ecologist suggests a possible answer, which is called a **hypothesis**—a statement of cause and effect. In many cases, several answers might be possible, and several different hypotheses can be proposed to explain the observations. Hypotheses arise from previous research, intuition, or inspiration. The origin of a hypothesis tells us nothing about its likelihood of being correct.

A hypothesis makes predictions, and the more precise predictions it makes the better. Predictions follow logically from the hypothesis, and mathematical reasoning is the most useful way to check on the logic of predictions. An example of a hypothesis is that pines do not grow under hardwoods because of a shortage of light. Alternative hypotheses might be that the cause is a shortage of pine seeds, or a shortage of soil water. Predictions from simple hypotheses like these are often straightforward: If you provide more light, pine seedlings will grow (under the light hypothesis). A hypothesis is tested by making observations to check the predictions—an experiment. An **experiment** is defined as any set of observations that test a hypothesis. Experiments can be manipulative or natural. We could provide light artificially under the mature forest canopy, or we could look for natural gaps in the forest canopy. The protocol for the experiments and the data to be obtained are called

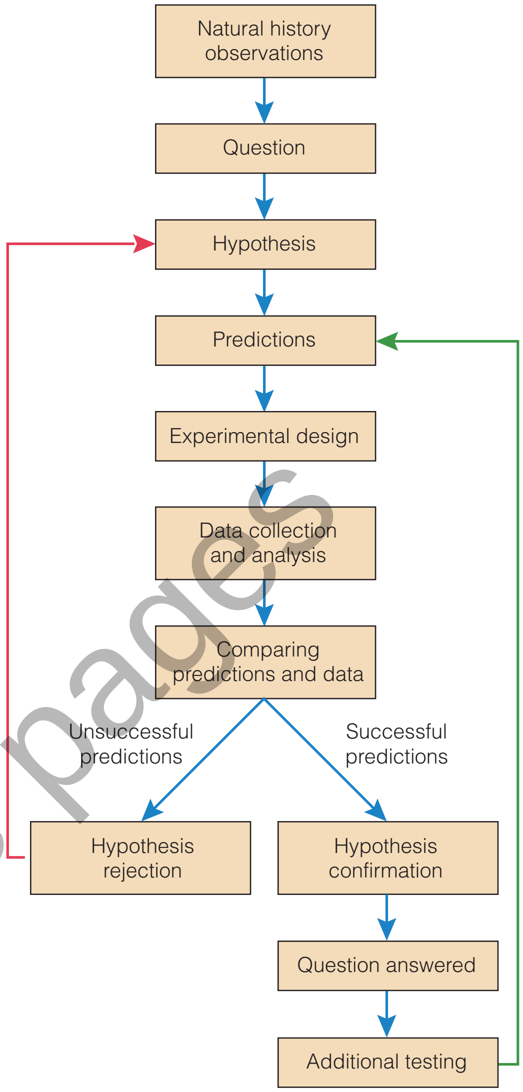

Figure 8 Schematic illustration of the scientific method as applied to ecological questions.

ESSAY

On Ecological Truth

We wish our scientists to speak the truth, and when politicians bend the truth they lose credibility. What is truth, and what in particular is the hallmark of ecological truth? The notion of truth is a profound one that philosophers discuss in detail and scientists just assume is simple.

Truth consists of correspondence with the facts. If we say that there are 23 elephants in a particular herd in the Serengeti, we are stating an ecological truth because we assume that if another person counted the elephants, he or she would get the same number. These kinds of facts are relatively simple, and scientists rarely get into arguments about them. Where arguments start is in the inferences that are drawn from whole sets of facts. For example, if we had counts of the same elephant herd over 20 years, and numbers were continually falling, we could say that this elephant population is declining in size. This statement is also an ecological truth if we have done our counting well and recorded all the data correctly.

But now suppose we wish to state that the elephant population is declining and that a disease is the cause of this decline. Is this statement an ecological truth? It is better to consider it an ecological hypothesis and to outline the predictions it makes about what we will find if we search for a disease organism in elephants dying in this particular area. We now enter a gray zone in which ecological truth is approximately equivalent to a supported hypothesis, one in which we checked the predictions and found them to be correct. But if a scientist wished to extend this argument to state that elephant populations all over east Africa are collapsing because of this disease, this is a more general hypothesis, and before we can consider it an ecological truth we would need to test its predictions by studying many more populations of elephants and their diseases. Many of our ecological ideas are in this incomplete stage because we lack the time, money, or personnel to gather the data to decide whether the general hypothesis is correct. So ecologists, like other scientists, must then face the key question of how to deal with uncertainty when we do not know if we have an ecological truth or not.

> *The central idea of this principle is to do no harm to the environment, to take no action that is not reversible, and to avoid risk.*

The key resolution to this dilemma for environmental management has been the precautionary principle: "Look before you leap," or "An ounce of prevention is worth a pound of cure." The precautionary principle is the ecological equivalent of part of the Hippocratic Oath in medicine: "Physician, do no harm." The central idea of this principle is to do no harm to the environment, to take no action that is not reversible, and to avoid risk. Ecological truth is never obvious in complex environmental issues and emerges more slowly than we might like, so we cannot wait for truth or certainty before deciding what to do about emerging problems in the environment, whether they concern declining elephant populations or introduced pest species.

the experimental design. Using the data that result from the experiments, we either accept or reject the hypothesis. And so the cycle begins again (Figure 8).

Many qualifications need to be attached to this simple scheme. Popper (1963) pointed out that we should always look for evidence that falsifies a hypothesis, and that progress in science consists of getting rid of incorrect ideas. In practice, we cannot achieve this ideal. We should also prefer simple hypotheses over complex ones, according to Popper, because we can reject simple hypotheses more quickly. This does not mean that we must be simpleminded. On the contrary, in ecology we must deal with complex hypotheses because the natural world is not simple. Every hypothesis must predict something and forbid other things from happening. The predictions of a hypothesis must say exactly what it allows and what it forbids. If a hypothesis predicts everything and forbids nothing, it is quite useless in science. The light hypothesis for pine seedlings both predicts more seedlings if you add more light and forbids more seedlings if you add more water.

Ecological systems are complex, and this causes difficulty in applying the simple method outlined in Figure 8. In some cases factors operate together, so it may not be a situation of light *or* water for pine seedlings but one of light *and* water. Systems in which many factors operate together are most difficult to analyze, and ecologists must be alert for their presence (Quinn and Dunham 1983). The principle, however, remains—no matter how complex the hypothesis, it must make some predictions that we can check in the physical world.

All ecological systems have an evolutionary history, and this provides another fertile source of possible explanations. There is controversy in ecology about whether one needs to invoke evolutionary history to explain present-day population and community dynamics.

Evolutionary hypotheses can be tested as Darwin did, by comparative methods but not by manipulative experiments (Diamond 1986).

Ecological hypotheses may be statistical in nature, but they do not fall into the “either A or B” category of hypotheses. Statistical hypotheses postulate quantitative relationships. For example, in North Carolina forests, pine seedling abundance (per m^2) is linearly related to incident light in summer. Tests of statistical hypotheses are well understood and are discussed in all statistics textbooks. They are tested in the same way indicated in Figure 8.

Some ecological hypotheses have been very fruitful in stimulating work, even though they are known to be incorrect. The progress of ecology, and of science in general, occurs in many ways, using mathematical models, laboratory experiments, and field studies.

Review Questions and Problems

1. Discuss the connotation of the words *ecologist* and *environmentalist*. Would you like to be labeled either of these names? Where in a public ranking of preferred professions would these two fall?
2. Look up the definition of *environment* in several standard dictionaries and in the *Oxford Dictionary of Ecology* (2006), and compare them. Is it possible to measure the environment of an individual? Are other individuals part of the environment of an individual?
3. Is it necessary to define a scientific subject before one can begin to discuss it? Contrast the introduction to several ecology textbooks with those of some areas of physics and chemistry, as well as other biological areas such as genetics and physiology.
4. A plant ecologist proposed the following hypothesis to explain the absence of trees from a grassland area: Periodic fires may prevent tree seedlings from becoming established in grassland. Is this a suitable hypothesis? How could you improve it?
5. Is it necessary to study the scientific method and the philosophy of science in order to understand how science works? Consider this question before and after reading the essays by Popper (1963) and Platt (1964).
6. Discuss the application of the distribution and abundance model to microbes and viruses.
7. Quinn and Dunham (1983) argue that the conventional methods of science cannot be applied to ecological questions because there is not just one cause; one effect and many factors act together to produce ecological changes. Discuss the problem of “multiple causes” and how scientists can deal with complex systems that have multiple causes.
8. A wildlife ecologist interested in protecting large mammals by means of wolf control analyzed data from six sites at which wolves had been removed for five consecutive years. On three of the sites, the prey species (moose and caribou) had increased, and on three of the sites prey populations did not change. How would you interpret these data in light of Figure 8?
9. Plot the data in Table 1 graphically, with gross national product (x-axis) versus total fertility rate (y-axis). How tight is the relationship between these two variables? Discuss the reasons for the overall form of this relationship, and the reasons why there might be variation or spread in the data.

Overview Question

Does ecology progress as rapidly as physics? How can we measure progress in the sciences, and what might limit the rate of progress in different sciences? Will there be an “end to science”?

Suggested Readings

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