ANDREWARTHA

and

BIRCH

and Abundance of Animals

THE DISTRIBUTION AND ABUNDANCE *of* ANIMALS

By

H. G. ANDREWARTHA

Waite Agricultural Research Institute, University of Adelaide

and

L. C. BIRCH

Department of Zoology, University of Sydney

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PART I

Introduction

CHAPTER 1

The Scope of Ecology

In solving ecological problems we are concerned with what animals do *in their capacity as whole, living animals, not as dead animals or as a series of parts of animals. We have next to study the circumstances under which they do these things, and, most important of all, the limiting factors which prevent them from doing certain other things. By solving these questions it is possible to discover the reasons for the* distribution and numbers of animals in nature.

ELTON (1927, p. 34)

1.0 THE TWO SORTS OF ECOLOGY

IN ITS full context the quotation which heads this chapter emphasized the difference between the older disciplines of anatomy, histology, taxonomy, physiology, etc., and the newer one of ecology, in which, as Elton said, we have to study the living animal in the circumstances in which it is found in nature. Our purpose, in doing this, is to explain why a certain kind of animal is found in certain areas but not in others; why they are numerous in one place but scarce in another; why they are more numerous this year than they were last; and so on. This problem has been tackled in two very different ways.

It was appreciated from the very first that the same, or a similar, group of species is likely to be found in the same sort of "habitat" (see sec. 2.2 for the meaning of "habitat"). So it became popular to study these communities of animals; and to many it has seemed as if this were the very essence of ecology. In order to help with the study of communities, Elton (1927, p. 63) used the term "niche."

The best way to indicate briefly the scope of community ecology is to explain the meaning of "niche." In the paragraph in which he used this term Elton said that all communities of plants and animals have a similar ground-plan; they all have their herbivores, carnivores, and scavengers. In a wood there may be certain caterpillars which eat the leaves of trees, foxes which hunt rabbits and mice, beetles which catch springtails, and so on. "It is convenient to have some term to describe the status of an animal in its community, to indicate what it is *doing* and not merely what it looks like, and the term used is 'niche.' . . . The 'niche' of an animal means its place in the biotic environment, *its relations to food and enemies*." Thus the caterpillar and the mouse broadly occupy similar niches because they eat plants; the fox and

the ladybird also fit broadly into similar niches because they both eat other animals in the community.

There are many papers in technical journals which report studies of communities of animals without stressing, or even mentioning, the niches which the different sorts occupy. At their worst, these may be mere descriptive lists; but the better ones usually report more or less quantitatively the relative numbers of the different sorts of animals. If the methods of the plant sociologists are followed—and they often are—the different species may be classified according to their "dominance" in the community (Kontkanen, 1948, 1949).

There is a difference of opinion about the meaning of "community"; some would stress the "ecological relationship" between species, whereas others would agree that any assemblage of species which is usually found in the same "habitat" is a community (Kontkanen, 1950). The "habitat" is a subjective concept, because the boundaries must be arbitrarily fixed by the student (sec. 2.2). The disagreement about the constitution of a community is academic and not important in practice, because the enormous task of unraveling the ecological relationships in even a simple community has usually proved impracticable. Instead, we are given descriptive accounts of all the animals that may be found in a certain "habitat." Or, if this prove to be too ambitious, the study may be restricted to a taxonomic group, perhaps a family or an order. Characteristic titles for papers in this field are: "Analysis of the Animal Community in a Beech Forest"; "An Ecological Study of the Saltatoria of Point Pelee"; or "The Tree-Hole Habitat with Emphasis on the Pselaphid Beetle Fauna."

These studies are justified by the hope that collectively they will discover the laws governing niches, that is, the relationships between the members of communities. Progress has been summarized from time to time, and the reader will know books by Pearse (1926), Elton (1927), Clements and Shelford (1939), Allee *et al.* (1949), Dice (1952), and others. All will agree that there is much more to be learned in this field. Nevertheless, these studies have been going on long enough now for us to be fairly sure that, no matter how mature the science of "community ecology" may become, it is not likely to give rise to a satisfactory, or even to any, general theory about "the distribution and numbers of animals in nature." There are two reasons for this. When too much emphasis is put on the community, too little attention is paid to the species whose distribution and abundance have to be explained. The distribution and abundance of a species cannot be explained by studying only its relations with the plants and animals in its "community." There are certain other important components of environment which also require to be considered.

But there are other zoölogists who have a practical and urgent interest in the distribution and abundance of animals. These are the ones who are concerned with the insects which may harm crops or livestock, or the vertebrates which are valued for their flesh or fur or even for the fun of shooting them. Papers

written by these men have such a wide range of titles that it is not possible to select characteristic ones. Only occasionally does one meet the word "ecology." When it occurs, it is used in a different context. "Ecological Studies of *Eutettix tenellus*" and "Ecology and Management of *Zenaidura macroura*" are two examples. Note that these titles imply that the ecology of a certain species has been investigated, not the "ecology" of a forest or a lake.

The two meanings are so distinct that the time may have come to give them different names. We cannot use "synecology" and "autecology" in this context. The meanings of these words have become attenuated (Chapman, 1931, p. 5; Allee *et al.*, 1949, pp. 48, 227); but in none of their meanings do they discriminate between that sort of ecology which leads to an explanation of the distribution and abundance of animals and that sort which describes the relationships of members of communities. In French a distinction is made between "la biocénotique" and "l'écologie"; and Kontkanen (1950, p. 9) suggested that "biocoenotics" might be used in all languages to cover the study of communities. If a new name is needed, this one seems to recognize the real cleavage which has developed in methods and knowledge, and it is etymologically satisfactory. But perhaps it would be best merely to speak of the "ecology" of a certain species or the "ecology" of a certain community.

The literature dealing with species of harmful insects and useful fishes, birds, and mammals is enormous. It contains, if one is prepared to search deeply, ample material from which to build a wide and satisfying general theory of ecology as we use this word to refer to the distribution and abundance of animals in nature. This has not hitherto been done; that is why we decided to write this book.

1.1 THE REASONS WHY DISTRIBUTION AND ABUNDANCE SHOULD BE REGARDED AS DIFFERENT ASPECTS OF THE SAME PROBLEM

In studying the ecology of an animal, we seek to answer the questions: Why does this animal inhabit so much and no more of the earth? Why is it abundant in some parts of its distribution and rare in others? Why is it sometimes abundant and sometimes rare? These are all problems of distribution and abundance.

The concept of *distribution* is well understood by naturalists. The distribution of a species coincides with the broad geographic limits inside which the species may be found more or less permanently established. It has become customary to separate distribution from abundance, although Elton (1927) was careful to avoid this error. However necessary this abstraction may be as a methodological device, the separation should never be allowed to persist in the final synthesis, for distribution and abundance are but the obverse and reverse aspects of the same problem. This becomes quite clear when we observe

closely the way animals are actually distributed in nature. Inside the distribution there may be favorable zones where a high level of abundance is maintained; but near the limits of the distribution there may be a marginal zone which is sometimes inhabited and sometimes not and which, in general, is a zone characterized by low numbers. Outside the distribution there are none. This interaction between distribution and abundance may be illustrated by the following example, which is based on the ecology of a certain grasshopper in Australia (see sec. 13.12). We did not have quite enough empirically determined facts to complete the example, so we filled in the gaps with imaginary values. These values are possible ones, and the example may be regarded as being essentially realistic.

The distribution of these grasshoppers is bounded on one side (coastward) by a humid zone, where arable farming is practiced; it is bounded on the other side by desert. The area where the grasshoppers are found is just too arid for arable farming, but hardy grasses and shrubs provide pasturage for sheep. The weather is unkind. The summer is hot and extremely arid; evaporation from an exposed surface of water may exceed 40 inches, and this may be tenfold the amount of rain that falls during the same period. The only plants that remain green during summer are certain xerophytic shrubs and trees which the grasshoppers do not eat. The winter is the wet season, and usually there are grasses and other herbs for the grasshoppers to eat. But the rainfall is unreliable; sometimes so little rain falls that there is no food for the grasshoppers, and most of them die from starvation without laying any eggs; at other times there may be so much rain that diseases spread widely among the grasshoppers. Notwithstanding these risks, the grasshoppers are numerous throughout much of their distribution. Occasionally, when the weather is unusually kind, they may become extremely abundant and remain so for several years. They are not found in the desert to the north or in the humid zone to the south.

The chief causes of high death-rates among the grasshoppers are those which we have listed in Table 1.01. By methods which will be described fully in section 13.124, we estimated the probabilities that are shown in the first three rows in the column headed "A" in Table 1.01. These probabilities express the chance that any one generation will meet with catastrophe from the cause named in the first column. It is also the chance that such a catastrophe will occur in any one year, because this species completes one generation every year. We lacked empirical evidence about the frequency of outbreaks of disease, so we filled in the fourth row with an imaginary figure. All the figures in the last two columns are imaginary. The figures under "A" refer to a certain district which is near the center of the distribution of the grasshoppers; it is a place where we know the grasshoppers are usually numerous. Locality "B" is arbitrarily supposed to be near the southern (humid) boundary, and "C" near or outside the northern (arid) boundary of the distribution of the grasshoppers.