Animal Ecology

Charles Elton (1927)

CHAPTER V

THE ANIMAL COMMUNITY

"The large fish eat the small fish; the small fish eat the water insecti ; the water insects eat plants and mud."

"Large fowl cannot eat small grain."

"One hill cannot shelter two tigers."-CHINESE PROVERBS.

Every animal is (1,2) closely linked with a number of other animals living round it, and these relations in an animal community are largely food relations. (3) Man himself is in the centre of such an animal community, as is shown by his relations to plague-carrying rats and (4) to malaria or the diseases of his domestic animals, *e.g.* liver-rot in sheep. (5) The dependence of man upon other animals is best shown when he invades and upsets the animal communities of a new country, *e.g.* the white man in Hawaii. (6) These interrelations between animals appear fearfully complex at first sight, but are less difficult to study if the following four principles are realised: (7) The first is that of *Food-chains* and the *Food-cycle.* Food is one of the most important factors in the life of animals, and in most communities (8) the species are arranged in food-chains which (9) combine to form a whole food-cycle. This is closely bound up with the second principle, (10) the *Size of Food.* Although animals vary much in size, anyone species of animal only eats food between certain limits of size, both lower and (11) upper, which (12) are illustrated by examples of a toad, a fly, and a bird. (13) This principle applied to primitive man, but no longer holds for civilised man, and (14) although there are certain exceptions to it in nature, it is a principle of great importance. (15) The third principle is that of *Niches.* By a niche, is meant the animal's place in its community, its relations to food and enemies, and to some extent to other factors also. (16), (17), (18), (19), (20) A number of examples of niches can be given, many of which show that the same niche may be filled by entirely different animals in different parts of the world. (21) The fourth idea is that of the *Pyramid of Numbers* in a community, by which is meant the greater abundance of animals at the base of food-chains, and the comparative scarcity of animals at the end of such chains. (22) Examples of this principle are given, but, as is the case with all work upon animal communities, good data are very scarce at present.

1. IF you go out on to the Malvern Hills in July you will find some of the hot limestone pastures on the lower slopes covered with ant-hills made by a little yellow ant *(Acanthomyops flavus).* These are low hummocks about a foot in diameter, clothed with plants, some of which are different from those of the surrounding pasture. This ant, itself forming highly organised colonies, is the centre of a closely-knit community of other animals. You may find green woodpeckers digging great holes in the ant-hills, in order to secure the ants and their pupae. If you run up quickly to one of these places from which a woodpecker has been disturbed, you may find that a robber ant *(Myrmica scabrinodis)* has seized the opportunity to carry off one of the pupae left behind by the yellow ants in their flight. The latter with

unending labour keep building up the hills with new soil, and on this soil there grows a special set of plants. Wild thyme *(Thymus serpyllum)* is particularly common there, and its flowers attract the favourable notice of a red-tailed bumble-bee *(Bombus lapidarius)* which visits them to gather nectar. Another animal visits these ant-hills for a different purpose: rabbits, in common with many other mammals, have the peculiar habit of depositing their dung in particular spots, often on some low hummock or tree-stump. They also use ant-hills for this purpose, and thus provide humus which counteracts to some extent the eroding effects of the woodpeckers. It is interesting now to find that wild thyme is detested by rabbits as a food,138 which fact perhaps explains its prevalence on the ant-hills. There is a moth *(Pempelia subornatella)* whose larvae make silken tubes among the roots of wild thyme on such ant-hills; then there is a great army of hangers-on, guests, and parasites in the nests themselves; and so the story could be continued indefinitely. But even this slight sketch enables one to get some idea of the complexity of animal interrelations in a small area.

2. One might leave the ants and follow out the effects of the rabbits elsewhere. There are dor-beetles *(Geotrupes)* which dig holes sometimes as much as four feet deep, in which they store pellets of rabbit-dung for their own private use, Rabbits themselves have far-reaching effects upon vegetation, and in many parts of England they are one of the most important factors controlling the nature and direction of ecological succession in plant communities, owing to the fact that they have a special scale of preferences as to food, and eat down some species more than others. Some of the remarkable results of "rabbit action" on vegetation may be read about in a very interesting book by Farrow.[19] Since rabbits may influence plant communities in this way, it is obvious that they have indirectly a very important influence upon other animals also. Taking another line of investigation, we might follow out the fortunes and activities of the green woodpeckers, to find them preying on the big red and black ant *(Formica rufa)* which builds its nests in woods, and which in turn has a host of other animals linked up with it.

If we turned to the sea, or a fresh-water pond, or the inside of a horse, we should find similar communities of animals, and in every case we should notice that food is the factor which plays the biggest part in their lives, and that it forms the connecting link between members of the communities.

3. In England we do not realise sufficiently vividly that man is surrounded by vast and intricate animal communities, and that his actions often produce on the animals effects which are usually quite unexpected in their nature-that in fact man is only one animal in a large community of other ones. This ignorance is largely to be attributed to town life. It is no exaggeration to say that our relations with the other members of the animal communities to which we belong have had a big influence on the course of history. For instance: the Black Death of the Middle Ages, which killed off more than half the people in Europe, was the disease which we call plague. Plague is carried by rats, which may form a permanent reservoir of the plague bacilli, from which the disease is originally transmitted to human beings by the bites of rat fleas. From this point it may either spread by more rat fleas or else under certain conditions by the breathing of infected air. Plague was still a serious menace to life in the seventeenth century, and finally flared up in the Great Plague of London in 1665, which swept away some hundred thousand people. Men at that time were still quite ignorant of the connection between rats and the spread of the disease, and we even find that orders were given for the destruction of cats and dogs because it was suspected that they were carriers of plague.[149] And there seemed no reason why plague should not have continued indefinitely to threaten the lives of people in England; but after the end of the seventeenth

century it practically disappeared from this country. This disappearance was partly due to the better conditions under which people were living, but there was also another reason. The dying down of the disease coincided with certain interesting events in the rat world. The common rat of Europe had been up to that time the Black or Ship Rat *(R. rattus),* which is a very effective plague-carrier owing to its habit of living in houses in rather close contact with man. Now, in 1727 great hordes of rats belonging to another species, the Brown Rat *(R. norvegicus),* were seen marching westwards into Russia, and swimming across the Volga. This invasion was the prelude to the complete occupation of Europe by brown rats.87 Furthermore, in most places they have driven out and destroyed the original black rats (which are now chiefly found on ships), and at the same time have adopted habits which do not bring them into such close contact with man as was the case with the black rat. The brown rat went to live chiefly in the sewers which were being installed in some of the European towns as a result of the onrush of civilisation, so that plague cannot so easily be spread in Europe nowadays by the agency of rats. These important historical events among rats have probably contributed a great deal to the cessation of serious plague epidemics in man in Europe, although they are not the only factors which have caused a dying down of the disease. But it is probable that the small outbreak of plague in Suffolk in the year 1910 was prevented from spreading widely owing to the absence of very close contact between man and rats.[71] We have described this example of the rats at some length, since it shows how events of enormous import to man may take place in the animal world, without anyone being aware of them.

4. The history of malaria in Great Britain is another example of the way in which we have unintentionally interfered with animals and produced most surprising results. Up to the end of the eighteenth century malaria was rife in the low-lying parts of Scotland and England, as also was liver-rot in sheep. No one in those days knew the causes or mechanisms of transmission of either of these two diseases; but at about that time very large parts of the country were drained in order to reclaim land for agricultural purposes, and this had the effect of practically wiping out malaria and greatly reducing liver-rot-quite unintentionally 1 We know now that malaria is caused by a protozoan which is spread to man by certain blood-sucking mosquitoes whose larvae live in stagnant water, and that the larva of the liver-fluke has to pass through one stage of its life-history in a fresh-water snail (usually *Limnaea truncatula).* The existence of malaria depends on an abundance of mosquitoes, while that of liver-rot is bound up with the distribution and numbers of the snail. With the draining of land both these animals disappeared or became much rarer.[13b]

5. On the whole, however, we have been settled in this country for such a long time that we seem to have struck a fairly level balance with the animals around us; and it is because the mechanism of animal society runs comparatively smoothly that it is hard to remember the number of important ways in which wild animals affect man, as, for instance, in the case of earthworms which carryon such a heavy industry in the soil, or the whole delicately adjusted process of control of the numbers of herbivorous insects. It is interesting therefore to consider the sort of thing that happens when man invades a new country and attempts to exploit its resources, disturbing in the process the balance of nature. Some keen gardener, intent upon making Hawaii even more beautiful than before, introduced a plant called *Lantana camara,* which in its native home of Mexico causes no trouble to anybody. Meanwhile, some one else had also improved the amenities of the place by introducing turtle-doves from China, which, unlike any of the native birds, fed eagerly upon the berries of *Lantana.* The combined effects of the vegetative powers of the plant and the spreading of seeds by the turtle-doves were to make the *Lantana* multiply exceedingly and become a serious pest on the grazing country.

Indian mynah birds were also introduced, and they too fed upon *Lantana* berries. After a few years the birds of both species had increased enormously in numbers. But there is another

PLATE VI

(a) A typical animal community in the plankton of a tarn in the English Lake District. Three important key-industry animals are shown: *Diaptomus*, *Daphnia* and *Bosmina*.

(b) Effect of "rabbit pressure" on grass in the Malvern Hills. The plants are closely nibbled by rabbits. The white web on the furze bush was constructed by a minute mite (*Erythraeus regalis*, Koch var.) which was present in enormous numbers.

side to the story. Formerly the grasslands and young sugar-cane plantations had been ravaged yearly by vast numbers of army-worm caterpillars, but the mynahs also fed upon these caterpillars and succeeded to a large extent in keeping them in check, so that the outbreaks became less severe. About this time certain insects were introduced in order to try and check the spread of *Lantana,* and several of these (in particular a species of Agromyzid fly) did actually destroy so much seed that the *Lantana* began to decrease. As a result of this, the mynahs also began to decrease in numbers to such an extent that there began to occur again severe outbreaks of army-worm caterpillars. It was then found that when the *Lantana* had been removed in many places, other introduced shrubs came in, some of which are even more difficult to eradicate than the original *Lantana.*[73]

6. It is clear that animals are organised into a complex society, as complex and as fascinating to study as human society. At first sight we might despair of discovering any general principles regulating animal communities. But careful study of simple communities shows that there are several principles which enable us to analyse an animal community into its parts, and in the light of which much of the apparent complication disappears. These principles will be considered under four headings:

A. Food-chains and the food-cycle.
B. Size of food.
C. Niches.
D. The pyramid of numbers.

Food-chains and the Food-cycle

7. We shall see in a later chapter what a vast number of animals can be found in even a small district. It is natural to ask: "What are they all doing?" The answer to this is in many cases that they are not doing anything. All cold-blooded animals and a large number of warm-blooded ones spend an unexpectedly large proportion of their time doing nothing at all, or at any rate, nothing in particular. For instance, Percival[12b] says of the African rhinoceros: "After drinking they play…the rhino appears at his best at night and gambols in sheer lightness of heart. I have seen them romping like a lot of overgrown pigs in the neighbourhood of the drinking place."

Animals are not always struggling for existence, but when they do begin, they spend the greater part of their lives eating. Feeding is such a universal and commonplace business that we are inclined to forget its importance. The primary driving force of all animals is the necessity of finding the right kind of food and enough of it. Food is the burning question in animal society, and the whole structure and activities of the community are dependent upon questions of food-supply. We are not concerned here with the various devices employed by animals to enable them to obtain their food, or with the physiological processes which enable them to utilise in their tissues the energy derived from it. It is sufficient to bear in mind that animals have to depend ultimately upon plants for their supplies of energy, since plants alone are able to turn raw sunlight and chemicals into a form edible to animals. Consequently herbivores are the basic class in animal society. Another difference between animals and plants is that while plants are all competing for much the same class of food, animals have the most varied diets, and there is a great divergence in their food habits. The herbivores are usually preyed upon by carnivores, which get the energy of the sunlight at third-hand, and these again may be preyed upon by other carnivores, and so on, until we reach an animal which has no enemies, and which forms, as it were, a terminus on this food cycle. There are, in fact, chains of animals linked together by food, and all dependent in the long run upon plants. We refer to these as " food-chains," and to all the food-chains in a community as the "food-cycle."

8. Starting from herbivorous animals of various sizes, there are as a rule a number of food-chains radiating outwards, in which the carnivores become larger and larger, while the parasites are smaller than their hosts. For instance, in a pine wood there are various species of aphids or plant-lice, which suck the juices of the tree, and which are preyed on by spiders. Small birds such as tits and warblers eat all these small animals, and are in turn destroyed by hawks. In an oak wood there are worms in the soil, feeding upon fallen leaves of plants, and themselves eaten by thrushes and blackbirds, which are in turn hunted and eaten by sparrow-hawks. In the same wood there are mice, one of whose staple foods is acorns, and these form the chief food of the tawny owl. In the sea, diatoms form the basic plant food, and there are a number of crustacea (chiefly copepods) which turn these algae into food which can be eaten by larger animals. Copepods are living winnowing fans, and they form what may be called a "key industry" in the sea. The term "key-industry" is a useful one, and is used to denote animals which feed upon plants and which are so numerous as to have a very large number of animals dependent upon them. This point is considered again in the section on "Niches."

9. Extremely little work has been done so far on food-cycles, and the number of examples which have been worked out in even the roughest way can be counted on the fingers of one hand. The diagram shown in Fig. 3 shows part of a marine plankton community, which has been studied by Hardy,[102] and which is arranged to show the food-chains leading up to the herring at different times of the latter's life. To complete the picture we should include the dogfish, which attacks the herring itself. Fig. 4 shows the food-cycle on a high arctic island, and is chosen because it is possible in such a place to work out the interrelations of its impoverished fauna fairly completely.

At whatever animal community we look, we find that it is organised in a similar way. Sometimes plants are not the immediate basis of the food-cycle. This is the case with scavengers, and with such associations as the fauna of temporary fresh-water pools and of the abyssal parts of the sea where the immediate basic food is mud and detritus; and the same is true of many parasitic faunas. In all these cases, which are peculiar, the food-supply is of course ultimately derived from plants, but owing to the isolation of the animals it is convenient to treat them as a separate community. Certain animals have succeeded in telescoping the particular food-chain to which they belong. The whale-bone whale manages to collect by means of its sieve-like apparatus enough copepods and pteropods to supply its vast wants, and is not dependent on a series of intermediate species to produce food large enough for it to deal with effectively. This leads us on to a more detailed consideration of the problem of

Size of Food

10. Size has a remarkably great influence on the organisation of animal communities. We have already seen how animals form food-chains in which the species become progressively larger in size or, in the case of parasites, smaller in size. A little consideration will show that size is the main reason underlying the existence of these food-chains, and that it explains many of the phenomena connected with the food cycle. There are very definite limits, both upper and lower, to the size of food which a carnivorous animal can cat. It cannot catch and destroy animals *above* a certain size, because it is not strong or skilful enough. In the animal

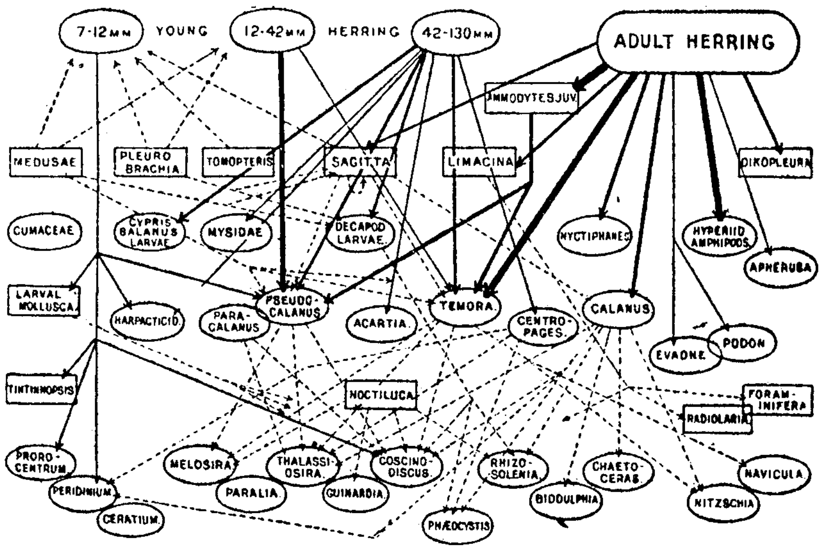

FIG. 3.— Diagram showing the general food relations of the herring to other members of the North Sea plankton community. Note the effect of herring size at different ages upon its food. (From Hardy.[102])

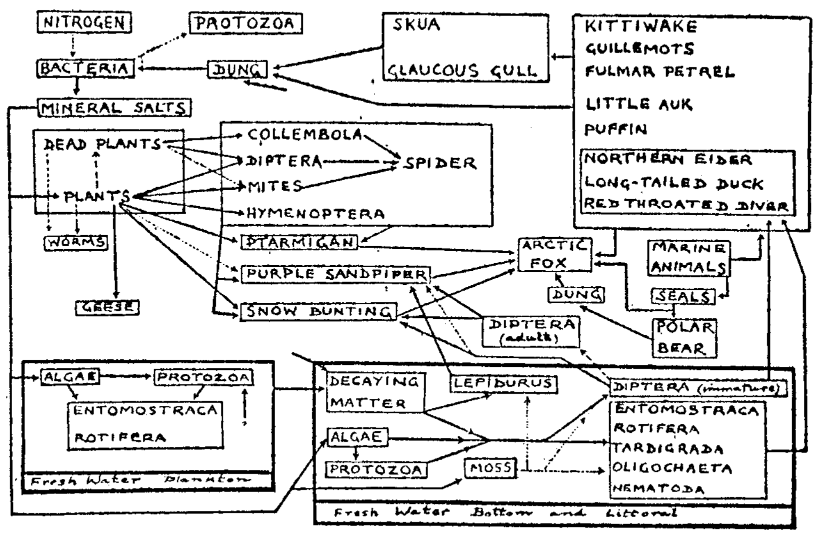

FIG. 4.— Food-cycle among the animals on Bear Island, a barren spot in the arctic zone, south of Spitsbergen. (The dotted lines represent probable food relations not yet proved.) The best way to read the diagram is to start at "marine animals") and follow the arrows. (From Summerhayes and Elton.[25])

world, fighting weight counts for as much as it does among ourselves, and a small animal can no more tackle a large one successfully than a light-weight boxer can knock out a trained man four stone heavier than himself. This is obvious enough in a broad way: spiders do not catch elephants in their webs, nor do water scorpions prey on geese. Also the structure of an animal often puts limits to the size of food which it can get into its mouth. At the same time a carnivore cannot subsist on animals *below* a certain size, because it becomes impossible at a certain point to catch enough to supply its needs. If you have ever got lost on the moors and tried to make a square meal of bilberries, you will at once see the force of this reasoning. It depends, however, to a large extent on the number of the prey: foxes find it worthwhile to live entirely on mice in the years when the latter are very abundant, but prey on larger animals like rabbits at other times.

11. It is thus plain that the size of the prey of carnivorous animals is limited in the upward direction by its strength and ability to catch the prey, and in the downward direction by the feasibility of getting enough of the smaller food to satisfy its needs, the latter factor being also strongly influenced by the numbers as well as by the size of its food. The food of every carnivorous animal lies therefore between certain size limits, which depend partly on its own size and partly on other factors. There is an *optimum* size of food which is the one usually eaten, and the limits actually possible are not usually realised in practice. (It is as well to point out that herbivorous animals are not strictly limited by the size of their plant-food, except in special cases such as seed-eating birds, honey-collecting insects etc., owing to the fact that the plants cannot usually run away, or make much resistance to being eaten.) We have very little information as to the exact relative sizes of enemies and their prey, but future work will no doubt show that the relation is fairly regular throughout all animal communities.

12. Three examples will serve to illustrate the part played by size. There lives in the forests round Lake Victoria a kind of toad which is able to adjust its size to the needs of the moment. When attacked by a certain snake the toad swells itself out and becomes puffed up to such an extent that the snake is quite unable to cope with it, and the toad thus achieves its object, unlike the frog in Aesop's fable.[3c] Carpenter[3a] has pointed out another curious case of the importance of size in food. The tsetse fly *(Glossina palpalis),* whose ecology was studied by him in the region of Lake Victoria, can suck the blood of many mammals and birds, in which the size of the blood corpuscles varies from 7 to 18μ, but is unable to suck that of the lungfish, since the corpuscles of the latter (41μ in diameter) are too large to pass up the proboscis of the fly. A third case is that noticed by Vallentin[77b] in the Falkland Islands. He found that the black curlew *(Haematopus quoyi)* ate limpets *(Patella aenea)* on the rocks at low tide, but was only able to dislodge those of moderate size, not usually more than 45 millimetres across.

13. These are three rather curious cases of what is a universal phenomenon. Man is the only animal which can deal with almost any size of food, and even he has only been able to do this during the later part of his history. It appears that the very early ancestors of man must have eaten food of a very limited range of size-such things as shellfish, fruits, mushrooms, and small mammals. Later on, man developed the art of hunting and trapping large animals, and he was thus able to increase the size of his food in the *upward* direction, and this opened up possibilities of obtaining food in greater bulk and variety. After the hunting stage came the agricultural stage, and this consisted essentially in the further development of the use of large animals, now in a domesticated state, and in the invention of means of dealing with foods much *smaller* than had previously been possible, by obtaining great quantities of small seeds in a short time. All other animals except man have their food strictly confined within rather

narrow limits of size. The whale-bone whale can feed on tiny crustacea not a thousandth of its bulk, while the killer whale can destroy enormous cuttle-fish; but it is only man who has the power of eating small, large, and medium sized foods indiscriminately. This is one of the most important ways in which man has obtained control over his, surroundings, and it is pretty clear that if other animals had the same power, there would not be anything like the same variety and specialisation that there is among them, since the elaborate and complex arrangements of the food-cycles of animal communities would automatically disappear. For the very existence of food-chains is due mainly to the fact that any one animal can only live on food of a certain size. Each stage in an ordinary food-chain has the effect of making a smaller food into a larger' one, and so making it available to a larger animal. But since there are upper and lower limits to the size of animals, a progressive food-chain cannot contain more than a certain number of links, and usually has less than five.

14. There is another reason why food-chains stop at a certain point; this is explained in the section on the Pyramid of Numbers. Leaving aside the question of parasites at present, it may be taken as a fairly general rule that the enemy is larger than the animal upon which it preys. (This idea is contained in the usual meaning of the word "carnivore.") But such is not invariably the case. Fierceness, skill, or some other special adaptation can make up for small size. The arctic skua pursues and terrorises kittiwake gulls and compels them to disgorge their last meal. It does this mainly by naked bluff, since it is, as a matter of fact, rather less in weight than the gull, but is more determined and looks larger owing to a great mass of fluffy feathers. In fact, when we are dealing with the higher animals such as birds, mammals, and the social ants and bees, the psychology of the animals very often plays a large part in determining the relative sizes of enemies and their prey. Two types of behaviour may be noticed. The strength of the prey and therefore its virtual size may be reduced; this is done by several devices, of which the commonest are poison and fear. Some snakes are able to paralyse and kill by both these methods, and so can cope with larger animals than would otherwise be possible. Stoats are able to paralyse rabbits with fear, -and so reduce the speed and strength of the latter. It is owing to this that the stoat can be smaller than its prey. The fox, which does not possess this power of paralysing animals with fear, is considerably larger than the rabbit. The second point is that animals are able to increase their own effective size by flock tactics. Killer whales in the Antarctic seas have been seen to unite in parties of three or four in order to break up the thick ice upon which seals, their prey, are sleeping.[150] Wolves are another example. Most wolves are about half the linear size of the deer which they hunt, but by uniting in packs they become as formidable as one very large animal. The Tibetan wolf, which eats small gazelles, etc., hunts singly or in twos and threes.[43a] On the other hand, herbivores often band together in flocks in order to increase their own powers of defence. This usually means increased strength, but other factors come in too. Ants have achieved what is perhaps the most successful solution of the size problem, since they form organised colonies whose size is entirely fluid according to circumstances, Schweitzer[88] noted a column of driver ants in Angola march past for thirty-six hours. They are able by the mass action of their terrible battalions to destroy animals many times their own size *(e.g.* whole litters of the hunting dog[121]*),* and at the same time can carry the smallest of foods. It must be remembered, therefore, that the idea of food-chains of animals of progressively larger size is only true in a general way, and that there are a number of exceptions. Having considered the far-reaching effects of size on the organisation of animal communities, we are now in a position to consider the subject of

Niches

15. It should be pretty clear by now that although the actual species of animals are different in different habitats, the ground plan of every animal community is much the same. In every community we should find herbivorous and carnivorous and scavenging animals. We can go further than this, however: in every kind of wood in England we should find some species of aphid, preyed upon by some species of ladybird. Many of the latter live exclusively on aphids. That is why they make such good controllers of aphid plagues in orchards. When they have eaten all the pest insects they just die of starvation, instead of turning their attention to some other species of animal, as so many carnivores do under similar circumstances. There are many animals which have equally well-defined food habits. A fox carries on the very definite business of killing and eating rabbits and mice and some kinds of birds. The beetles of the genus *Stenus* pursue and catch springtails *(Collembola)* by means of their extensile tongues. Lions feed on large ungulates-in many places almost entirely zebras. Instances could be multiplied indefinitely. It is therefore 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 I' niche." Animals have all manner of externa1 factors acting upon them—chemical, physical, and biotic-and the "niche" of an animal means its place in the biotic environment, *its relations to food and enemies.* Thy ecologist should cultivate the habit of looking at animals from this point of view as well as from the ordinary standpoints of appearance, names, affinities, and past history . When an ecologist says "there goes a badger" he should include in his thoughts some definite idea of the animal's place in the community to which it belongs, just as if he had said "there goes the vicar."

16. The niche of an animal can be defined to a large extent by its size and food habits. We have already referred to the various key-industry animals which exist, and we have used the term to denote herbivorous animals which are sufficiently numerous to support a series of carnivores. There is in every typical community a series of herbivores ranging from small ones *(e.g.* aphids) to large ones *(e.g.* deer). Within the herbivores of anyone size there may be further differentiation according to food habits. Special niches are more easily distinguished among carnivores, and some instances have already been given.

The importance of studying niches is partly that it enables us to see how very different animal communities may resemble each other in the essentials of organisation. For instance, there is the niche which is filled by birds of prey which eat small mammals such as shrews and mice. In an oak wood this niche is filled by tawny owls, while in the open grassland it is occupied by kestrels. The existence of this carnivore niche is dependent on the further fact that mice form a definite herbivore niche in many different associations, although the actual species of mice may be quite different. Or we might take as a niche all the carnivores which prey upon small mammals, and distinguish them from those which prey upon insects. When we do this it is immediately seen that the niches about which we have been speaking are only smaller subdivisions of the old conceptions of carnivore, herbivore, insectivore, etc., and that we are only attempting to give more accurate and detailed definitions of the food habits of animals.

17. There is often an extraordinarily close parallelism between niches in widely separated communities. In the arctic regions we find the arctic fox which, among other things, subsists upon the eggs of guillemots, while in winter it relies partly on the remains of seals killed by polar bears. Turning to tropical Africa, we find that the spotted hyaena destroys large numbers of ostrich eggs, and also lives largely upon the remains of zebras killed by lions.[12a] The arctic fox and the hyaena thus occupy the same two niches-the former seasonally, and the

latter all the time. Another instance is the similarity between the sand-martins, which one may see in early summer in a place like the Thames valley, hawking for insects over the river, and the bee-eaters in the upper part of the White Nile, which have precisely similar habits. Both have the same rather distinct food habits, and both, in addition, make their nests in the sides of sand cliffs forming the edge of the river valleys in which they live. (Abel Chapman[850] says of the bee-eaters that "the whole cliff-face appeared aflame with the masses of these encarmined creatures.") These examples illustrate the tendency which exists for animals in widely separated parts of the world to drift into similar occupations, and it is seen also that it is convenient sometimes to include other factors than food alone when describing the niche of any animal. Of course, a great many animals do not have simple food habits and do not confine themselves religiously to one kind of food. But in even these animals there is usually some regular rhythm in their food habits, or some regularity in their diverse foods. As can be said of every other problem connected with animal communities, very little deliberate work has been done on the subject, although much information can be found in a scattered form, and only awaits careful coordination in order to yield a rich crop of ideas. The various books and journals of ornithology and entomology are like a row of beehives containing an immense amount of valuable honey, which has been stored up in separate cells by the bees that made it. The advantage, and at the same time the difficulty, of ecological work is that it attempts to provide conceptions which can link up into some complete scheme the colossal store of facts about natural history which has accumulated up to date in this rather hap hazard manner. This applies with particular force to facts about the food habits of animals. Until more organised information about the subject is available, it is only possible to give a few instances of some of the more clear-cut niches which happen to have been worked out.

18. One of the biggest niches is that occupied by small sap-suckers, of which one of the biggest groups is that of the plant-lice or aphids. The animals preying upon aphids form a rather distinct niche also. Of these the most important are the coccinellid beetles known as ladybirds, together with the larvae of syrphid flies (cf. Fig. 5) and of lacewings. The niche

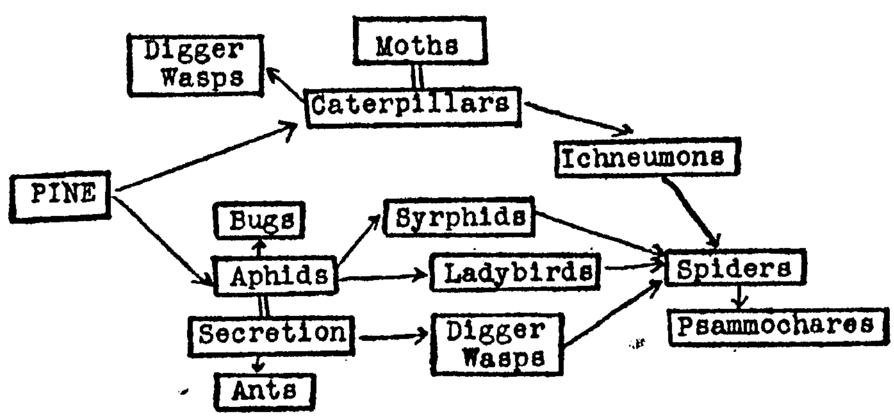

FIG. 5.—Food-cycle on young pine-trees on Oxshott Common. (From Richards.[18])

in the sea and in fresh water which is analogous to that of, aphids on land is filled by copepods, which are mainly diatom eaters. This niche occurs all over the world, and has a number of well-defined carnivore niches associated with it. If we take a group of animals like the herbivorous grass-eating mammals, we find that they can be divided 'into smaller niches according to the size of the animals. There is the mouse niche, filled by various species in different parts of the world; the rabbit niche, of larger size, filled by rabbits and hares in the palae-arctic region and in North America, by the agouti and viscacha in South America, by wallabies in Australia, and by animals like the hyrax, the spring buck, and the mouse deer 56 in Africa. In the same way it can be shown that there is a special niche of carnivorous snakes which prey upon other snakes-a niche which is filled by different species in different countries. In South America there is the mussarama, a large snake four of five feet in length' which is not itself poisonous, but preys exclusively upon other snakes' many of which are poisonous, being itself immune to the venons of lachesis and rattlesnake, but not to colubrine poisons. In the United States the niche is filled by the king-snake which has similar habits, while in India there is a snake called the hamadryad which preys up another (in this case non-poisonous) snakes.[86a]

19. Another widespread niche among animals is that occupied by species which pick ticks off other animals. For instance, the African tick-bird feeds entirely upon the ticks which live upon the skin of ungulates, and is so closely dependent upon its mammalian "host" that it makes its nest of the latter's hair *(e.g.* of the hartebeest).[12f] In England, starlings can often be seen performing the same office for sheep and deer. A similar niche is occupied on the Galapagos Islands by a species of scarlet land-crab, which has been observed picking ticks off the skin of the great aquatic lizards *(Amblyrhynchus)*.[36C] Another niche, rather analogous to the last one, is that occupied by various species of birds, which follow herds of large mammals in order to catch the insects which are disturbed by the feet of the animals. Chapman[85d] saw elephants in the Sudan being followed by kites and grey herons; Percival[12g] says that the buff-backed egret follows elephants and buffalo in Kenya for the same purpose; in Paraguay 860 there are the Aru blackbirds which feed upon insects disturbed by the feet of cattle; while in England wagtails attend cattle and sheep in the same way.

20. There is a definite niche which is usually filled by earthworms in the soil, the species of worm differing in different parts of the world. But on coral islands their place may be largely taken by land-crabs. Wood-Jones[107a] states that on Cocos-Keeling Island, coconut husks are one of the most important source of humus in the soil, and in the rotting husks land-crabs (chiefly of the genus *Cardiosoma)* make burrows and do the same work that earthworms do in our own country. (There are as a matter of fact earthworms as well on these islands.) On the coral reefs which cover such a large part of the coast in tropical regions, there is a definite niche filled by animals which browse upon the corals, just as herbivorous mammals browse upon vegetation on land. There are enormous numbers of holothurians or sea-cucumbers which feed entirely in this way. Darwin 30 gives a very good description of this niche. Speaking also of Cocos-Keeling Island, he says:

> "The number of species of Holothuria, and of the individuals which swarm on every part of these coral-reefs, is extraordinarily great; and many ship-loads are annually freighted, as is well known, for China with the trepang, which is a species of this genus. The amount of coral yearly consumed, and ground down into the finest mud, by these several creatures, and probably by many other kinds, must be immense. These facts are, however, of more importance in another point of view, as showing us that there are living checks to the growth of coral-reefs, and that the almost universal law of' consume and be consumed,' holds good even with the polypifers forming those massive bulwarks, which are able to withstand the force of the open ocean."

This passage, besides showing that the coral-eating niche has a geological significance, illustrates the wide grasp of ecological principles possessed by Darwin, a fact which continually strikes the reader of his works. We have now said enough to show what is meant by an ecological niche, and how the study of these niches helps us to see the fundamental similarity between many animal communities which may appear very different superficially. The niche of an animal may to some extent be defined by its numbers. This leads us on to the last subject of this chapter,

The Pyramid of Numbers

21. "One hill cannot shelter two tigers." In other and less interesting words, many carnivorous animals, especially at or near the end of a food-chain, have some system of territories, whereby it is arranged that each individual, or pair, or family, has an area of country sufficiently large to supply its food requirements. Hawks divide up the country in this way, and Eliot Howard's work[9] has shown that similar territory systems playa very important part in the lives of warblers. We can approach the matter also from this point of view: the smaller an animal the commoner it is on the whole. This is familiar enough as a general fact. If you are studying the fauna of an oak wood in summer, you will find vast numbers of small herbivorous insects like aphids, a large number of spiders and carnivorous ground beetles, a fair number of small warblers, and only one or two hawks. Similarly in a small pond, the numbers of protozoa may run into millions, those of *Daphnia* and *Cyclops* into hundreds of thousands, while there will be far fewer beetle larvae, and only a very few small fish. To put the matter more definitely, the animals at the base of a food-chain are relatively abundant, while those at the end are relatively few in numbers, and there is a progressive decrease in between the two extremes. The reason for this fact is simple enough. The small herbivorous animals which form the key-industries in the community are able to increase at a very high rate (chiefly by virtue of their small size), and are therefore able to provide a large margin of numbers over and above that which would be necessary to maintain their population in the absence of enemies. This margin supports a set of carnivores, which are larger in size and fewer in numbers. These carnivores in turn can only provide a still smaller margin, owing to their large size which makes them increase more slowly, and to their smaller numbers. Finally, a point, is reached at which we find a carnivore *(e.g.* the lynx or the peregrine falcon) whose numbers are so small that it cannot support any further stage in the food-chain. There is obviously a lower limit in the density of numbers of its food at which it ceases to be worth while for a carnivore to eat that food, owing to the labour and time that is involved in the process. It is because of these number relations that carnivores tend to be much more wide-ranging and less strictly confined to one habitat than herbivores.

22. This arrangement of numbers in the community, the relative decrease in numbers at each stage in a food-chain, is characteristically found in animal communities all over the world, and to it we have applied the term " 'pyramid of numbers." It results, as we have seen, from the two facts *(a)* that smaller animals are preyed upon usually by larger animals, and *(b)* that small animals can increase faster than large ones, and so are able to support the latter.

The general existence of this pyramid in numbers hardly requires proving, since it is a matter of common observation in the field. Actual figures for the relative numbers of different stages in a food-chain are very hard to obtain in the present state of our knowledge. But three examples will help to crystallise the idea of this " pyramid." Birge and Juday[92] have calculated that the material which can be used as food by the plankton rotifers and crustacea of Lake Mendota in North America weighs twelve to eighteen times as much as they do. (The fish which eat the crustacea would weigh still less.) Again, Mawson[93] estimated that one pair of skuas *(Megalestris)* on Haswell I. in the Antarctic regions, required about fifty to one hundred Adelie penguins to keep them supplied with food (in the form of eggs and young of the penguins); while Percival[12d] states that one lion will kill some fifty zebras per year, which gives us some idea of the large numbers of such a slow-breeding animal as the zebra which are required to produce this extra margin of numbers.