TEXT-BOOKS OF ANIMAL BIOLOGY

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ANIMAL ECOLOGY

BY

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WITH AN INTRODUCTION BY

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ANIMAL ECOLOGY

CHAPTER I

INTRODUCTION

"Faunists, as you observe, are too apt to acquiesce in bare descriptions and a few synonyms; the reason for this is plain, because all that may be done at home in a man's study, but the investigation of the life and conversation of animals is a concern of much more trouble and difficulty, and is not to be attained but by the active and inquisitive, and by those that reside much in the country."—GILBERT WHITE, 1771.

1. ECOLOGY is a new name for a very old subject. It simply means scientific natural history. To a great many zoologists the word "natural history" brings up a rather clear vision of parties of naturalists going forth on excursion, prepared to swoop down on any rarity which will serve to swell the local list of species. It is a fact that natural history has fallen into disrepute among zoologists, at any rate in England, and since it is a very serious matter that a third of the whole subject of zoology should be neglected by scientists, we may ask for reasons. The discoveries of Charles Darwin in the middle of the nineteenth century gave a tremendous impetus to the study of species and the classification of animals. Although Linnæus had laid the foundation of this work many years before, it was found that previous descriptions of species were far too rough and ready, and that a revision and reorganisation of the whole subject was necessary. It was further realised that many of the brilliant observations of the older naturalists were rendered practically useless through the insufficient identification of the animals upon which they had worked. Half the zoological world thereupon drifted into museums

and spent the next fifty years doing the work of description and classification which was to lay the foundations for the scientific ecology of the twentieth century. The rest of the zoologists retired into laboratories, and there occupied their time with detailed work upon the morphology and physiology of animals. It was an age of studying whole problems on many animals, rather than the whole biology of any one animal. The morphologist does not require the identification of his specimens below orders or families or perhaps (in extreme cases) genera. The physiologist takes the nearest convenient animal, generally a parasite or a pet of man, and works out his problems on them. The point is that most morphology and physiology could be done without knowing the exact name of the animal which was being studied, while ecological work could not. Hence the temporary dying down of scientific work on animal ecology.

2. Meanwhile a vast number of local natural history societies burst into bloom all over Britain, and these bent their energies towards collecting and storing up in museums the local animals and plants. This work was of immense value, as it provided the material for classifying animals properly. But as time went on, and the groundwork of systematics was covered and consolidated, the collecting instinct went through the various stages which turn a practical and useful activity into a mania. At the present day, local natural history societies, however much pleasure they may give to their members, usually perform no scientific function, and in many cases the records which are made are of less value than the paper upon which they are written. Miall commented on this fact as long ago as 1897 when he said: "Natural history . . . is encumbered by multitudes of facts which are recorded only because they are easy to record." [79] * Such is the history of these societies. Like the bamboo, they burst into flower, produced enormous masses of seed, and then died with the effort. But however this may be, it is necessary for zoologists to realise that the work of the last fifty years has made field work on animals a practical possibility. It was of little use making observations

* The small numbers refer to the bibliography at the end of this book.

on an animal unless you knew its name. Scientific ecology was first started some thirty years ago by botanists, who finished their classification sooner than the zoologists, because there are fewer species of plants than of animals, and because plants do not rush away when you try to collect them. Animal ecologists have followed the lead of plant ecologists and copied most of their methods, without inventing many new ones of their own. It is one of the objects of this book to show that zoologists require quite special methods of their own in order to cope properly with the problems which face them in animal ecology.

3. When we take a broad historical view, it becomes evident that men have studied animals in their natural surroundings for thousands of years—ever since the first men started to catch animals for food and clothing; that the subject was developed into a science by the brilliant naturalists before and at the time of Charles Darwin; and that the discoveries of Darwin, himself a magnificent field naturalist, had the remarkable effect of sending the whole zoological world flocking indoors, where they remained hard at work for fifty years or more, and whence they are now beginning to put forth cautious heads again into the open air. But the open air feels very cold, and it has become such a normal proceeding for a zoologist to take up either a morphological or physiological problem that he finds it rather a disconcerting and disturbing experience to go out of doors and study animals in their natural conditions. This is not surprising when we consider that he has never had any opportunity of becoming trained in such work. In spite of this, the work badly needs doing; the fascination of it lies in the fact that there are such a number of interesting problems to be found, so many to choose from, and requiring so much energy and resource to solve. Adams says: "Here, then, is a resource, at present largely unworked by many biologists, where a wealth of ideas and explanations lies strewn over the surface and only need to be picked up in order to be utilised by those acquainted with this method of interpretation," [1b] while Tansley, speaking of plant ecology, says: "Every genuine worker in science is an explorer, who is continually

meeting fresh things and fresh situations, to which he has to adapt his material and mental equipment. This is conspicuously true of our subject, and is one of the greatest attractions of ecology to the student who is at once eager, imaginative, and determined. To the lover of prescribed routine methods with the certainty of ' safe ' results the study of ecology is not to be recommended." [15a]

CHAPTER II

THE DISTRIBUTION OF ANIMAL COMMUNITIES

Each habitat (1) has living in it a characteristic community of animals; (2) these can be classified in various ways and (3) their great variety and richness is due to the comparative specialisation of most species of animals. (4) It is convenient to study the zonation of such communities along the various big gradients in environmental conditions, such as that from the poles to the equator, which (5) shows the dominating influence of plants upon the distribution of animals, in forming special local conditions and (6) by producing sharp boundaries to the habitats so that (7) animal communities are more sharply separated than they would otherwise be. This is clearly shown by (8) the vertical zones of communities on a mountain-side, which also illustrate the principle that (9) the members of each community can be divided into those " exclusive " to and (10) into those " characteristic " of it, while the remaining species, which form the bulk of the community, occur in more than one association. (11) Other vertical gradients are that of light in the sea and (12) that of salts in water. (13) Each large zone can be subdivided into smaller gradients of habitat, *e.g.* water-content of the soil, and (14) these again into still smaller ones, until we reach single species of animals, which in turn can be shown to contain gradients in internal conditions supporting characteristic communities of parasites. (15) In such ways the differences between communities can be classified and studied as a preliminary to studying the fundamental resemblances amongst them.

1. ONE of the first things with which an ecologist has to deal is the fact that each different kind of habitat contains a characteristic set of animals. We call these animal associations, or better, animal communities, for we shall see later on that they are not mere assemblages of species living together, but form closely-knit communities or societies comparable to our own. Up to the present time animal ecologists have been very largely occupied with a general description and classification of the various animal habitats and of the fauna living in them. Preliminary biological surveys have been undertaken in most civilised countries except England and China, where animal ecology lags behind in a peculiar way. In particular

we might mention the work of the American Bureau of Biological Survey (which was first started in order to study problems raised by the introduction of the English sparrow into the United States), and of other institutions in that country, and similar surveys undertaken under the initiative of the late Dr. Annandale in India. It is clearly necessary to have a list of the animals in different habitats before one can proceed to study the more intricate problems of animal communities. We shall return to the question of biological surveys in the chapter on " Methods."

2. Various schemes have been proposed for the classification of animal communities, some very useful and others completely absurd. Since, however, no one adopts the latter, they merely serve as healthy examples of what to avoid, namely, the making of too many definitions and the inventing of a host of unnecessary technical terms. It should always be remembered that the professional ecologist has to rely, and always will have to rely, for a great many of his data, upon the observations of men like fishermen, gamekeepers, local naturalists, and, in fact, all manner of people who are not professional scientists at all. The life, habits, and distribution of animals are often such difficult things to ascertain and so variable from time to time, that it will always be absolutely essential to use the unique knowledge of men who have been studying animals in one place for a good many years. It is a comparatively simple matter to make a preliminary biological survey and accumulate lists of the animals in different communities. This preliminary work requires, of course, great energy and perseverance, and a skilled acquaintance with the ways of animals; but it is when one penetrates into the more intimate problems of animal life, and attempts to construct the food-cycles which will be discussed later on, that the immensity of the task begins to appear and the difficulty of obtaining the right class of data is discovered. It is therefore worth emphasising the vital importance of keeping in touch with all practical men who spend much of their lives among wild animals. To do this effectually it is desirable that ecology should not be made to appear much more abstruse and difficult

than it really is, and that it should not be possible to say that " ecology consists in saying what every one knows in language that nobody can understand." The writer has learnt a far greater number of interesting and invaluable ecological facts about the social organisation of animals from gamekeepers and private naturalists, and from the writings of men like W. H. Hudson, than from trained zoologists. There is something to be said for the view of an anonymous writer in *Nature*, who wrote: " The notion that the truth can be sought in books is still widely prevalent and the present dearth of illiterate men constitutes a serious menace to the advancement of knowledge." Even if this is so, it is at the same time true that there is more ecology in the Old Testament or the plays of Shakespeare than in most of the zoological textbooks ever published!

All this being so, there seems to be no point in making elaborate and academic classifications of animal communities. After all, what is to be said for a scientist who calls the community of animals living in ponds the " tiphic association," or refers to the art of gardening as " chronic hemerecology " ?

3. It is important, however, to get some general idea of the variety and distribution of the different animal communities found in the world. The existence of such a rich variety of communities is to be attributed to two factors. In the first place, no one animal is sufficiently elastic in its organisation to withstand the wide range of environmental conditions which exist in the world, and secondly, nearly all animals tend during the course of evolution to become more or less specialised for life in a narrow range of environmental conditions, for by being so specialised they can be more efficient. This tendency towards specialisation is abundantly shown throughout the fossil record and is reflected in the numerous and varied animal communities of the present day. Primarily, there is specialisation to meet particular climatic and other physical and chemical factors, and secondarily, animals become adapted to a special set of biotic conditions—food, enemies, etc. The effect of the various environmental factors upon animals is a

subject which will be followed up separately in the next chapter.

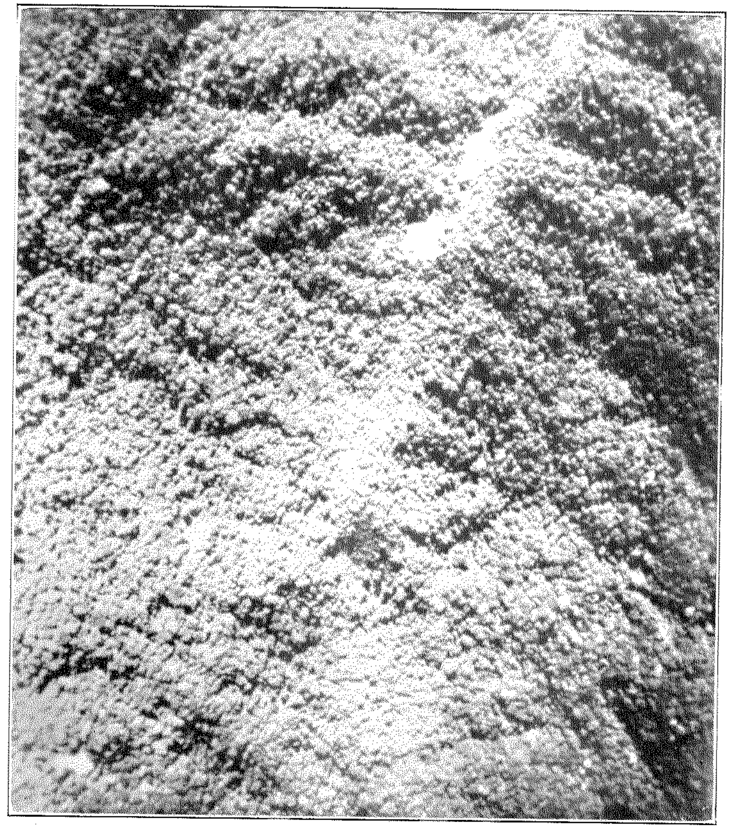
4. One way of giving some idea of the range of different animal habitats, and of the communities living in them, is to take some of the big gradients in environment and show how the communities change as we pass from one end to the other. The biggest of these is the gradient in temperature and light intensity between the poles and the equator, which owes its existence to the globular shape of the world. At the one extreme there are the regions of polar ice-pack, with their peculiar animal communities living in continuous daylight during the summer and continuous darkness in the winter, and with corresponding abrupt seasonal changes in temperature. At the other end of the scale we have equatorial rain forest with a totally different set of animals adapted to life in a continuously hot climate, and in many cases in continuous semi-darkness, in the shade of the tropical trees. An animal like Bosman's Potto sees less light throughout the year than the Arctic fox. In between these extremes we have animal communities accustomed to a moderate amount of heat and light.

5. These examples serve to introduce a very important idea, namely, the effect of vegetation upon the habitats and distribution of animals.

Although a tropical rain forest partly owes its existence to the intense sunlight of the tropics, yet inside the forest it is quite dark, and it is clear that plants have the effect of translating one climate into another, and that an animal living in or under a plant community and dependent on it, may be living under totally different climatic conditions from those existing outside. Each plant association therefore carries with it, or rather in it, a special local " climate " which is peculiar to itself. Broadly speaking, plants have a blanketing effect, since they cut off rain, and radiant energy like light and heat. Their general effect is therefore to tone down the intensity of any natural climate. At the same time they reduce the amount of evaporation from the soil surface, and so make the air damper than it otherwise would be.

Looking at the matter very broadly, in the far north there

PLATE I



Aerial photograph of a climax tropical forest in Burma (taken by Captain C. R. Robbins). Each lump in the photograph represents a forest tree some two or three hundred feet high. A ridge runs diagonally across the photo, and in the upper right-hand corner there are two white patches, which are landslides.

is very sparse vegetation, which does not always cover the ground at all completely. As we go south the vegetation becomes more dense and higher until we reach a zone with scattered trees. These are separated by wide intervals owing to the fact that the soil is too shallow (being frozen below a certain depth) to allow of sufficient root development except by extensive growth sideways. Then we find true forests, but still not very luxuriant. Finally, there are the immense rain forests of the equatorial belt. The gradation consists essentially first of a gradual filling up of the soil by roots, and then a covering up of the surface by vegetation.

6. There is a further important way in which plant communities affect animals. When we look at two plant communities growing next to one another, it is usually noticeable that the junction between the two is comparatively sharply marked. Examples of this are the zones of vegetation round the edge of a lake or up the side of a mountain. The reason for this sharp demarcation between plant communities is simple. Plants are usually competing for light, and if one plant in a community manages to outstrip the others in its growth it is able to cut off much of the light from them, and it then becomes *dominant*. This is the condition found in most temperate plant communities. Examples are the common heather (*Calluna*), or the beech trees in a wood, or the rushes (*Juncus*) in a marshy area. The process of competition is not always so simple as this, and there may be all manner of complicated factors affecting the relative growth of the competing species, but the final battle is usually for light. In some cases the winning species kills off other competitors, not by shading them, but by producing great quantities of dead leaves which swamp the smaller plants below, or by some other means. The main phenomenon of dominance remains the same. Now at the junctions of two plant communities there is also a battle for light going on, and it resolves itself mainly into a battle between the two respective dominants. Just as within the community, so between two different dominants, no compromise is possible in a battle for light. If one plant wins, it wins completely. Now every plant has a certain set

of optimum conditions for maximum growth, and as conditions depart from this optimum, growth becomes less efficient. Since each dominant has different optimum conditions, there is always a certain point in an environmental gradient where one dominant, and therefore one community, changes over fairly abruptly into another. There may be originally a regular and gradual gradient in, say, water-content of the soil, as from the edge of a lake up on to a dry moor; but the existence of dominance in plants causes this to be transformed into a series of sharply marked zones of vegetation, which to some extent mask the original gradient, and may even react on the surroundings so as to convert the conditions themselves into a step-like series.

7. It is clear, then, that because green plants feed by means of sunlight, the boundaries of their communities tend to be rather sharply defined; and since we have seen that each plant community carries with it a special set of " climatic " conditions for the animals living in it, the rather sudden difference in conditions at the edges of the plant communities will be reflected in the animals. This means that the species of animals will tend to be subdivided into separate ones adapted to different plant zones, instead of graded series showing no sudden differences. It also means that animal communities are made much more distinct from one another than would be the case if they were all living in one continuous gradient in conditions, or in a series of open associations of plants like arctic fjaeldmark (stony desert). It would be infinitely more difficult to study animal associations if this were not the case, for we should not have those convenient divisions of the whole fauna into communities which are so useful for working purposes. It is sometimes assumed in discussions on the origin of species that the environmental conditions affecting animals are always in the form of gradients. It is clear that such is by no means always the case.

8. As has been mentioned above, the abrupt transitions between plant communities are particularly well seen on the sides of mountains, where there are vertical zones of vegetation corresponding on a small scale to the big zones of latitude.

In America they are usually referred to as " life zones," and the existence of great mountain ranges in that country is one of the reasons why ecology has attracted more attention there. In England, where the mountain ranges are in the north, we do not see the impressive spectacle of great series of vegetation zones which have so much attracted the American ecologist. This vertical zonation is most striking in the tropics, where, within the same day, one may be eating wild bananas at sea-level and wild strawberries on the mountains. One of the best descriptions of this phenomenon is given by A. R. Wallace in the account of his travels through Java.[57]

The work of botanists has given us fairly clear ideas about the distribution of zones of vegetation, but we are still in great ignorance as to the exact distribution and boundaries of the animal communities in these life zones, and of their relation to the plants. A good deal of work has been done by Americans upon certain groups of animals (chiefly birds and mammals), and in particular may be mentioned the extremely fine account of the Yosemite region of the Sierra Nevada by Grinnell and Storer,[40] in which are given accurate data of the distribution of vertebrates in relation to life zones, together with a mass of interesting notes on the ecology of the animals.

9. There is a further important point in regard to the distribution and composition of animal communities. If we take the community of animals living, say, in the Canadian zone, we should find that a definite percentage are confined to that zone, and in fact that the distribution of some of the animals is strictly determined by the type of vegetation. These species we speak of as " exclusive " to that community. The game-birds found in Great Britain afford good examples of this. The ptarmigan (*Lagopus mutus*) lives in the alpine zone of vegetation, while the red grouse (*Lagopus scoticus*) replaces it at lower levels on the heather moors. Another bird, the capercaillie (*Tetrao urogallus*), lives in coniferous woods, while the pheasant (*Phasianus colchicus*) occurs chiefly in deciduous woods. Finally, the common partridge (*Perdix perdix*) comes in cultivated areas with grassland, etc. We see here examples of birds which are exclusive to certain plant

associations, and we may also note that they are all living a similar life as regards food and general habits. Each association has some kind of large vegetarian bird, although the actual species is different in each case. Another well-known example is the common grass-mouse (*Microtus agrestis*) which, except when it is extremely abundant and " boils over " into neighbouring habitats, is chiefly found living underground in grassland, where it feeds on the roots of the grass. A great number of vegetarian insects are attached to one species of plant, and if that plant only occurs in one association, the animal is also limited in the same way. The oak (*Quercus robur*) supports hundreds of insects peculiar to itself, and if we include parasites the number will be far greater.

10. Continuing our survey of one zone, we should find that there are certain species which occur in particularly large numbers there, although they are not exclusively confined to it. These we call " characteristic " species. A good example of this type is the long-tailed mouse (*Apodemus sylvaticus*) which occurs in woods, but is not confined to them. Trapping data for one area near Oxford showed that 82 per cent. of specimens were caught in woods, while 18 per cent. occurred outside in young plantations and even occasionally in the open. Here the animal is not so strictly limited to one habitat as, for instance, *Microtus*, but we are quite justified in calling it a wood-mouse in this district. Thorpe [122] has described some of the exclusive and characteristic British birds with reference to plant associations.

In most cases in which we have any complete knowledge (and they are few) it is found that these two classes of animals—the exclusives and the characteristics—may often form only a comparatively small section of the whole community, that there are many species of animals which range freely over several zones of vegetation, either because they are not limited by the direct or indirect effects of the vegetation, or because they can withstand a greater range of environment than the others. As an example of this type of distribution we may take the common bank vole (*Evotomys glareolus*) which, in contrast to the *Apodemus* mentioned above, comes both in

woodland and in wood margin, shrub communities, and young plantations. The actual figures for comparison with *Apodemus* are as follows : 47 per cent. of the specimens in woods and 53 per cent. outside, chiefly in shrub or young tree habitats.

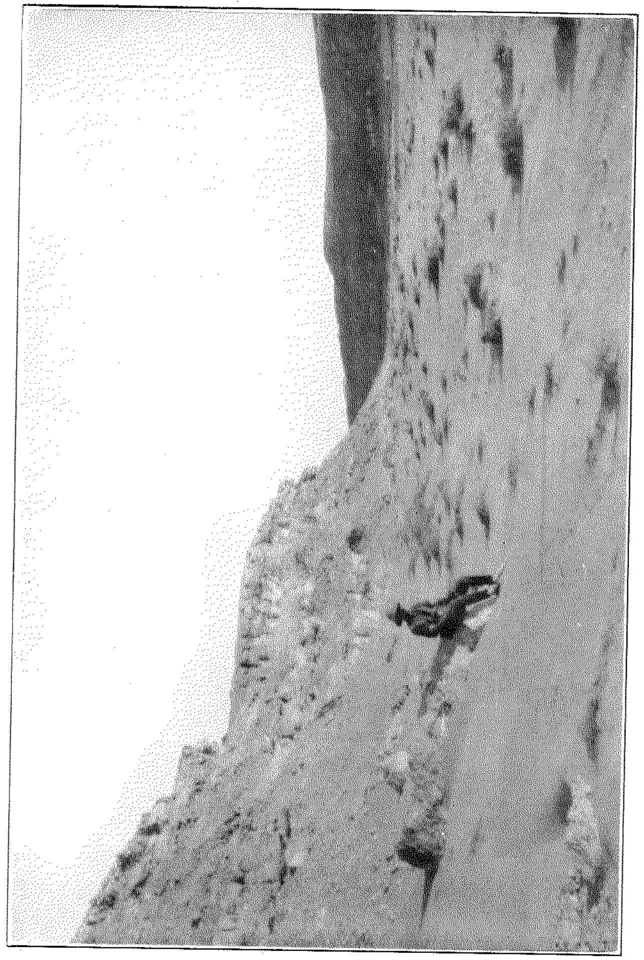
It may be, in fact, often rather an arbitrary proceeding to split up the animals living on, say, a mountain-side into communities corresponding to the exclusive and characteristic species of each life zone, and it should be realised quite clearly and constantly borne in mind when doing field work, that many common and important species come in more than one zone. Richards, after several years' study of the animals of an English heath, says : " The commonest animals in a plant community are often those most common elsewhere." [18a] At the same time it is probably true that animals living in several zones of vegetation show a marked tendency to have their limits of distribution coinciding with the edges of the plant zones. This is only natural in view of the step-like nature of the gradient in environment produced by the plant communities.

11. Another important vertical gradient is that found in the sea and in fresh-water lakes, and this is caused by the reduction in the amount of light penetrating the water as the depth increases. This gradient shows itself both in the free-living communities (*plankton*) and in those living on the bottom (*benthos*). As we go deeper down the plants become scarcer owing to lack of light, until at great depths there are no plants at all, and the animals living in such places have to depend for their living upon the dead bodies of organisms falling from the well-lighted zone above, or upon each other. There is the same tendency for the plants to form zones as on land, and one of the most interesting things about marine communities is the fact that certain animals which have become adapted to a sedentary existence compete with the plants (seaweeds of various kinds) and in some cases completely dominate them. The reason for this is that in the sea, and to a lesser extent in fresh water, it is possible for an animal to sit still and have its food brought to it in the water, while on land it has to go and get it. Web-spinning spiders are almost the only group of land animals which has perfected a

means of staying in the same place and obtaining the animals carried along in the air. In the tropics certain big spiders are actually able to snare small birds in their webs. In the sea an enormous number of animals sit still in one place and practically have their food wafted into their mouths. Indeed, food is probably not usually a limiting factor for such animals, and competition is for space to sit on. Hence it is that we find these animals behaving superficially like plants. Over great areas of the tropical seas (dependent probably on certain temperature conditions of the sea, or upon the plankton living in such waters) corals almost completely replace seaweeds on the seashore and shallow waters, where they feed like other animals on plankton organisms or upon small organic particles in the water. Corals on a reef usually form zones, each dominated by one or more species, just as in plants. The zonation is apparently determined by gradients in such factors as surf-action, amount of silt in the water, etc. Amongst the corals grow various calcareous algæ which resemble them very closely in outward appearance. As we go farther from the equator, plants become relatively more and more abundant on the shores of the oceans, but even in Arctic regions certain groups of animals, *e.g.* hydroids, may form zones between other zones composed of seaweeds.[25a]

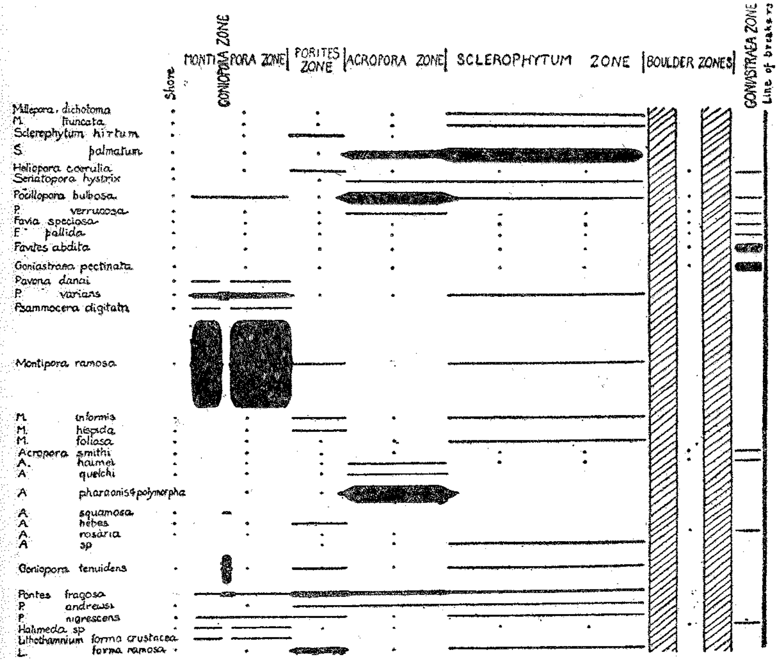
12. There is another vertical gradient in conditions which is clear-cut and of universal occurrence. This is the gradient in salt content of the water from mountain regions down to sea-level. Through the action of rain all manner of substances are continually being washed out of the rocks and soil. These pass into streams and rivers and accumulate temporarily in lakes and ponds at various levels. But since the salts are always being washed down, we find that on the whole the higher we go the purer is the water. Exceptions must be made to this rule in the case of places which have the higher parts of their mountain ranges composed of very soluble rocks, or in places like Central Asia, which have high plateaux on which many salt lakes develop. But, on the whole, we can distinguish an upland or alpine zone of waters containing few salts and often slightly acid in reaction. Lower down, the

PLATE II



The photograph (taken by Dr. K. S. Sandford in the Eastern Egyptian Desert in 1926) shows a typical limestone desert with blown sand and rock escarpments. This locality had had no rain for at least four years, and yet supported an open vegetation (probably owing to the supply of dew) and a fauna consisting of gazelles, ibex, together with a good many birds, lizards, insects, etc.

rivers and standing waters contain considerably more salts (*e.g.* places like the Norfolk Broads or the meres of Lancashire and Cheshire). Then there is a rather sudden increase in the steepness of the gradient through brackish water lagoons and estuaries to the sea itself. The sea, having been there



The thickness of the black stripes indicates the abundance of each species at various distances from the shore.

FIG. 1.—Zonation of corals (together with a few calcareous algæ) on a reef in the New Hebrides, showing that the phenomenon of dominance exists among corals, just as among plants. The left-hand side of the diagram is the shore of the island, while the right-hand side is the outer edge of the reef. (From Baker.[104])

much longer than the inland lakes and ponds, contains enormously more salts than the latter, but really it is only one end of a gradient which started high up in the mountains. There are well-marked different associations of animals in all these types of waters. Of course, other factors than salt content are important (particularly temperature), but the salt content itself is undoubtedly very important as a controlling factor, since it acts not only directly but also by affecting the hydrogen ion concentration of the water.

13. Within each of the big zones which owe their existence to major differences in climate there are numerous smaller gradients in outer conditions, each of which gives rise to a series of more or less well-marked associations of plants and animals. These gradients are caused by local variations in soil and climate, or by biotic factors such as grazing by animals. One obvious example is the gradient in the amount of water in the soil. At one end we may find the animal community of a dry heather moor, and at the other the community of free-floating and free-swimming animals which form the plankton of a lake. Between these two extremes there would be zones of marsh, reed swamp, and so on, each with a distinctive set of animals. These various zones are due to the fact that at one end of the gradient there is much soil and practically no water (at any rate in summer), while at the other there is much water and very little soil, the proportion of soil and water gradually changing in between.

14. We can carry the subdivision of animal communities further and split up one ordinary plant association, like an oak wood, into several animal habitats, *e.g.* tree-tops, tree-trunks, lower vegetation, ground surface, and underground, and we should find that each of these habitats contained an animal community which could be treated to some extent at least as a self-contained unit. Again, each species of plant has a number of animals dependent upon it, and one way of studying the ecology of the animals would be to take each plant separately and work out its fauna. Finally, each animal may contain within its own body a small fauna of parasites, and these again can be split up into associations according to the part of the body which they inhabit. If we examine the parasites of a mouse, for instance, we find that the upper part of the intestine, the lower part, the cæcum, the skin, the ears, each have their peculiar fauna.

It is obviously impossible to enumerate all the different gradients in the environment and all the different communities of animals which inhabit them. One habitat alone, the edge of a pond, or the ears of mammals, would require a whole book if it were to be treated in an adequate way. The aim of the foregoing sketch of the whole subject is to show that the term " animal community " is really a very elastic one, since we can use it to describe on the one hand the fauna of equatorial forest, and on the other hand the fauna of a mouse's cæcum.

For general descriptions of the animal communities of the more important habitats, the reader may be referred to a book on animal geography by Hesse,[111] and to a more recent book by Haviland.[109]

15. The attention of ecologists has been directed hitherto mainly towards describing the differences between animal communities rather than to the fundamental similarity between them all. The study of these differences forms a kind of animal ethnology, while the study of the resemblances may be compared to human sociology (soon to become social science). As a matter of fact, although a very large body of facts of the first type has been accumulated, few important generalisations have as yet been made from it. So much is this the case that many biologists view with despair the prospect of trying to learn anything about ecology, since the subject appears to them at first sight as a mass of uncoordinated and indigestible facts. It is quite certain that some powerful digestive juice is required which will aid in the assimilation of this mass of interesting but unrelated facts. We have to face the fact that while ecological work is fascinating to do, it is unbearably dull to read about, and this must be because there are so many separate interesting facts and tiny problems in the lives of animals, but few ideas to link the facts together. It seems certain that the key to the situation lies in the study of animal communities from the sociological point of view. This branch of ecology is treated in Chapter V., but first of all it is necessary to say something about the subject of ecological succession—an important phenomenon discovered by botanists, since it enables us to get a fuller understanding of the distribution and relations of animal and plant communities.

CHAPTER III

ECOLOGICAL SUCCESSION

A number of changes (1) are always taking place in animal communities, (2) one of the most important of which is ecological succession, which (3) causes plant associations to move about slowly on the earth's surface, and (4) is partly due to an unstable environment and partly to plant development which typically consists (5) of a *sere* of associations starting with a bare area and ending with a climax association. (6) Each region has a typical set of seres on different types of country which (7) may be studied in various ways, of which the best is direct observation of the changes as in (8) the heather moor described by Ritchie or (9) the changes following the flooding and redraining of the Yser region described by Massart or (10) a hay infusion; but (11) indirect evidence may be obtained as in the case of Shelford's tiger beetles. (12) The stages in succession are not sharply separated and (13) raise a number of interesting problems about competition between species of animals, which (14) may be best studied in very simple communities. (15) In the sea, succession in dominant sessile animals may closely resemble that of land plants, while (16) on land, animals often control the direction of succession in the plants. Therefore (17) plant ecologists cannot afford to ignore animals, while a knowledge of plant succession is essential for animal ecologists.

1. WE have spoken of animal communities so frequently in the last chapter that the reader may be in danger of becoming hypnotised by the mere word "community" into thinking that the assemblage of animals in each habitat forms a completely separate unit, isolated from its surroundings and quite permanent and indestructible. Nothing could be farther from the true state of affairs. The personnel of every community of animals is constantly changing with the ebb and flow of the seasons, with changing weather, and a number of other periodic rhythms in the outer environment. As a result of this it is never possible to find all the members of an animal community active or even on the spot at all at any one moment. To this subject we shall return in the chapter on the Time Factor in Animal Communities, since its

discussion comes more suitably under the structure of animal communities than under their distribution.

2. There is another type of change going on in nearly all communities, the gradual change known as *ecological succession*, and with this we will now deal. Such changes are sometimes huge and last a long time, like the advance and retreat of ice ages with their accompanying pendulum swing from a temperate climate with beech and oak forests and chaffinches, to an arctic one with tundra and snow buntings, or even the complete blotting out of all life by a thick sheet of ice. They may, on the other hand, be on a small scale. Mr. J. D. Brown watched for some years the inhabitants of a hollow in a beech tree, and the ecological succession of the fauna. At first an owl used it for nesting purposes, but as the tissues of the tree grew round the entrance to the hollow it became too small for owls to get into, and the place was then occupied by nesting starlings. Later the hole grew smaller still until after some years no bird could get in, and instead a colony of wasps inhabited it. The last episode in this story was the complete closing up of the entrance-hole. This example may sound trivial, but it is an instance of the kind of changes which are going on continuously in the environment of animals.

3. If it were possible for an ecologist to go up in a balloon and stay there for several hundred years quietly observing the countryside below him, he would no doubt notice a number of curious things before he died, but above all he would notice that the zones of vegetation appeared to be moving about slowly and deliberately in different directions. The plants round the edges of ponds would be seen marching inwards towards the centre until no trace was left of what had once been pieces of standing water in a field. Woods might be seen advancing over grassland or heaths, always preceded by a vanguard of shrubs and smaller trees, or in other places they might be retreating; and he might see even from that height a faint brown scar marking the warren inhabited by the rabbits which were bringing this about. Again and again fires would devastate parts of the country, low-lying areas would be flooded, or pieces of water dried up, and in every

case it would take a good many years for the vegetation to reach its former state. Although bare areas would constantly be formed through various agencies, only a short time would elapse before they were clothed with plants once more.

There are very few really permanent bare areas to be met with in nature. Rocks which appear bare at a distance are nearly always covered with lichens, and usually support a definite though meagre fauna, ranging from rotifers to eagles. Apparently barren places like lakes contain a huge microscopic flora and fauna, and even temporary pools of rain-water are colonised with almost miraculous rapidity by protozoa and other small animals.

4. It is the exception rather than the rule for any habitat to remain the same for a long period of years. Slow geological processes, like erosion and deposition by rivers and by the sea, are at work everywhere. Then there are sudden disasters, like fires, floods, droughts, avalanches, the introduction of civilised Europeans and of rabbits, any of which may destroy much of the existing vegetation. There is a third kind of change which is extremely important but not so obvious, and is the more interesting since its movements are orderly and often predictable. This is the process known as the *development* of plant communities. Development is a term used by plant ecologists in a special technical sense, to include changes in plant communities which are solely or largely brought about by the activities of the plants themselves. Plants, like many animals, are constantly moulting, and the dead leaves produced accumulate in the soil below them and help to form humus. This humus changes the character of the soil in such a way that it may actually become no longer suitable for the plants that live there, with the result that other species come in and replace them. Sometimes the seedlings of the dominant plant (*e.g.* a forest tree) are unable to grow up properly in the shade of their own parents, while those of other trees can. This again leads to the gradual replacement of one community by another.

When a bare area is formed by any of the agencies we have mentioned, *e.g.* the changing course of a river, it is first colonised by mosses or algæ or lichens; these are driven out by low herbs, which kill the pioneer mosses by their shade; these again may be followed by a shrub stage; and finally a woodland community is formed, with some of the earlier pioneers still living in the shade of the trees.

This woodland may form a comparatively stable phase, and is then called a climax association, or it may give way to one or more further forest stages dominated by different species of trees in the manner described above. It is not really possible to separate development of communities from succession caused by extrinsic changes, such as the gradual leaching out of salts from the soil or other such factors unconnected with the plants themselves. The important idea to grasp is that plants react on their surroundings and in many cases *drive themselves out*. In the early stages of colonisation of bare areas the succession is to a large extent a matter of the time taken for the different plants to get there and grow up; for obviously mosses can colonise more quickly than trees.

5. In any one region the kind of climax reached depends primarily upon the climate. In high Arctic regions succession may never get beyond a closed association of lichens, containing no animals whatsoever. In milder Arctic regions a low shrub climax is attained, while farther south the natural climax is forest or in some cases heath, according to whether the climate is of a continental or an oceanic type. Sometimes ecological succession is held up by other agencies than climate and prevented from reaching its natural climax. In such cases it is a common custom to refer to the stage at which it stops as a sub-climax. A great deal of grassland and heath comes under this heading, for further development is prevented by grazing animals, which destroy the seedlings of the stage next in succession. An area of typical heather moor in the New Forest was fenced off for several years from grazing ponies and cattle by its owner, with the immediate result that birches and pines appeared by natural colonisation, and the young pines, although slower in growth than the birches, will ultimately replace them and form a pine wood. Here grazing was the sole factor preventing normal ecological

succession. The same thing is well known to occur in a great many places when heather or grass is protected, the important animals varying in different places, being usually cattle, sheep, horses, or rabbits, or even mice.

6. We begin to see that the succession of plant communities does not take place at random, but in a series of orderly stages, which can be predicted with some accuracy. The exact type of communities and the order in which they replace one another depend upon the climate and soil and other local factors, such as grazing. It is possible to classify different series of stages in succession in any one area, the term " sere " being used to denote a complete change from a bare area in water or soil up

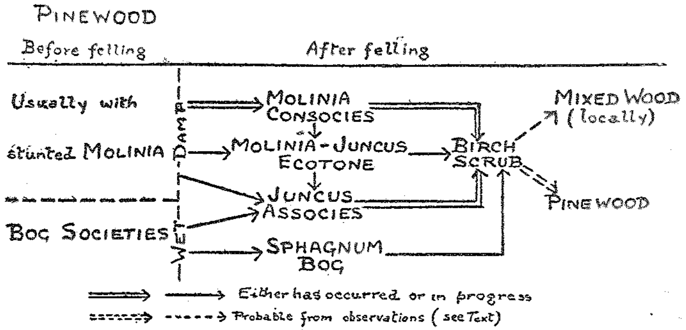
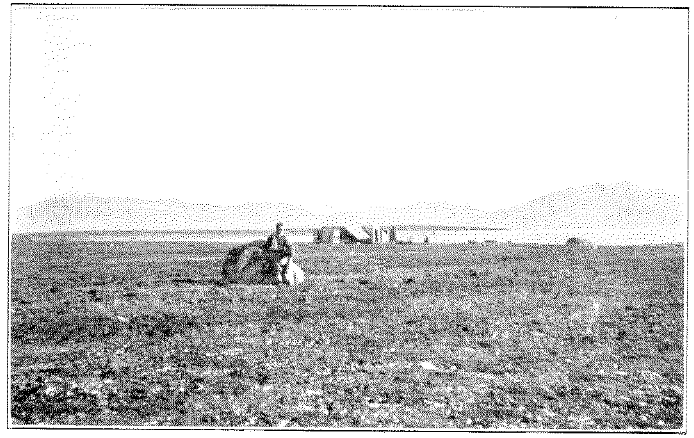


FIG. 2.—The diagram shows the stages in ecological succession following colonisation of damp bare areas formed by felling of a pine wood on Oxshott Common. The succession is different on the drier areas. (From Summerhayes and Williams.[120])

to a climax like pine wood (*cf.* Fig 2). Each type of soil, etc., has a different type of " sere " which tends to develop upon it, but they all have one character in common : bare areas are usually very wet or very dry, and the tendency of succession is always to establish a climax which is living in soil of an intermediate wetness—a type of vegetation called " mesophytic," of which a typical example is an oak wood. Thus a dry rock surface gains ultimately a fairly damp soil by the deposition of humus, while a water-logged soil is gradually raised above the water-level by the same agency, so that there tends to appear a habitat in which the expenditure by plants and by direct loss from the soil is suitably balanced by the

PLATE III



(*a*) A typical stretch of high arctic dry tundra, inhabited by reindeer, arctic fox, etc. (The photograph was taken in August, 1924, by Dr. K. S. Sandford, on Reindeer Peninsula, North Spitsbergen.)

(*b*) Drifting pack-ice near North-East Land (Spitsbergen Archipelago), with the bearded seal (*Erignathus barbatus*) lying on a floe. (Photographed by Mr. J. D. Brown, July, 1923.)

income of water, and extremes of environment are avoided. This is, of course, only a rough generalisation and applies especially to temperate regions, but it explains why we often get seres on very different kinds of bare areas converging towards the same final climax.

7. The account of this subject given above is necessarily brief, and a much fuller account is given by Tansley in his book *Practical Plant Ecology*,[15] which is essential to the work of all animal ecologists. Clements has treated the whole subject in stupendous detail in his monograph *Plant Succession*,[39] which is illustrated by a very fine series of photographs of plant communities.

Let us now consider a few examples of succession in animal and plant communities. It is clearly impracticable to take more than a few species as examples of changes in whole communities, and naturally the exclusives afford the most striking ones. There are several ways in which animal succession can be studied. The best way is to watch one spot changing over a series of years and record what happens to the fauna. This is the method least practised, but the most likely to lead to productive results, since we stand a good chance of seeing how the structure of the communities is altered as one grades into another. Yapp [31] says: " We may perhaps regard the organisms, both plants and animals, occupying any given habitat, as woven into a complex but unstable web of life. The character of the web may change as new organisms appear on the scene and old ones disappear during the phases of succession, but the web itself remains." It is just the changes in this " web " about which we know so little at present, and that is why study of the actual changes will always be the most valuable.

8. One of the most interesting and clear-cut examples of succession, recorded by Ritchie,[13a] is so striking that it has been often quoted, and is worth quoting again here. He describes the manner in which a typical heather moor in the south of Scotland, with its normal inhabitant, the red grouse (*Lagopus scoticus*), was converted in the short space of fifteen years into a waste of rushes and docks, inhabited by a huge

colony of black-headed gulls (*Larus ridibundus*), and then in about ten years turned back again into a moor like the original one. These events were brought about by the arrival of a few pairs of gulls which nested there for the first time in about 1892. The gulls were protected by the owner, and after fifteen years they had increased prodigiously until there were well over 3,000 birds nesting. The occupation of the ground by gulls, with its accompanying manuring and trampling of the soil, caused the heather to disappear gradually and to give way to coarse grass. The grass was then largely replaced by rushes (*Juncus*), and the latter ultimately by a mass of docks (*Rumex*). At the same time pools of water formed among the vegetation and attracted numbers of teal (*Anas crecca*). The grouse meanwhile had vanished. Then protection of the gulls ceased, and their numbers began to decrease again, until in 1917 there were less than sixty gulls nesting, the teal had practically disappeared, and the grouse were beginning to return. In fact, with the cessation of "gull action" on the ground the place gradually returned to its original state as a heather moor. As Ritchie remarks, there must have been a huge number of similar changes among the lower animals which also would be profoundly affected by the changes in vegetation.

9. Another striking story is that told us by Massart,[35] who studied the changes wrought during the war by the flooding of parts of Belgium in the Yser district. Here the sea was allowed by the Belgian engineers to inundate the country in order to prevent the advance of the German army. The sea-water killed off practically every single plant in this district, and all available places were very soon colonised by marine animals and plants, space being valuable in the sea. When the country was drained again at the end of the war, ecological succession was seen taking place on a generous scale. At first the bare "sea-bottom" was colonised by a flora of salt-marsh plants, but these gave way gradually to an almost normal vegetation until in many places the only traces of the advance and retreat of the sea were the skeletons of barnacles (*Balanus*) and mussels (*Mytilus*) on fences and notice-boards, and the presence

of prawns (*Palæmonetes varians*) left behind in some of the shell holes.

10. Ecological succession may easily be studied experimentally by making a hay infusion in water and leaving it exposed to the air for several weeks. Bacteria are the first things to become abundant, since they live upon the decaying vegetable matter. Then various protozoa appear, and it is possible to see a whole animal community being gradually built up, as each new species arrives and multiplies and fits into its proper niche. In a hay infusion the bacteria are followed by small ciliate protozoa of the *Paramecium* type, which subsist upon bacteria and also by absorbing substances in solution and in suspension in the water. Then there are larger hypotrichous ciliates, which prey upon bacteria and also upon the smaller ciliates. Eventually the whole culture may degenerate owing to the exhaustion of food material for the bacteria and therefore for the animals dependent on them. On the other hand, green plants, in the form of small algæ, may arrive and colonise the culture. These will be able to subsist for a long time, and may change the character of the whole community by providing a different type of food. Succession in hay infusions is particularly fascinating, since it can be studied anywhere, and does not last over a very long time.

11. Another method of determining the course of animal succession is to work from a knowledge of the succession relations of the plant communities (gained either from direct observation or from deduction and comparison with other districts) and then work out the animal communities of each plant zone. It is then possible to say in a general way what animals will replace existing ones when succession does occur. This was done by Shelford,[20] who studied the tiger beetles of the genus *Cicindela* (carnivorous ground beetles of variegated colours) in a sere of plant communities on the shores of Lake Michigan. The lake-level has been falling gradually of late years, and there can be seen all stages in succession on the bare areas left behind on the shores. On the lake margin was *Cicindela cuprascens*, whose larvæ live in wettish sand. Young

cottonwoods colonise this ground, and another species of tiger beetle (*C. lepida*) then replaces the first one. In the old cottonwoods, where conditions are different with grass and young pine seedlings, *C. formosa* took the place of *C. lepida*. Then with the formation of a dominant pine community on the ridges still another species, *C. scutellaris*, replaces the previous one and continues to live on into the next stage in succession, a black oak community; but it gradually becomes scarcer with the change to white oak, until a stage is reached with no tiger beetles at all. With the following red oak stage there arrives *C. sexguttata*, which persists afterwards in clearings, but when the climax association of beech and maple has been reached tiger beetles again disappear altogether. Here there can be distinguished at least eight stages in the development of plant associations, and five different species of tiger beetle, none of which come in more than two plant zones.

12. It is important to note that we have to deal in this case with a genus of animals which tends to form species which are exclusive or confined to one or two plant associations. In England there seems to be the same tendency among the species of *Cicindela*. But this kind of strict limitation to plant associations is probably rather unusual, especially among carnivorous animals. Exception must be made in the case of some of the great host of herbivorous animals (in particular insects) which are attached to one species of plant only. But even in these cases the plant itself, and therefore the animal, is not usually confined to one plant association. In practice, succession in animal communities is an infinitely more complicated affair. One reason for this is the great lag of animals behind plants, due to their different powers of dispersal. Another reason is that the survival of only a few of the earlier plants in the later stages will enable a great number of animals to hang on also, and these of course cannot be separated in their inter-relations with the newcomers. For instance, on areas in the south of England where pine woods have grown up over and largely replaced heather (*Calluna*), there are still many patches of heather growing in the more open places, and these have been found to contain the typical heather communities of animals, showing that the animals are in this case affected rather by the food, shelter, etc., provided by the heather than by the general physical " climate " produced by the pine wood.[18c] It is when we try to work out the food relations of the animals that the presence of small patches of earlier pioneer animals in a climax association becomes such a complicating factor. In fact, succession (at any rate in animals) does not take place with the beautiful simplicity which we could desire, and it is better to realise this fact once and for all rather than to try and reduce the whole phenomenon to a set of rules which are always broken in practice! The present state of our knowledge of succession is very meagre, and this ignorance is to a large extent due to lack of exact knowledge about the factors which limit animals in their distribution and numbers. The work done so far has necessarily been restricted to showing the changes in exclusive species of one genus, or in the picking out of one or two salient features in the changes as an indication of the sort of thing that is taking place. Work like that done by Shelford, and observations like those of Ritchie and Massart, make it quite clear that succession is an important phenomenon in animal life; the next stage of the inquiry is the discovery of the exact manner in which succession affects whole communities.

13. It will be as well at this point to remind the reader that most of the work done so far upon animal succession has been static and not dynamic in character; that the cases in which the whole thing has been seen to happen are few in number and, although extremely valuable and interesting, of necessity incompletely worked out.

Given a good ecological survey of animal communities and a knowledge of the local plant seres, we can predict in a general way the course of succession among the animals, but in doing so we are in danger of making a good many assumptions, and we do not get any clear conception of the exact way in which one species replaces another. Does it drive the other one out by competition? and if so, what precisely do we mean by competition? Or do changing conditions destroy or drive out the first arrival, making thereby an empty niche for another animal which quietly replaces it without ever becoming "red in tooth and claw" at all? Succession brings the ecologist face to face with the whole problem of competition among animals, a problem which does not puzzle most people because they seldom if ever think out its implications at all carefully. At the present time it is well known that the American grey squirrel is replacing the native red squirrel in various parts of England, but it is entirely unknown why this is occurring, and no good explanation seems to exist. And yet, more is known about squirrels than about most other animals. In ecological succession among animals there are thousands of similar cases cropping up, practically all of which are as little accounted for as that of the squirrels. There is plenty of work to do in ecology.

14. It is probable that accurate data about the succession in animal communities will be most easily and successfully obtained by taking very small and limited communities living in peculiar habitats, for it is here that the number of species is reduced to reasonable proportions. Experience has shown that the general study of animal communities is best carried out on simple communities such as those of Arctic regions or of brackish water. Habitats in which succession can be studied quickly and conveniently are the dead bodies of animals, the dead bodies of plants (*e.g.* logs, or fungi), the dung of mammals, marine timber, temporary pools, and so on. The ecologist will be able to find a number of such habitats wherever he is; and they all contain on a small scale similar communities to those found in woods or lakes. In such places succession is always in progress and, what is more important, in quick progress. The writer has found that it is almost impossible to make even a superficial study of succession in any large and complicated community, owing to the appalling amount of mere collecting which is required, and the trouble of getting the collected material identified. When one has to include seasonal changes throughout the year as well, the work becomes first of all disheartening, then terrific, and finally impossible. Much of this mental strain can be avoided by choosing simple communities, and the results as contributions to the general

theory of succession are probably just as valuable. In any case, it is desirable that botanists and animal ecologists should cooperate in such studies, and in most cases a team of several people is required for the proper working out of the animals. It is probable, however, that in the simpler cases one man could do very valuable work.

15. We have not spoken so far of succession in the sea. Owing to the peculiar importance of sessile animals on the shores and slopes of the sea, it is not uncommon to find plant and animal succession becoming rather closely related. Wilson [82] watched the succession on bare areas on the shores of California at La Jolla, and found that the pioneers were colonial diatoms which formed the first community. These were followed by an association of colonial hydroids (mostly *Obelia*), and the latter were then replaced by a seaweed (*Ectocarpus*), which became dominant after some four months. Further stages were foreshadowed, and it appeared that the whole would ultimately develop into a climax association of other seaweeds (chiefly kelp). The interesting thing about this sere is the fact that the second stage in succession is formed by sessile animals, and is sandwiched between two plant stages. The zonation of animals and plants in the intertidal zone in other regions is often an alternation of animal and plant dominance, *e.g. Balanus* or *Mytilus* and seaweeds, in the temperate regions. On coral islands succession may consist almost entirely of a series of animal zones with only an occasional plant zone formed of calcareous algæ.[104] In such cases it is perfectly legitimate to refer to the most abundant animal as the "dominant" species, but in most animal communities the term has little meaning owing to the different methods of feeding adopted by animals and plants. It is perhaps better to avoid the use of the term "dominant" in the cases of animals except for sessile aquatic species, since dominance implies occupying more space or getting more light than other species.

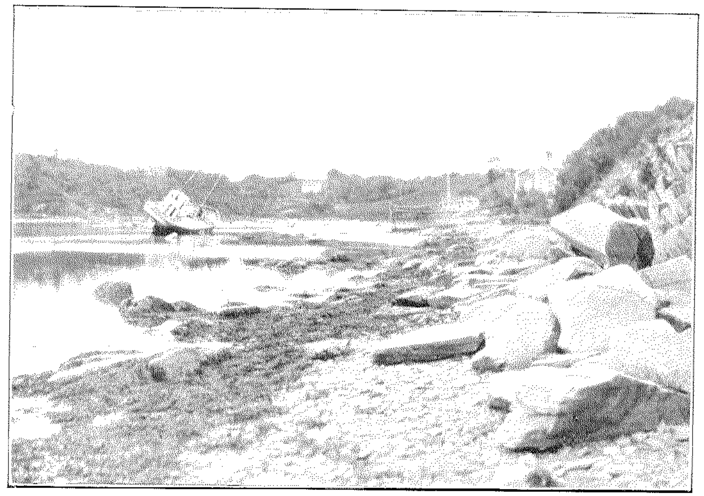
16. We have just pointed out that animals play an important part in ecological succession in the sea; but it should also be realised that they also have very important effects in a different

sort of way upon plant succession on land. Herbivorous animals are often the prime controlling factor in the particular kind of succession which takes place on an area. Farrow [8a] says: "It is thus seen that variation in the intensity of the rabbit attack alone is sufficient to change the dominant type of vegetation in Breckland from pine woodland to dwarf grass-heath vegetation through the phases of *Calluna* heath and *Carex arenaria*, and that for each given intensity of rabbit attack there is a certain associated vegetation." He showed that there were definite zones of vegetation round each rabbit colony and even each hole, since the distance from the colony resulted in different intensities of attack. The curious fact also appears that *Carex arenaria* will dominate *Calluna* when both are eaten down intensely. It is the relative intensity of attack that matters. The example quoted here is only one of many which could be given, although the situation has not been worked out so ingeniously or fully for any other animals or place.

17. Hofman's work [83] has made it probable that the influence of rodents in burying seeds of conifers may sometimes determine the type of succession which starts after a forest fire. The Douglas Fir (*Pseudotsuga taxifolia*) is a dominant tree over large parts of the Cascade and Coast region of Washington and Oregon. When the seed crops are light they are largely destroyed by an insect (*Megastigmus spermotrophus*) and by rodents. But when there is an unusually heavy crop large quantities of surplus seed are collected and stored in caches by the rodents. Since in many cases the animals do not return to the caches the seeds remain there for a good many years, and if there is a fire in the forest or the trees are cut down, large quantities of the stored seed germinate. More of the Douglas fir seed than of other species of trees such as hemlock and cedar is cached by rodents, so that the Douglas has accordingly an advantage in the early stages of succession. The same thing holds good for the white pine; its seeds are much eaten by rodents, which gather them and store them in the ground. But here other factors such as germination come in and affect the succession.

PLATE IV

(*a*) A semi-permanent pond in Oxfordshire (permanent except in drought years, when it dries up completely). Various successive zones of aquatic and marsh plants lead finally to grazed grassland on the right, and to elm trees on the left.



(*b*) Zonation of habitats on the sea-shore at low tide of Norway (Svolvaer), showing gradation from sea to land, through seaweeds (*Fucus*, etc.), drift-line, shingle, rocks, up to pasture or birchwoods.

18. One more example may be given of the way in which animals and plants are intimately bound up together in ecological succession. Cooper [84] has studied the relation of the white pine blister rust to succession in the New England and the Adirondacks. This disease is a very important one, and the most critical point in its life-history, from the point of view of controlling it, is its occurrence at one stage on the various species of wild gooseberries (*Ribes*). Cooper found that the distribution of *Ribes* was to an important extent affected by the distribution of fruit-eating birds, and that changes in the character of the birds during ecological succession resulted in a failure of the gooseberry seeds to spread in sufficient numbers to establish many new plants, after a certain stage in succession had been reached. The normal succession in places where the original forest had been cleared and then allowed to grow up again is as follows: first a stage with rank grass and weeds; this is followed by a shrub stage, in which plants like raspberry, blackberry, juniper, etc., are important. At this point the species of *Ribes*, though relatively unimportant, reach their maximum abundance. The shrub stage is followed by one with trees, of which the most important are white pine, aspen, birch, and maple. Finally a climax of other species may be reached. But the important point is the appearance of the first trees, for at this stage the bird fauna changes considerably and the number of fruit-eating, or at any rate gooseberry-eating, birds diminishes suddenly. The *Ribes* is able to exist in the shade of these later forest stages of succession, but cannot produce fruit in any quantity, and so, unless birds bring in new seeds from outside, the *Ribes* is bound to die out ultimately. As we have seen, the corresponding changes in the bird species prevent any large amount of seed getting into the forest after these stages, and this reacts upon the rust.

19. It is obvious that a knowledge of animals may be of enormous value to botanists working on plant succession. At the same time it is necessary for the animal ecologist to have a good general knowledge of plant succession in the region where he is working. It enables him to classify and

understand plant communities, and therefore animal communities, much more easily than he can otherwise do, by providing an idea which links up a number of otherwise rather isolated facts. Furthermore, as will be shown later on, succession of communities, which is nothing more than a migration of the animals' environment, plays an important part in the slow dispersal of animals. Again, as we have pointed out, the intricate problems of competition between different species of animals can be studied to advantage in a series of changing communities. Tansley's *Types of British Vegetation* [16] is the standard work in which the plant associations of Britain are described, and in many cases the probable lines of succession in the associations are given also. It is essential to have access to this book if one is carrying out any extensive work in the way of preliminary surveys or studies in ecological succession.

CHAPTER IV

ENVIRONMENTAL FACTORS

The ecologist is (1) concerned with *what animals do*, and with the factors which prevent them from doing various things; (2) the study of factors which limit species to particular habitats lies on the borderlines of so many subjects, that (3) he requires amongst other things a slight knowledge of a great many scattered subjects. (4), (5), (6), (7) The ecology of the copepod *Eurytemora* can be taken as a good example of the methods by which such problems may be studied, and illustrates several points, *e.g.* (8) the fact that animals usually have appropriate psychological reactions by which they find a suitable habitat, so that (9) the ecologist does not need to concern himself very much with the physiological limits which animals can endure; and (10) the fact that animals are not completely hemmed in by their environment, but by only a few limiting factors, which (11) may, however, be difficult to discover, since (12) the factor which appears to be the cause may turn out to be only correlated with the true cause. (13), (14) Examples of limiting factors to the distribution of species are: hydrogen ion concentration of water; (15) water supply and shelter; (16) temperature; (17) food plants; and (18) interrelations with other animals. The last subject is so huge and complicated, that it requires special treatment—as the study of animal communities.

1. It will probably have occurred to the reader, if he has got as far as this, that rather little is known about animal ecology. This is, of course, all to the good in one way, since one of the most attractive things about the subject is the fact that it is possible for almost any one doing ecological work on the right lines to strike upon some new and exciting fact or idea. At the same time it is often rather difficult to know what are the best methods to adopt in tackling the various problems which arise during the course of the work. This is particularly true of the branch of ecology dealt with in the present chapter. Much of the work that is done under the name of ecology is not ecology at all, but either pure physiology—*i.e.* finding out how animals work internally—or pure geology or meteorology, or some other science concerned primarily with the