GROWTH AND REGULATION OF ANIMAL POPULATIONS

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preface

The point of this book is to indicate briefly the present state of theory relating to the number and kinds of animals and plants that are found in nature. The subject is sufficiently new and the various attempts at constructing such a theory are so diverse that at present there is no convenient short, comprehensible term to designate this theory. "Ecology," the general term, is concerned with the interaction between organisms and their environment in the broadest possible sense. Our problem here is somewhat more narrow and excludes, to a large degree, simple description of the natural world, on one hand, and much of the physiological reaction of individual organisms to their private worlds, on the other. We will be primarily concerned with interactions between individual animals that live in association with each other, insofar as these interactions in some way alter the number and kinds of these animals. Every reader will find some material in this book that appears trivially obvious to him. I doubt, however, that all of it will appear obvious to any one person or that any two readers will be in agreement as to which parts are obvious. Bear with me when I repeat, in a naive-sounding way, things you already know.

On occasion I will be forced to use algebraic notation. Everything stated in a mathematical form, however, will also be said verbally. If you have an allergy to notation, read only the prose and take my word for the rest.

By the end of the book I hope it will be clear that the problem of constructing a general theory of kind and abundance of animals is a real, empirically solvable problem; that we are not able to present a solution yet, but that the general procedures involved in such a solution are available at least in principle. I hope it will also be clear that this area represents an intellectual challenge of the first magnitude and that high-quality investigators are very much needed. The practical ramifications of this problem are as significant for the future survival of mankind as the solution to the problem of control of atom bombs.

The initial chapters describe in a general way the kinds of order and interaction that seem to exist in nature. We will then discuss some of the statistical properties that are used in the analysis of populations of individual species. With this background we will present experimental models of natural communities and some of the theory that has been constructed from them. Gradually we will generalize our experiments and theory until we return to the natural world, with perhaps a deeper comprehension than we had originally.

L. B. S.

Ann Arbor, Michigan
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Francis Evans, Nelson Hairston, Fred Smith, and Marston Bates of the University of Michigan, Sumner Richman of Lawrence College, and Joseph Armstrong of Monteith College, Wayne State University, have all contributed criticism and encouragement.

On rereading, I find that the entire document is in one sense a commentary on some ideas of my teacher, G. Evelyn Hutchinson of Yale University.

The errors are my own.

contents

chapter one	▸ Man in the Ecological World	1
chapter two	▸ Communities and Populations	8
chapter three	▸ The Ecological Niche in a General Sense	25
chapter four	▸ Life Insurance for Animals	33
chapter five	▸ Reproduction and Increase	45
chapter six	▸ Simple Changes in Populations	56
chapter seven	▸ Competition between Species	62
chapter eight	▸ Gause's Experiments and Their Implications	71
chapter nine	▸ Weakness of the Sigmoid Growth Model; Growth of Metazoan Populations	82
chapter ten	▸ Escape in Time and Space	107
chapter eleven	▸ Interactions between Metazoan Species	117
chapter twelve	▸ Prudent Predators and Efficient Prey	130

chapter thirteen ▶ Predator-Prey Interactions 143

chapter fourteen ▶ The Reality of Cycles 152

chapter fifteen ▶ Communities in Nature 160

chapter sixteen ▶ Speculation 167

Bibliography 173

Index 181

chapter one

Man in the Ecological World

No matter how unique man may be from the standpoint of intellect, esthetics, or metaphysics, he has the same overall biological demands as any other animal. Despite the apparent complexity, self-sufficiency, and independence of human civilization, the laws governing population growth and maintenance in plants and animals are very similar to those governing population growth and maintenance in man. We will assume these statements to be axiomatic; the necessary qualifications and explanations will become apparent from the remainder of the text. The text will not be particularly concerned with man himself, except as one of many examples of a highly social population. To avoid interrupting the discussion later, it may be well to indicate initially man's role in nature and the practical significance of studies of nonhuman population dynamics.

Several authors (Brown, 1954; Darling, 1955; Elton, 1958; Osborn, 1948; Sears, 1935; Vogt, 1948) have discussed man's role in nature, and a recent and impressive symposium volume (Thomas, 1956) discusses the effect of man on the earth. Without recounting the voluminous documentation in detail, certain conclusions may be drawn.

Civilization, particularly in its recent history, has been a major source of geologic change on the earth, equivalent in the magnitude of its effects to the natural geologic forces of rain and frost. The constructions arising from the efforts of man differ from other features on the face of the earth in their relative lack of stability. Without the activity of man most of these changes would never appear at all, and without man's care and maintenance most of them would disappear. For example, metals typically exist on the earth's natural surface in an oxidized state. Man's metal structures, however, are made of reduced metals. The process of changing metals from the oxidized to the reduced state is one of the major power-consuming processes of civilization. Again, large masses of nonmetallic rock are typically acted upon by water, heat, and gravity to produce solid masses with sloping sides. Most of man's buildings are vertical walled and hollow. It is noteworthy that the few mound-shaped solid structures built by man have lasted longer than even the languages spoken by their architects. To make improbable objects and maintain them against dissolution requires tremendous expenditures of energy. Recently this energy has been supplied by the rapid dissolution, instigated by man, of otherwise relatively stable geologic formations, such as coal beds or subterranean oil pools.

Man's construction and maintenance act to alter the direction of some geologic changes and to increase greatly the rate of others. For most of its history the nonhuman biological world has existed under conditions of relatively slow geologic change, but the new geology of man—the geology of the noösphere—to use Vernadsky's term (1944), has brought about relatively rapid change in the lives of many organisms. Foxes, for example, have vanished from the rocks of Manhattan but rats have expanded into the tunnels and sewers.

In addition to altering the geologic surface of the earth, man acts directly on biological systems. He has eliminated some of the large organisms that he considered at the time to be dangerous or useless. The wolf has been eliminated from eastern North America and the lion from most of the Indian peninsula and the entire Middle East. Man does his futile best to eliminate some other species, which accounts for the drainage canals being dug in the New Jersey marshes, in which the mosquitoes continue to breed. Often a species or a population vanishes by accident because it happens to be in the way of some other biological effort of man. Various fish populations have died in man's feud with the mosquitoes. Bayberry, snails, cedars, large ungulates—all have had their populations decimated because they share a parasite with man or one of man's creatures.

Since man has food requirements similar to those of the other large mammals, he encourages the increase of certain plants and animals that provide him with food and with the peculiarly human requirements of clothing and ornament. In this process man, assuming the role of director of evolution, has appropriated at least 10 percent of the earth's surface.

Mountains, oceans, deserts, and even rivers act as barriers to many animals and some species of plants. Communities of mutually tolerant species have developed inside these barriers. Occasionally an animal is rafted or blown or harassed across a barrier and may momentarily upset the structure of nature on the new land. In such a case the new organism may replace some existing species or simply fit in with only a slight change in the abundance of the other species; most likely it will be unable to become established in the new location and will die.

In the course of his daily commerce man roams the earth, crossing these barriers, carrying—on his person or in the recesses of his ship, plane, canoe, or pocket—pets, pests, weeds, parasites, improvements and ornaments, both plant and animal. Dogs, cats, goats, and pigs have been spilled into every port-of-call. Fleas, rats, flies, ants, lice, and infinite varieties of microorganisms have stowed away on almost every journey man has ever made. Although rat guards on hawsers may do the work for which they were introduced, how does one prevent escape of beetles from an airplane? Under this hail of immigrants, radical changes are occurring in the nonhuman world wherever mankind passes.

Not only is man the most shocking innovation since the first appearance of the terrestrial vertebrates, but his activities are proceeding at an accelerating rate. Not only are the numbers of men on the earth increasing at almost 3 percent per year, but the standard of living of all men is rising, with a concomitant increase in the per capita demands for fuel and raw materials of all sorts. The importance of man continues to increase and the possibility of the biological world ever being as stable as it was in prehuman time becomes more and more remote. How many men can the earth hold? We must abandon all pretense of saving intact any wilderness areas and consider that we will treat the earth as a combined garden and factory; all other species will either prove useful to man or will be eliminated; they will either adjust to the omnipresence of man or die. Answers to the question are now merely guesses, ranging from 7 billion to 200 billion, the difference in the estimates depending on how several subsidiary questions are answered.

Implicit in this picture of the future is a mental health problem: a world completely full of man and his activities could well be a maddening place. There is an esthetic problem: the beauty of the wilderness is very real. There is a political problem: a world full of men would be highly regimented, a world of an Aldous Huxley or Orwell fantasy.

Even more terrifying is the eventual biological problem. Many of the elements on the surface of the earth are now being used and reused. The carbon in our atmosphere has passed through living things several times since the world began. The nitrogen in your breakfast may have been through four other organisms in the last four years. In general, plants bind the various elements that make up living stuff in an energy-rich form, using light energy from the sun in the process of photosynthesis. This energy is respired as fast as it is made. We know this, since organic compounds by and large do not accumulate anywhere, which would be the case if energy were not being respired. Plants respire only about a third of the photosynthetically fixed energy. Two-thirds goes into supplying the food for all the nongreen things that are alive on the earth. Since it is known that energy does not accumulate, and in most of America we can look out a window and see vegetation that shows no sign of being chewed or decimated by animals, we can infer that much of the energy is consumed by animals after it leaves the living plants. Bacteria and molds fill the soil and the microarthropods feed on them. The fact that the grasshoppers, caterpillars, and other organisms that feed directly on the live plants do not denude the leaves, except during unusual periods, indicates that something other than food shortage is controlling the numbers of these herbivores, the obvious inference being that they are controlled by predators. If the predators and decomposers are responsible for the lack of accumulation of organic material, then they must be limited in their abundance by the quantity of organic plant material available. In short, the absence of the accumulation of organic material implies that there exists a balance in nature in at least one sense. How far man can alter this nice balance without causing excess or defect in the rate of utilization of carbon dioxide in the atmosphere or the rate of silting of lakes and rivers, and what the effect would be on man of tripling the carbon dioxide concentration in the atmosphere, we do not know.

In addition to the gross cycles of water and carbon there are cycles of reuse occurring in the less conspicuous elements such as vanadium, cobalt, molybdenum, and barium. Quite often these hinge in a large part on the biological activities of a relatively few species. For example, sea squirts are of major significance in the passage of vanadium through the sea. How are these cycles affected by man and how may his present activities be altering them? Some of man's disturbances of nature are harmless, but it is quite possible that some of them may have ramifications that will seriously alter man's world. It is, unfortunately, impossible to determine, at the present time, the complete implications of any disturbance of nature. We can confidently say that as human populations and human standards of living and rates of per capita environment consumption increase, the margin for error in judgment diminishes.

The normal activities of man cannot continue without constant disruption of nature. The spread of population and railroads in India that has seriously interfered with the mating behavior of the Indian rhino (Ripley, 1952) is a case that generates only a certain amount of intellectual and perhaps sentimental regret. But are we as certain that various other results of our population growth will create only a diminution of the variability of nature? Some may be much more dangerous than that.

The primary problem is to ensure, so far as possible, that the disturbance produced by man is reversible. By keeping a careful check on what we may call "man-associated" nature it may be possible to see the effects of disturbance while we can still change our activities. Agricultural procedures have repeatedly been altered when it was found that soil conditions were deteriorating too rapidly. In some cases this has actually restored a semblance of *status quo ante*. If, as is quite likely, vital aspects of man's ecology are dependent on undomesticated species, nature sanctuaries not only are of esthetic, sentimental, and recreational value but are indispensable reserves of biological raw material to be used for the retracing of our ecological steps. Such retracing may become necessary for the construction of a viable ecology. It is impossible to reconstruct a particular species once it is extinct. Some species and communities of species have critical limits of perturbation, beyond which they cannot recover. These limits of resilience of the natural world are not now known in any particular case. All we know is that they do exist and that we must somehow determine what they are.

The natural world seems infinitely complex to the casual observer. We must admit this complexity as an empirical fact. Descriptions of nature can, then, be in one of two forms: we can describe it in all its complexity or we can analyze it into simpler parts and describe them. A direct description will be accurate only to the degree that it mirrors the complexity of the subject. It is no easier to make predictions from such a description than from casual observation itself. This does not denigrate the value of such description. Anyone who has worked in nature on a specific problem involving prediction is struck with the accuracy of the observations of some laymen. An example of this occurred while I was traveling to Sarasota, Florida, to take charge of the red tide investigation, and started talking to a fisherman on a bus between Daytona Beach and Melbourne. His conclusions about red tide, modified in some details, were essentially identical with the conclusions I published two years and $80,000 later. The fisherman, unfortunately, could not precisely define the evidence and arguments that led to his conclusions. He was therefore simply guessing correctly.

In problems with little risk involved, an educated guess is an acceptable guide to decision. As the penalties for error increase, however, it is vital that most of the intuitive portion of the guessing procedure be replaced by publicly verifiable theory. Although the red tide was an economically significant problem, it had no life-or-death ramifications, and so the fisherman's clever guess or my simple-minded theory were sufficient guides for recommendations. Unfortunately, ecological problems in the broad sense do become matters of life and death. Man is examining his own habitat and cannot afford to destroy it. We cannot expect public administrators to be trained naturalists and at the same time develop the necessary information about law and economics. Moreover, there is no clear evidence that anyone can think as nature does; some of our very best naturalists have made unfortunate errors when they built on this semimystical foundation. On the other hand, there is some evidence to indicate that the man who makes the dry theoretical analysis must have some personal experience of the natural world. Occasionally, population theories made by pure mathematicians, astronomers, and statisticians have proven sterile or dangerous, or both. There is good reason, also, to believe that without formal training the statements made by the lover of nature are nothing more than an ecstatic cry having esthetic meaning only.

Our only alternative is to attempt to analyze nature so that it may be described in a rigorous way and so that predictions can be derived by publicly repeatable procedures. Such a description of nature is fragmentary in the sense that all the population equations, community theory, and sampling statistics in the world will not appear identical with an actual landscape. A Chinese mountain landscape screen or the description in the Canticles of a spring morning are more similar to nature itself but unfortunately have less predictive value than the "unnatural"-looking equations. After pulling out of the natural world the various tangled threads that can be rigorously analyzed, we will examine them with some care and then try to put them back together and see how closely this synthetic mathematical fabric resembles the tapestry from which it was pulled. The two will probably not look very much alike, but we should then be able to define, to some degree, the difference between what we know on theoretical grounds and what we must yet do before we can build safe predictions.

It goes without saying that the predictions are required immediately, and the theories are still primitive and show every sign of growing slowly. This is an untenable situation for which I can offer no easy solution.

chapter two

Communities and Populations

If you were to make a fence around any region of the earth's surface and list the kinds and numbers of organisms found within that fence, you would be starting to define the problem of population ecology. Making an actual list and count of this type, however, is a painful operation for several reasons. The three most obvious will be listed.

First, it takes something of an expert to distinguish one kind of animal from another, and becoming an expert on some groups of animals may require years of study. There are, for example, 200,000 kinds of beetles and 50,000 kinds of protozoa. Two hundred different species of arthropods alone may be found in the soil under a 5-inch diameter circle.

Second, the actual numbers of organisms involved is very high in some cases. A half-million arthropods per square meter of soil, 10 million protozoa per liter of sea water, a billion bacteria per meter of mud—these would in many instances be common figures.

The third objection is that it is difficult to determine how reliable and meaningful any particular count may be. How many of the organisms in the area examined really belong there and how many are just passing through? If you examined the area tomorrow, would the animals and plants be the same in numbers and kinds as they are today? If the boundaries of your area were shifted slightly, what would happen to the kinds and numbers of organisms in it? How far can any estimate be generalized?

Despite these problems there certainly does seem to be order in the natural world, and this order cries out for explanation. For example, a typical rural landscape, as seen from the side of a road, may include grassland or pasture land in the foreground, a row of bushes behind them, and in the distance a backdrop of trees. Another typical view might include a small pond, surrounded by marsh, with plowed land in the distance and a woodlot. It is obvious to the hunter that certain sorts of game will be found in forests rather than in the open fields, and it is clear that an angler will drop his hook in water rather than sand. Each of these intuitively recognized regions of the landscape may be called a "community."[1] The boundaries between the communities are usually readily recognizable by the boundaries between the most visible plants (referred to as dominant plants). Portions of the landscape can thus be catalogued in various ways. We can, for example, categorize on the basis of the geometric shape of the dominant vegetation—that is, grassland, forests, etc. Grassland is recognized by the arrangement of the dominant vegetation as a relatively low carpet of plants, each individual plant being relatively insignificant in size; forest, as a canopy of plants with most of the green portions at their tops, forming an open, shaded region around the stems or trunks of the individual plants. We normally think of grassland as something a man can look over the top of, and a forest as something a man walks through. Forests, grasslands, marshes, etc., can also be categorized in terms of the kinds of plants that form the dominant vegetation; an oak-hickory community, for example, is different from a spruce-hemlock forest community, and a buffalo-grass community is different from a dune-grass community.

Extensive field studies have made it possible, at least in parts of the United States, to map the location of different terrestrial communities, both by dominant vegetation type and general topography (Clements and Shelford, 1939) and by the associations of species, independent of topography (the biotic provinces of Dice).

[1] The term "community" is here used in a very broad sense, essentially identical with "ecosystem" as used by Dice (1952). The concept is more clearly defined on p. 11.

However, where a community covers a large area—for example, the Carolinian province, or the beech-maple community, in several states of the eastern United States—it is almost impossible to make detailed predictions about the flora or fauna of any subdivision of major ecological units, although it is generally possible to make some predictions about the kinds of organisms that will be present and the kind that will be absent. It is thus advisable to examine smaller regions of the earth's surface, which may prove more amenable to complete analysis. How are such areas to be chosen?

The eventual goal is to discover exactly what determines the numbers and kinds of organisms in each area. The area selected should therefore be one in which most or all of the various possible interactions between organisms, and between organisms and their environment, are comprehensible in local terms. A pond or small lake or even a relatively permanent puddle is more likely to meet these requirements than a field or forest of equal surface area or than the volume of water under an equal surface area in the ocean or one of the Great Lakes. There are two reasons for this. A pond or small lake is clearly differentiated from the surrounding countryside by a drastic change in physical properties, which in turn implies a sharp boundary in the distribution of most animals. Water and air are very different, and the kinds of organisms adapted to water are in general very different from the kinds of organisms adapted to air. Although a small oceanic area has the air-water interphase as its upper boundary, it is not bounded on the edges. Further, a pond or small lake is concave, which means that all passive organisms and their products will stay in the community and will leave the boundary of the pond only by active transport —either by their own movement, or by being carried by some other organism, or by some sudden flow of water. It is not surprising, therefore, that much of the modern theory of ecology has been developed in lakes and with aquatic organisms.

Even in the nonaquatic parts of nature, however, we want to be able to define subregions small enough to permit detailed analysis. Because of their tremendous size and complexity, whole forests and whole biotic provinces cannot be analyzed in detail. Enough work has been done in such areas to demonstrate the existence of regularities, but the more discrete and simple the systems studied, the more apparent these regularities become.