



The Ecological Survey of Animal Communities: With a Practical System of Classifying Habitats by Structural Characters

Author(s): Charles S. Elton and Richard S. Miller

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THE ECOLOGICAL SURVEY OF ANIMAL COMMUNITIES:
WITH A PRACTICAL SYSTEM OF CLASSIFYING HABITATS
BY STRUCTURAL CHARACTERS

BY CHARLES S. ELTON AND RICHARD S. MILLER*

Bureau of Animal Population, Department of Zoological Field Studies, Oxford

(*With one Figure in the Text*)

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1. DEVELOPMENT OF IDEAS

Nearly all animal ecologists have some views about the usefulness or otherwise of ecological surveys designed to describe the way in which species are grouped together in different places. The present paper seeks to clarify the position of community surveys in animal ecology, by contrasting as plainly as possible their theoretical aims with the practical limitations that hinder their achievement. At the same time a simplified system of assembling and classifying information about habitats at both a species and a community level is described, that seeks to recognize the limitations of the material without destroying the value of the integrated results.

The ideas and methods presented here are partly the result of a good many years of thought and observation by the senior author, and partly of three years spent at Oxford by the junior author, with a background of experience from the western United States. Our conclusions were finally formulated between August 1951 and March 1952, as the outcome of long discussions, based in particular upon field experience of Wytham Woods. This is an estate close to Oxford, with about a thousand acres of woodland and grassland. It is set on hills ringed below by farm lands that are in turn bounded on two sides by the great bend of the River Thames that gave Wytham its Saxon name. Here the University, which owns most of the land, has encouraged field research and allotted some parts of the hills as scientific nature reserves. The whole area is a representative south midland ecological complex on calcareous soils, with at least several thousand species of animals living on it.

During the final period of this study the Nature Conservancy made a grant which enabled Miller to devote his whole time to the work, and also provided for another bio-

* Now at the Biological Laboratories, Harvard University.

logist, Miss B. Macpherson, to manage the indexing side of the survey. We are most grateful to her for considerable help and valuable suggestions; also to some other research workers in the Bureau of Animal Population, especially Mr A. Macfadyen, Dr C. Overgaard Nielsen and Mr Eric Duffey, for the benefit of frequent discussion as well as for field material and information; and to Prof. Thomas Park and Dr Laurie Clark for kindly reading parts of the paper in manuscript and giving comments.

Although the mental development which has led up to this investigation has taken Elton about 35 years to follow through, the logic of its conclusions can be stated very simply. It is that whatever problem in natural population control or dynamics is being studied, one has to consider the working of density-dependent situations and therefore of biotic relations both within individual sections of the same population and between populations of different species. From this it follows that one needs to know about community ecology, in other words, to undertake ecological survey, even if it is at first only on a limited scale. This argument may be usefully illustrated by a brief résumé of the mental stages by which Elton arrived at the present position. It is to be supposed that other people may have followed a similar sequence of ideas, but the absence of a coherent general philosophy in the research of many animal ecologists suggests that the account of a particular person's struggles to make sense of the complexities of nature may have a certain value, especially as it began in the pioneer days of animal ecology in this country.

Starting with a strong desire to describe the ecological groupings of species, that is, the pattern of organic nature, Elton soon realized that animal communities differ fundamentally from vegetation units in the transfer of organic matter (and by implication potential energy) through numerous stages forming a network of biotic connexions between the populations of different species. This stage of thought was approached originally through the inspiration of Shelford's book, *Animal communities in Temperate America*, first read in 1920; by a series of reconnaissances in the years 1919–21 of sixty marl-pit ponds, an estuarine stream, and the sand-dune systems in the neighbourhood of Liverpool; also of various ponds and pools in the Lake District and around Oxford; and by surveys of Arctic plant and animal communities and soil formations in the Spitsbergen archipelago in 1921, 1923 and 1924 (Summerhayes & Elton, 1923, 1928). The last still remains the most complete attempt at a combined description of all plant and animal communities of a complex area of land, fresh water, seashore (and pack-ice), though it was not made in exact quantitative terms. Its chief large omission was the rich microfauna of soil and litter, since proved by Hammer (1944) to be a feature of Arctic regions.

The attractive notion that a small pond is a closed microcosm was soon dispelled, also the hope that it would be a simple system to study. There was bewildering variation from one to another, and great internal complexity within each. During Arctic surveys the bare elements of a connected ecosystem* (Tansley, 1935) of sea, land and fresh water could be observed, and could be visualized working as one organic 'machine' (in the sense used by Lotka, 1925). It was possible to view the system as a whole, though without material for exact population measurements. It was soon felt that any descriptive picture of species groupings needed complementing and extending by a more dynamic†

* 'Ecosystem' is the comprehensive term introduced by Tansley to mean plant and animal populations, together with the whole physical and chemical system in which they live.

† 'Dynamic' is used throughout this paper to cover the field of population ecology involving movements of individuals, rates of change of numbers or of natality and mortality, as well as energetics in the more restricted sense implied by some physicists.

interpretation, and that this would lead to ideas and methods of measurement arising out of the essential differences between plant and animal populations. This meant turning away from the main trend of workers like Shelford, who while they realized the existence of the food cycle and of energy transfer, were mainly concerned to define the lateral margins of the main habitats and species living in them, using physiology, behaviour and other adaptations as indicators. The Arctic made one see ecological processes in full swing. One of these is the circulation of matter (and energy) through the species network, a specially striking instance of this being the influence of sea birds locally upon the open and stunted vegetation of the ordinary tundra. In these situations a bird colony can, by making possible closed vegetation, have a paramount effect on the competition between different species of plants.

Another process, only vaguely understood and based upon a few puzzling occurrences, is that species of animals wholly characteristic of one zone (marine drift-line) are able to colonize a different zone (dry tundra) in the absence of related species normally found there. This was a recognition of the principle of competition, which we now believe to be a fundamental clue to understanding the variability of communities, and the limitation of their species composition (see §3). The first process—the productivity cycle—is essentially different in tempo in the plant and animal sections of a community complex. It is of course chemically different. But also the much greater mobility of most animal populations leads to frequent lateral and vertical exchanges between the faunas of different parts of major habitats, and this occurs rapidly and has a strong effect on community form (and, as we shall show, on the scale of habitat relations). With vegetation, such exchanges are usually only through slow vegetative growth and the spread of seeds, etc., into already solidly occupied ground, but most animal populations are spaced in an open manner that allows of immediate interaction by invaders and consequent biotic effects on populations there.

Recognition of the existence of what are now called 'consumer layers', of main 'key industry' species or groups in different 'ecological niches' through which large parts of the plant produced organic material passes, and of the 'pyramid of numbers' (Elton, 1927), led naturally to investigation of fluctuations in numbers of common or abundant forms, such as are especially sharply shown by rodents (Elton, 1924). It was realized that these fluctuations cause disturbances within communities, and that we needed to know how the upper and lower ranges of population density are controlled, as well as understanding what causes particular periodicity and any regional synchronization of the changes. From 1923 onwards for about 20 years Elton's attention was mainly diverted into research upon these fluctuations. The community concept was held in mind, and, indeed, applied with some thoroughness to the parasites of a small mammal population (Elton, Baker, Ford & Gardiner, 1931). This again revealed the chains and branching relationship between species, the variability of the species assemblages, but nevertheless the possibility of attaining a general picture of dispersion and limits.

In the years 1924–5 an attempt was made to start a full ecological survey, but it had to be abandoned for several reasons, especially the grave difficulties of attaining satisfactory taxonomic precision except through the direct labours of specialists. That situation, although often still difficult (as, for example, with the huge group of parasitic Hymenoptera), has radically improved during the last 25 years. This field study (done in co-operation with O. W. Richards) was on the ecological succession in communities

colonizing bare wet mud dredged from the Oxford Canal. The rapid and striking changes in fauna associated with the sequence from bare ground to willow thicket left a vivid impression of the power of vegetative and resulting microclimatic conditions to alter the composition of animal communities.

By the nineteen-thirties a general realization began to spread among animal ecologists that the controlling processes in animal populations are brought about primarily by density-dependent situations. Attention inevitably centred upon fluctuations, since these had been proved to occur everywhere in nature. A good many important mathematical theories were propounded, by Lotka, Volterra, Thompson, Nicholson and others; while some pioneer laboratory model experiments were being developed by Chapman and Gause. Both theory and practice also owed much to the work of Pearl, though this was not concerned directly with fluctuations. All these highly abstruse theories were really saying that limitation of numbers must be brought about primarily by biotic relationships. Such relationships can be reduced to five kinds: (1) intraspecific competition, (2) interspecific competition, (3) herbivore-plant relations, (4) predator-prey relations and (5) parasite-host relations. Other relationships, such as to climate and survival niches, were thought to have no power of acting in a regulatory manner, unless they combined in some way with the density-dependent processes mentioned above, some of which may be either opposed or symbiotic in character.

We had therefore reached the point at which the natural control of fluctuations, and therefore the limits of population density, could not be understood without knowing about biotic relations. As four out of five of the main classes of biotic relations mentioned above are between different species, it follows that some reconnaissance of species associations in nature is needed in order to understand the population ecology of any one of them. The only partial exception is the case of purely intraspecific competition, where the other four processes may take a secondary place, although they are usually going on as well.

There was a very important change of philosophical view coming in here, as the properties (the 'elasticity' as it were) of the biological network itself were given paramount importance, populations not being controlled just by factors like climate.

A property of interspecific relations is that they do not stop at one link in the chain. For all one can know to begin with, a large part or the whole community living in a particular habitat may be affected by the population density of any one species; and also other communities at quite considerable distances may be concerned. One only has to think of our summer migrant birds or the salmon to see the force of this point. There seemed no escaping the logic of this argument. One must try to map out, as it were, the species channels through which matter and energy move in the community complex, and seek at the same time to find how far oscillations in numbers of any one species are able or likely to extend their effects along these channels or even temporarily to exploit new ones. Some species would be more self-contained than others. Some would perhaps generate their own fluctuations, others would be strongly influenced from outside.

From about 1928, the animal that had been chosen for intensive study was the vole (*Microtus agrestis*), a grass-eating key species showing marked fluctuations in numbers, and itself the centre of an extensive assemblage of dependent and partially dependent enemies and parasites, and in competition with other herbivorous forms. By 1939 it had become likely that the primary control of its fluctuations must be sought in intraspecific

properties of the population (Elton, 1942), and that enemies and parasites occupied a subordinate importance in generating them. This idea has since gained strong evidence (Chitty, 1952). In the situations under study, interspecific controlling processes could often be ruled out. Nevertheless, the fluctuations of voles cause just that kind of periodic alteration of the supply channels of organic matter through other species that it was the original aim to study, such as changes in numbers of raptorial birds or of parasites and by the destruction of young trees.

This research on voles explored a number of lines, concerned either with the internal complexities of population structure and turn-over, or the ecological ties of the vole with other species. It involved a number of workers, whose activities cannot be reviewed here, but are described in the book mentioned above. One of the incidental but important elements in it was a set of quadrat experiments designed to show how the vole affects hill vegetation. The results (Summerhayes, 1941) were an elegant illustration of the truth that although the flow of energy through the species network goes only in one direction, from plants up through the successive consumer layers, the ecological influences acting through the properties of populations may act in either direction. Thus the grass feeds the vole, but the vole exerts a sufficiently powerful control upon the canopy of dominant grasses to alter the plant-species composition considerably. And this alteration is in the direction of enriching the whole community by making possible the survival of several other flowering plants and of mosses under competition with the dominant grass. These changes must involve further chain effects upon invertebrates, though they were not studied. This work fell into line with earlier experiments by botanists on the influence of rabbits upon chalk grassland (see Tansley, 1939) and of grazing animals upon pasture. The important idea contained in it is the mutual interaction of plants on animals and animals upon plants (frequently discussed in ideas of the biotic community, etc.) and of the mutual reaction of animals with one another (cf. competition; symbiosis in the conventional sense; also predator-prey relations as discussed by Elton, 1938). The point emphasized here is that a map of the paths and channels of energy flow through the species network does not in itself tell one the whole chain of effects; that can only be described in terms of populations and associated biological phenomena.

In the summer of 1942 Elton resumed an active interest in ecological surveys of whole communities, though little but planning and a few technical ideas could be developed until the War ended. But it was decided to organize a 'continuing ecological survey' in the Oxford region as soon as conditions made this possible. At that time it was visualized in rather bare form as a 'multiple correlation apparatus for assembling and handling ecological data on a large scale by uniform methods'. It was to take in the three counties of Oxfordshire, Berkshire and Buckinghamshire as general limits, Oxford being near the geographical centre; it would study all kinds of habitat and all groups of animals, and seek the co-operation of plant ecologists; and its central nucleus was to be a punch-card system on which ecological events could be recorded.

(It should perhaps be said that this decision to abandon special research upon small mammal populations, in favour of more general ecological survey, did not mean abandonment by the Bureau of earlier studies on populations, which were continued and have been expanded after the War by members of it who had already done much to develop them, especially by D. H. Chitty, P. H. Leslie and H. N. Southern. Indeed, the present working structure of the Bureau follows very closely the logical sequence discussed in §2:

community survey, population studies as such, and tracing energy flow through the species network. There are individuals following each of these three lines, independently, but inevitably with some productive influence upon each other.)

In 1943 Wytham Woods came into the hands of the University and later developed into the natural centre near Oxford for field studies on ecology. It was felt that a purely descriptive survey either on the Wicken Fen model (studies by separate taxonomic specialists, with no integration of methods or ideas, and practically no exact or standard habitat recording), or that of the more highly organized Studland Heath survey (where habitat recording was given a high place, but the plan was essentially a historical, mapping and statistical one), would not repay the labour expended on it.* But if it could be combined in a logical and practical way with the special population studies that were likely to be done in increasing amount at Oxford, something of a new character might be developed. But there were no illusions about the magnitude or duration of the task, which is of a kind that has hitherto discouraged the great majority of ecologists from trying to make any continuing community survey at all. The present paper is only intended to give an outline of ideas, and record a modest beginning of working out a convenient standard method for making habitat records for animals. The methods of assembling them in a form that can clear the way for the real task of understanding the balance of forces in an ecosystem will be dealt with in a separate paper.

2. OUTLINE OF REQUIREMENTS

From the foregoing argument, developed in a particular historical form, we can state the general requirements of an ecological survey. These can be subdivided into *Theoretical* and *Practical*, though it is not possible to separate them entirely logically without making almost incomprehensible abstractions.

(a) THEORETICAL REQUIREMENTS

The ultimate and proper aim of an ecological survey, however difficult its achievement may seem at the present level of our knowledge, is to ascertain and measure the population and dynamic relationships of all the species of organisms living in a place over some period of time. An ecological survey is not just a catalogue of the biological properties of individual species or a list of species, or a series of censuses. It is, or is heading towards, a synthesis that will describe not only the parts of a complex system but the interaction and balance between them, and the dynamic properties of the system as a whole.

The early organic chemist must have felt very much as the animal ecologist often does now. It must have seemed dangerous and vain to look beyond, say formaldehyde or a benzene ring, towards higher complexities. Yet organic chemists now seem to move with great confidence amidst compounds of complicated structure, built together by steady research upon related chemical compounds and on the general properties of such systems. Perhaps it is fairer to assess the present position of the animal ecologist as comparable with that of the *inorganic* chemist at the time of Dalton! The 'elements' of the ecologist are whole organisms, themselves chemically heterogeneous and organized into interspersed population systems living chiefly outside the laboratory, so that the task will be much bigger for us. But unless the aim of relating in logical, if possible in predictable

* For the plans of these surveys see Gardiner & Tansley (1923-32) and Diver & Good (1934). It should be noted that while the Wicken Fen results have been published, those of the Studland Heath survey have only partly appeared, because of the War.

form, the mixed species that live as communities in nature is woven into the working philosophy of all ecologists, the study of individual species alone will become quite one-sided and partially sterile. In many directions it has already become so. Our impression is that although general ideas, such as the food-web and density-dependent control of populations, are known to most ecologists, they are not usually focused on their studies. This point has been better made by Darwin a hundred years ago, when he was writing about the struggle for existence: 'Yet unless it be thoroughly engrained in the mind, the whole economy of nature, with every fact on distribution, rarity, abundance, extinction, and variation, will be dimly seen or quite misunderstood' (*The Origin of Species*, ch. 3).

Leaving aside for the moment what is meant by 'a place', an ecological survey can be done in three phases, which follow in a logical order as knowledge increases. All three are required for a complete understanding of communities.

(i) *The species network*

One can make species lists, learn the life history (and with animals, behaviour) and tolerance limits of each species, and establish a more or less qualitative picture or chart of biotic relationships—the functional niches of species. Research of this kind forms the essential starting point for ecological survey. This paragraph may appear a rather brief way of mentioning the mountains of information comprised by most field zoology done up to the present. There is, of course, no intention of depreciating its importance in saying that it contains a mass of information which, except so far as it has been integrated within the theories of evolution and genetics, is still largely an amorphous body of knowledge about separate species.

The addition of quantitative census methods, as done increasingly of late years, increases the scope of interpretation (by introducing the notion of population) and is valuable in developing special technical devices for collecting and counting different groups of organisms. Ecological survey of animals cannot be done by any single method of observing and collecting. Nevertheless, many of the methods we have already are still in a trial stage, their degree of accuracy being imperfectly known. But here again, censuses are a stage in research, not an end in themselves.

It is worth remembering that a chart of the ramifications of species relationships could be made without ever defining what 'a place' is, though it is usually set in the coordinates of some actual place or type of habitat. Such relationships do not necessarily imply co-existence or simultaneous activity of all the species in one topographical community, in the sense that they are interspersed and dynamically interacting in one place at one time. Biotic relations, by the movements of animals, go across all so-called habitat boundaries that may be set up for convenience, and the after-effects or the indirect effects of plant or animal activity may establish just as important dynamic relationships as those found between co-existent populations. A food-web does, however, normally imply that the species charted are organized into one or more topographically grouped communities or 'centres of action'.

This first stage (mapping the species assemblages and their biotic network), to which most ecological survey has so far been limited, may broadly be defined as the natural history and statistical stage. Difficult enough in itself, and still at an elementary level of knowledge, it is only a jumping-off stage for the study of the community in action, considered as a system of events and processes operating in mixed populations.

(ii) *Population processes and population balance*

It is common for ecological text-books and monographs to start from some description of the physical and chemical environment, develop this theme through a sort of geography towards a picture of vegetation types, and finally reach the animals somewhere in the midst of it all. At the theoretical level, it seems to us valuable to emphasize first of all the intrinsic properties of the animal species network itself. This network can be considered, in terms of concepts laid down by Lotka (1925), as an assemblage of interspersed populations of different species maintained by numerous separate and hereditarily transmitted gene systems and reacting with the environment essentially by concentrating and selecting materials and potential energy from it. In doing this, various species are ultimately competing for a common source of energy (that captured from the sun by plants), and quantitative ecology has the task of finding out how this energy becomes shared out between different populations. The first way of approaching this problem is to study the principles of population, as giving some measure of the success of each species in the struggle.

Populations considered as actively working kinetic systems possess three main properties: the component forces of increase and decrease, interspersion amongst other species, and individual movements. Study of the last of these is often included in the natural history stage of investigation, though not from the special point of view required for the analysis of population processes. Adaptation and development of the actuarial methods originally worked out for human populations has made it possible to investigate the interplay between the forces of fertility and mortality in wild populations, the situations controlling the rates of natural increase and the limits of population density—usually operating in fluctuating systems. Although the subject is partly illuminated, it is also greatly obscured for the ordinary ecologist by the brilliant cloud of mathematical theory that has evolved, especially around the question of oscillations in numbers. Nevertheless, these theories have managed to make a useful framework of general propositions about increase rates, interspersion and movements (with the implications of biotic relationships arising from the two latter). Few of these propositions have, however, yet received direct proof from field studies.

There is an enormous amount of work to be done on the properties of particular populations of single species, just as the natural history side of ecology can become absorbed in research on habits and life histories. Reproductive biology, causes of mortality, population structure by age and sex, changes in time (such as can be measured by successive censuses), movements of marked individuals, seasonal mass movements, can all be successfully studied in their own right. As has been pointed out in §1, eventually the necessity for invoking density-dependent relations, not only among members of the same species but between populations of different species, for the understanding of population processes, brings the ecologist back to community questions.

The greatest of the population mathematicians, Volterra, saw quite clearly that there would have to be a general theory of interrelations, as well as special theorems concerning, say, predator-prey relations between two species only. His rather tentative excursion into this further field (Volterra & D'Ancona, 1935) well illustrates the logic of community analysis, and it has implications about the number of consumer layers found in nature. Gause, one of the greatest experimenters on population ecology, devoted his

last research on this subject in an attempt to create a small community of nine species of Protozoa in the test-tube. He was successful, over the very short period of the experiments, in maintaining eight of them, which began to settle down into some sort of balanced state after initial fluctuations. Of the objects of this work he said: 'Since the general criterion of a system's organization is the existence of stable relations maintained by regulatory processes, we must clearly determine by means of some sort of dynamic methods whether or not this definition is applicable to the biocenosis. Does the latter exhibit features of composition and structure, maintained by regulation? In other words, can certain combinations of organisms be stable and there be no intermediate combinations between them, even given intermediate conditions' (Transl. from Gause, 1936).

(iii) *Energy paths and energy flow*

As zoologists we are so thoroughly used to regarding animals as solid bodies, forming parts of populations, that it is not always easy to keep in mind the physical or physiological significance of community ecology. The central physiological fact in community organization is, of course, the exploitation through the manifold connexions of the species network of energy derived from the sun and materials derived from the earth. Lotka has expressed this idea inimitably by defining the plants and animals in a community as a series of connected energy transformers: 'The fundamental equations of kinetics... may appear at first sight to contain no hint of dynamical, of energetic implications: These can be read into the equations only by calling to mind the physical nature of certain of the components whose masses X appear in the equations. These components—aggregates of living organisms—are, in their physical relations, *energy transformers*.... The entire body of all these species of organisms, together with certain inorganic structures, constitute one great world-wide transformer. It is well to accustom the mind to think of this as one vast unit, one great empire.' (Lotka, 1925, ch. 24).

Although everyone is aware that our primary and sole organic energy source is the sun, and that plants make this available in potential form to animals, the further fate of this energy after entering the animal consumer layers of a community has received comparatively little attention from ecologists. There are two reasons for this. One is that the practical measurement of energy consumption is not an easy matter, and leads into a good deal of purely physiological research. The other is that to a great degree population size gives an indirect measure of the amount of potential energy that a species has at any moment, since this is some function of the amount of organic matter. We find, therefore, a good deal of fundamental research in ecology upon productivity of populations, often combined with the calculation of biomass as well as numbers. Biomass is obtained by multiplying the census figure by a function for size, which should properly take account of the effects of sex and age distribution. This function may be just an index like length of body (which can be used for comparing similar sorts of animals), but it usually has to be expressed as volume or as wet or dry weight. Biomass calculations have been used widely in marine and fresh-water ecology, especially in connexion with the productivity or harvest-values of fish populations and their food supply.

But demographic measurements, even allowing for size differences among species, are at best a very rough and awkward index of the amount of potential energy in a body, and they do not at all measure the amount of energy that has gone into the building of that body, or the rate at which it is being used or lost. Thus population indices can be very

misleading in this respect. It is therefore necessary also to measure metabolic rates in order to get a correct and detailed picture of energy flow through organic systems. Earlier workers like Petersen, in his classical investigation of fish productivity in shallow seas (see Petersen & Jensen, 1911) and Bornebusch (1930), working on the soil fauna of woodland, saw the need for expressing ecological relations between species at the three levels of description, population process and energy consumption.

Ideas on the subject have been summarized most correctly by Macfadyen (1948), who takes into account the pioneer work of Thienemann and of Lindeman. He points out that the energy coming into an animal through its food is partly used up and partly handed on, and that which is used up can (unlike most of the matter itself) only be exploited once, and passes out of the body eventually in metabolic heat that is thereafter wasted as far as the organic network is concerned. Any quantity of potential energy entering from plants and passing through the consumer layers and the food-web therefore gradually diminishes until it has reached the uttermost link in the food chains. One of the interesting points that will be brought out in the later discussion of habitats is the very large amount of potential energy that is left in decaying plant and to a lesser extent animal bodies, and forms the basis for special centres of community action.

When we remember that metabolic rates of animals vary not only with age and sex activity, but with day and night and other climatic conditions from hour to hour and month to month, it is not surprising that we have as yet no reliable record of energy flow through a whole community or even a single species population in the wild. At present it is still chiefly a general idea with only limited quantitative data to clothe it, but one that binds together fundamentally the activities of all species living in one place, and at all times.

Place and time. So far, the general properties of the species network have been discussed without considering the patterns of their dispersion in place and time. In this way it is possible to give first importance to the far-reaching ramifications of the network and to its dynamic properties, rather than to the local arrangement of any part of it. Just as we can think of the physical-geographical system of the world as a huge heat-engine run by the sun's radiation power (Lotka, 1925), we may usefully think of the organic network as a tangled 'capillary system' of relatively small 'channels' through which energy derived from the sun's light passes. The spatial and temporal distributions of either of these systems are secondary to the nature of the system as a whole, though of the highest importance ecologically.

It is in discussing the topographical and temporal setting of the species network that it becomes most difficult to distinguish between theoretical and practical requirements, because so much of what passes for objective information about species groupings is, and indeed has to be, collected in an arbitrary statistical manner dependent for its habitat subdivisions upon subjective ideas of the observer. As the question is treated in §4 we will only make a few general points here, taking first the question of *place*.

There are really three questions involved when we ask how the general species network varies from one place to another. First, we know a great deal about the different kinds of physical-geographical patterns, and these can be classified as 'habitats' for plant and animal communities. There is obviously a great deal of repetition of these habitats—that is, they can be grouped into recognizable types like stream, pond, sand dune, alpine rocks or rocky seashore. We also know that animals are all to some extent specialists, both

physiologically and ecologically, in that a species of insect or a fish has a limited range of tolerance to temperature, or certain fixed requirements of food, or needs certain environmental structures for breeding. But the individual instances or loci of each habitat type are never *exactly* repeated. Each habitat type is, after all, not a rigidly connected system but a combination of numerous features that vary. On this ground alone, we must be prepared for differences in species composition and in their abundance from place to place within 'the same habitat', i.e. because owing to the inadequacy and subjectiveness of our observation of habitats, they are never really quite the same even when they appear so; and because we also usually put into one broad group a range of loci between which we can recognize differences.

The second question concerns vegetation. The considerations just mentioned apply to plants, as well as to animals, chances of dispersal and complexities of competition among plant populations making for still greater variability in animal habitats, that are not by any means compensated for by the integrating effects of plant dominance upon subordinate or associated species.

Thirdly, there are similar processes at work in animal populations that are discussed in § 3.

One of the great requirements for a survey is therefore to find out how far individual and local assemblages of species are repeated elsewhere; how far a given habitat type will contain the same assemblage; how far, indeed, we can rely on taxonomic species as units of ecological equivalence between different communities. The principles of classifying habitats need to be related to those that govern population relationships. And much of the confusion that has arisen in this branch of ecology has been caused by the fact that organisms are themselves important parts of the habitat of other organisms, or create changes in the environment that affect other species; but the implications of this fact have not been followed through.

Apart from being implicit in all study of process, *time* has a special importance in community ecology because of the cyclical and historical changes that occur everywhere in nature. The chief cyclical influences of the environment are day and night, tides and annual seasons, but there are also the less regular recurrent changes in weather, state of vegetation, etc. These temporal cycles make necessary a study of activity rhythms in species, which in turn very deeply affect other dependent species.

A survey also clearly needs to take into account not only ecological succession of a more or less predictable seral character, but as much as possible of the unique history of the area. The value of the historical approach is well shown in Diver's work (1933) at South Haven Peninsula, where the gradual building of a large shingle, sand-dune and lagoon system was traced in records since the sixteenth century.

Ecological succession is also important theoretically because it is one of the clearly established guarantees that communities have some orderly arrangement.

(b) PRACTICAL REQUIREMENTS

We may without too much paradox state that the primary requirement for doing an ecological survey is a clear and active working philosophy. The chief other practical requirements for a full-scale ecological survey, apart from the normal resources needed in ecological research, would seem to be:

(i) Taxonomic soundness, i.e. a guarantee that as far as possible the populations treated as separate units are groups homogeneous enough for the purpose in view.

- (ii) Continuity of research in place and time.
- (iii) Standard methods for recording habitats, analogous to the standard criteria of taxonomy for organisms.
- (iv) A system of collecting and processing specimens and records from the field and from experiments and classifying them into community systems.

(i) *Taxonomy*

In the primary stages of an ecological survey the species is the chief unit of study. This usually means the broad conception of a species dealt with in most taxonomic text-books. It is doubtful whether the minute subdivisions of some aggregate species are always relevant to the purpose of animal ecological survey at its present stage of work. Thus, it may be just practically impossible to name correctly every bit of *Rubus* coming into a field situation. Indeed, 'bramble' becomes a more useful term than '*Rubus*', and one may have to ignore the existence of several hundred apomictic species, while knowing well enough that they display all kinds of ecological differences. On the other hand, the occurrence of such ecological strains as those of the European malaria-carrying *Anopheles*, distinguishable only by minute morphological differences in early life-history stages but of crucial importance in determining disease transmission, warns us that eventually every 'species' we use will be found to have races within it, and that some of these will be found to matter very much ecologically. But this is no reason for being defeatist about the use of taxonomy. One might just as well say that advances in chemistry would never have been expected without knowing in advance the properties of every isotope of each element. The difficulties here can partly be overcome by doing the main survey continuously on one limited area, where the 'minor species' can be known or assumed from special studies.

There is enormous inconvenience and a good deal of wasted time for ecologists in mere changes of nomenclature unaccompanied by substantive discovery of new genetic groupings. One of the hopes of all ecological surveyors is a stabilized nomenclature. The frequent discovery of really new groupings, such as genuine species 'splits' and ecotypic races, makes it necessary to keep a voucher collection on some sampling basis, of the specimens on which the survey is built up. This is also a safeguard against mistakes in identification from existing taxonomic classification.

(ii) *Continuity*

There are several reasons for requiring continuity of research. One is the huge complexity of any area we can find for study, so that a survey is bound to take many years; another is that communities themselves change with time. The best way of ensuring continuity is to choose an area of sufficient size that has some guarantee of safety from catastrophic change in land use. This means using either a dedicated and well-managed nature reserve, or an estate on which the land usage is going to remain more or less the same, or on which its rotation system can be forecast in general terms (as with a long-term forestry working plan). The place should be fairly large, because among the chief biotic factors influencing the communities are the research workers themselves, who often display quite strong destructive tendencies (as by removing considerable samples of the habitat or of the populations) or desire to alter it, usually in the direction of simplifying the environment or causing animals to change their habits (as with the large scale use of

nest-boxes, or by live-trapping). From experience of Wytham Woods, 1000 acres is by no means too large an area, since many of the constituent habitats are local and small in extent, and populations of the larger species not very dense. Also the ecologist usually wishes to study numerous replicates of the habitat loci he is working in.

On the other hand, as Prof. Thomas Park has pointed out to us, deliberately planned alteration of the habitat (and constituent species of the community) is a valuable method whose use as a powerful tool in ecology has been little exploited. The catastrophic scale on which man is at present rather recklessly interfering by mechanical, chemical and biological means with existing ecosystems should not deter ecologists from scientific experiments of more modest dimensions. But as the repercussions of any experiment of the kind are unlikely to be limited to the immediately observed parts of the community and surrounding habitat, their implications for a continuing ecological survey on the same area need very careful forethought. It seems not unlikely that surveys and experiments will have to be done, at least partly, on different scientific reserves—an eventuality discussed in the White Paper on Conservation (Ministry of Town and Country Planning, 1947, p. 18).

The use of a common working area helps to overcome one of the chief difficulties in building up ecological survey on this scale. It is both impracticable and undesirable to try and make any rigid organization for such work, the pursuit of which needs a variety of research minds working along largely individual lines. But the fact of working together on the same area tends to bring about co-operation in various directions, and it should be the aim of any survey to show that its work has a long-term value to ecological science, and to enlist their voluntary help in adding to it.

Finally, it is absolutely necessary to have a permanent clearing-house for handling and storing the results of the survey, and working out standard methods that can be tried by individuals and small research groups doing field studies elsewhere. This is not the same as saying that all ecological survey should be centralized—far from it; only that we need at least one centre (preferably more) that is giving its attention to ecology of the species network, not from a purely taxonomic point of view.

(iii) *Classification of habitats*

In an earlier paper Elton (1949) urged the need for arriving at an agreed system of classifying habitats, one that would improve the completeness of individual species records and make them suitable for building up into community lists. Suppose we take the sort of field records that field naturalists or zoologists usually publish about species. A beetle will be recorded 'on flowers', or 'by sweeping' or 'on nettles', or 'under dead elm bark', or 'visiting sap at dusk'. With this will usually be given the date and place. But we immediately want to know: On what flowers, where, when, what weather, how many? By sweeping what? The field layer of vegetation is usually implied; but was it in or outside a wood, if in a wood under what trees? On leaf or flower of nettle, in what major habitat? What kind of elm? In a hedgerow, or edge of a wood, in a wood (if so what mixture of trees) or a timber-yard; under bark of a standing dead trunk (at what height), dead branch, log on ground? Sap of what tree, at what height, in what numbers, at what time of day—Greenwich Mean Time?

Casual questions like these that flock to be answered suggest that a great part not only of natural history but of professional zoological observation on habitats is very poor in

quality. It lacks a general ecological setting or context. This means that much of the observation, in so far as it might be built into an ecological picture, is running away to waste. The size of this drain, measured in human labour, must be very great. We believe this state of affairs to be caused by lack of research on what can be done to associate field records of animals with utilizable habitat data, and by the absence of any standard set of principles or language wherewith to make the records.

There are two ways in which this situation can be tackled. One is the limited one of making improvements in one's own field records, and those of one's immediate co-workers. But the progress of knowledge about distribution, habitats, habits and seasonal occurrence of animals, especially of insects, depends on a very large number of observers. Many events are noticed by chance or the opportunity to follow them fully falls to one person with some local advantage or special knowledge of a group. So it seemed to us well worth trying to evolve a system of recording habitats which could be used by any good field naturalist, with the hope that it would also be used—and improved through trial—by ecologists and zoologists. On the whole, we take the view that the habitat records of naturalists are usually either too vague or too fragmentary, while those of intensive ecological research are too elaborate and tend to describe unique situations in detail unnecessary for our purposes. The requirement here would seem to be something falling midway between these extremes, and based on commonly recognizable criteria. Perhaps this point (as far as *animal* ecology is concerned) might be found somewhere between the statement of the person who records a species as occurring 'in all suitable habitats' and the quadrat-strewn description of a piece of vegetation likely to be seen in the *Journal of Ecology*!

(iv) *Processing of material*

The organization in detail of an ecological survey involves a number of operations, including indexing and analysis of records, which have never hitherto been fully explored. The system evolved at Oxford will be reported elsewhere, but is briefly noted in §4 (c). The procedure is complicated, but not more difficult than learning an additional language or statistical technique (burdens that many biologists shoulder as a matter of course), and is justified by the integration of ecological knowledge about communities which it will make possible, and which ecological theory requires.

3. LIMITATIONS AND OPPORTUNITIES OF ECOLOGICAL SURVEYS

In the previous sections we have said why we believe that the complexity of nature is not in itself a reason for studying it only in small bits, as is the usual practice of zoologists. The tradition in science of seeking to reduce phenomena to their barest terms has been overwhelmingly profitable, and we do not seek to underestimate its value. The ecology of animal populations has received some of its most illuminating ideas from extremely simplified laboratory experiments. There is certainly great need for more experiments like those of Gause, Thomas Park and Crombie—remote as they may at first sight appear from nature in the raw. Nevertheless, natural populations live in communities and are adapted to this life, and we know that such communities may commonly include at least 25 to 200 or many more species of animals (not even counting parasites), living as interspersed populations that have some dynamic relationships, direct or indirect. In other words, *the complexity of nature is a fact of nature, and has to be studied as such*. After the

pieces of the puzzle have been described, studied and measured, we still have to fit them together into a pattern. The puzzle, in ecology, is, however, not a static pattern—we are studying parts of a complex biological ‘machine’ or factory of connected machines (Lotka’s ‘transformers’). In undertaking such a formidable synthesis, it is necessary to be clear about the limitations inherent in general ecological surveys. But there are corresponding opportunities for finding out something more about the real world in which animals live, and therefore the forces that control their populations and have influenced their evolution and adaptation both as individuals and populations.

Because surveys must take up a great deal of time and labour and technical ingenuity, their aims should be clear, progressive and knit into ideas of dynamic ecology. They have to show a convincing reason for their existence, and not just accumulate a vague mass of field records. To many types of mind they will not appeal psychologically. They cannot be done as short projects for research degrees; though such projects can be highly useful contributions to them. They must be much more self-propelled intellectually than a mere indexing unit, a library or than most taxonomic museums, i.e. they fail in their purpose unless they stir up and produce new ideas about the shape and flow of the organic world.

The limitations inferred above are not just the evident technical obstacles to making integrated sense of the interwoven lives of so many different species. Certain intrinsic characteristics of the species population network also introduce elements of unpredictability into the composition of communities to which some reference needs to be made here. Within the structure of the pyramid of consumer layers that an animal community broadly shows, we can divide density-dependent interrelations into (1) those between members of the same species, or between species of the same consumer layer, usually defined under the term ‘competition’, though they may also include symbiosis in some meaning of the term, as may those in the next category; (2) those between herbivorous species and their food, enemies and their prey, and parasites and their hosts; (3) certain relationships with other features of the environment, particularly space and cover, and such essential substances as are needed besides food. The third class of relationship apparently only acts in this way in conjunction with the interpopulation pressures in (1) and (2). Otherwise, the physical environment (e.g. climate), though affecting the rates of population change, does not do so in a density-dependent manner; it can, of course, cause or help to cause decrease to extinction in the marginal habitats of a species. These ideas are well known theoretically, though they will no doubt be modified in future; but they seem to represent substantially the present outlook of most population ecologists.

Each of the three main classes of ecological relationship within communities described above exhibits properties that cause or are likely to cause changes in the numbers and composition of species living in any place. Quite apart from how they are caused, we know that quite large fluctuations in numbers are common in the field. These unquestionably lead to local (usually temporary) extinction of populations—whether in small patches or more widely. For example, on a several thousand acre hill tenanted by voles (*Microtus*), a very high proportion of the ground may be entirely without voles at a period of low numbers. Similarly, one has had the experience of trying to plan field work for ecology students, and found that in a particular summer the oak caterpillars had devoured leaves on most of the oak trees, leaving a second crop of leaves practically untenanted by insects, and that independently the usually enormous aphid populations of sycamore trees had become so scarce that their enemies (lacewings, ladybirds, Syrphid fly larvae, etc.) were

practically absent. Innumerable examples of this kind could be cited; many have been recorded during less than ten years' survey of Wytham Woods.

It follows from this that ecological surveys will always carry the limitation that their lists and counts of species are not constants but selections from a range of varying situations. But they carry the corresponding advantage of giving chances for measuring (and up to a certain point analysing) such demographic changes and balances.

Competition can be divided roughly into that between members of the same species (intraspecific) and that between populations of different species (interspecific). The former can indeed set the stage for the operation of the latter; here we only wish to mention the tendency for intraspecific competition to generate fluctuations in numbers. Nicholson (1950) has done laboratory experiments with pure cultures of one species of blowfly in which violent oscillations developed through competition for food among individuals of different ages. Chitty (1952) believes that vole fluctuations in the field are generated by direct physical competition amongst animals of different age classes. These two examples have a particular interest in showing that purely intraspecific relationships may cause fluctuations in numbers, a conclusion arrived at also on theoretical grounds by Bernardelli and Leslie (see Leslie, 1945). It may turn out that the regular and strong cycles in populations of animals like the red salmon (*Onchorhynchus nerka*) in western North America and of the cockchafer beetle (*Melolontha*) in Europe are to be explained in these ways. However caused, they result in recurrent change and disturbance in the communities to which they belong. There are, for example, whole regions of Switzerland where adult *Melolontha* are scarce in two years out of three, leaving vacant one considerable element in the leaf-eating fauna of broad-leaved trees (Decoppet, 1920).

Interspecific competition, in the more limited and correct use of the notion, refers to the situations in which one species affects the population of another by a process of *interference*, i.e. by reducing the reproductive efficiency or increasing the mortality of its competitor. Or both species may be acting in such a way on each other. The term has, however, been widely applied to the processes leading up to such things as ecological adaptive radiation in allied species, and particularly to the good evidence that species of the same genus rather tend either to occur in different habitats in space or time, or if co-existing to have different food habits. Such evidence is usually interpreted in support of competition as an important influence in evolution, though by itself it does not in any way prove that interference accompanied the process of natural selection postulated. It just suggests that allied species tend to evolve into different ecological niches, which is another way of stating that the facts exist and that one believes in natural selection. There is very little field information to give satisfactory proof of interspecific competition at work in these species, most of that adduced being equally explicable by selective processes acting through other density-dependent population pressures. The distinction was not clearly realized by Elton (1946) in his analysis of the genus/species composition of plant and animal communities. The question not yet answered is whether such competition, *sensu stricto*, is going on daily in the lives of many species, or whether it occurs at long intervals or crises in their evolution. This point has been partly discussed by Udvardy (1951) for birds. It is probable that animal ecologists have been a great deal influenced by the obvious reality of day-to-day competition among so many plants. There is, nevertheless, laboratory evidence about animals, supported by some theory, that is so strong and persuasive that it must be taken into account in theories about community

ecology. The remarkable laboratory population studies made by Gause, by Thomas Park and his colleagues, and by Crombie, provide complete demographic demonstrations of how only one of two species of similar habits grown together in the same culture usually survive. The 'reaction' does not necessarily go only in one direction. By varying the conditions of experiments it was possible to change the outcome of competition by (1) a slight difference in food medium (Gause, 1935: *Paramecium caudatum* and *aurelia*); (2) the presence or absence of a parasite (Park, 1948: *Tribolium confusum* and *castaneum*); (3) varying the initial relative numbers (Park, Gregg & Luthermann, 1941: *Tribolium confusum* and *Gnathocerus cornutus*; *G. cornutus* and *Trogoderma versicolor*). It could also be shown that stable combination of two fairly similar species could be ensured by (1) a slight difference in food habits (Gause, 1935: *Paramecium bursaria* and *caudatum*); (2) the provision of a single type of artificial cover for one life stage of the more vulnerable species (Crombie, 1946: *Tribolium confusum* and *Oryzaephilus surinamensis*).

Four features of Park's experiments with the two species of *Tribolium* are especially relevant to thinking about field communities. First, in a given set of laboratory conditions, he was only able to register a statistical probability about the results, even after years of exhaustive research and very exact control of the known conditions. The results of individual experiments were indeterminable beforehand. This at any rate suggests that it may be even more difficult to ascertain the nature of the controlling processes in field situations involving much more complex factors. Secondly, the influence of a protozoan parasite on the outcome of the competition illustrates in a relatively simplified form how one type of density-dependent process may interact with another. Thirdly, the results of competition were not decided quickly; the two species could co-exist for up to two years or more before the final extinction of one of them. The fourth feature was the well-marked irregular fluctuations both in single-species and mixed cultures, not explained at present.

The field evidence about true interspecific competition is so slender that it only amounts to a few examples that seem to follow the lines of such laboratory experiments. Two only will be mentioned here. Trägårdh (1927) counted the breeding galleries of pine bark-beetles in Sweden, and found that although there could be as many as nine species on one tree, each had a particular ecological niche either in time or place. Normally *Blastophagus* (= *Myelophilus*) *piniperda* occupied the lower, and *B. minor* the upper region of the trunks, with some overlap. But on a small island where *minor* was not seen, *piniperda* extended much higher up the trees. A third species *Ips* (= *Orthotomicus*) *longicollis* could co-exist throughout the zones of both *Blastophagus*, because it lived more in the outer part of the bark. The similarity here to Crombie's experimental triangle of species, with *Rhizopertha dominica* and *Sitotroga cerealella* competing inside wheat grains, but co-existing with *Oryzaephilus surinamensis* which lives outside them, is striking (Crombie, 1944).

Brian (1952) noted the natural nesting habitats of four species of ants in an area of cut-over pinewood in Scotland, and also offered them various kinds of artificial cover. In old tree stumps *Formica fusca* and *Myrmica scabrinodis* were dominant species; away from stumps *M. rubra* and *scabrinodis* were the commonest nesters, *Formica* being unable to make natural mounds large enough to protect itself from climate. A fourth ant, *Leptothorax acervorum*, was local, living only in some hard stumps, and being a smaller species was protected from onslaught by the size of its nest galleries. But elsewhere it often lives in soft rotting fallen branches (as in Wytham Woods, where *Formica fusca* is

scarce). When artificial cover was introduced, usually neither *Myrmica* species was able to maintain itself for long against *Formica*, except where the latter only made a weak colony or occasionally for some other reason. 'Monopoly was achieved by direct aggression accompanied by the destruction of opposing workers.' Similarly, *Myrmica rubra*-colonists were usually replaced by *scabrinodis*, though the interference was not normally in the form of destructive wars.

The importance of interspecific competition has been stressed, because ecological surveys could supply a great deal of information about it, in so far as the process is ascertainable by certain kinds of demographic observation. It is to be supposed that recurrent decrease in numbers of any species creates some kind of ecological vacuum, which will tend to be reoccupied by other species that would not normally be able to maintain themselves in face of competition. This is essentially what happened when Brian's ants were given new cover to spread into. It seems also most likely that quite minor changes in the habitat, whether of climate, structure, vegetation or animal species will tend to upset any temporary balance that has been reached. The laboratory experiments show how slight a change might accomplish this. We should also be prepared to find fairly slow trends in population set up by competition, lasting a number of years before they are complete.

With regard to *predator-prey* and *parasite-host* relationships, no extended discussion is necessary, for there are numerous well-known examples of predators and parasite populations being affected by the numbers of the species they depend on. The reverse relationship is less well established by field measurements, but is generally accepted as one of the chief forms of natural control of populations. General changes in numbers, habits and even species composition (e.g. through arrival of unusual predators or through local extinction or emigration) are associated with such fluctuations. That the exact results of these interactions may show some features like those mentioned under competition is suggested by laboratory experiments and by the mathematical theories. The balance is very unstable in these simplified laboratory models, and no one has yet succeeded in maintaining a prey and its enemy, or an insect host and its parasite, for a consecutive series of fluctuations, without either breaking off the interaction at intervals (Utida, 1950) or adopting artificial aids, like adding individuals of one or both species intermittently to the cultures (Gause, 1934).

The fact that the introduction of artificial cover into laboratory cultures of interacting populations may completely change the results shows how similar variations in the structure of the habitat may produce changes in natural communities—as, indeed, is known from the ordinary observations of naturalists on the habits of wild animals.

Such considerations finally lead to the question of *ecological niches*. This is a much more elusive concept than was supposed either by Elton (1927) or Grinnell (1928) when they independently started using the term. There is no difficulty in seeing the reality of a very broad distinction of ecological function, such as between herbivore and carnivore. The distinctions get a bit blurred if we divide up carnivores into separate niches, since a carnivore may in fact 'belong' to more than one consumer layer. At the other end of the scale, each species has a unique ecological niche in the sense that its particular mosaic of abilities and habits is unique. In between the broad consumer type and the species, one may create any number of 'niches', by choosing some well-marked type of habit: 'mouse-eater', 'conifer-needle feeder', 'bark-beetle' and so on. What ecologists usually

imply by such groupings is that within them interspecific competition occurs or may occur. But when one considers an actual example like the grain-beetle *Rhizopertha dominica* competing with the grain-moth *Sitotroga cerealella* (in laboratory culture), it is seen that the similarities of habit (larvae feeding inside wheat grains, etc.) that bring about competition can be matched by considerable differences in other properties of the species (they will have different parasites; they have different life spans; they presumably have different tolerance ranges to climate). Lack (1946) pointed out how in a period of vole abundance in Europe, various raptorial birds that normally have different food niches, or at any rate ranges of food, may temporarily feed on voles, and come into a common 'niche'.

We think, therefore, that analysis of communities should pay attention more to tracing the consequences of one species in a key position being replaced by another, than trying to classify all the functions of species into a few niches. It is equally important to know (a) what groups of species occupy certain broad food niches *and are in a state of dynamic (competition) balance* with one another, (b) what secondary consequences occur in the species network if such balance is changed.

4. HABITAT STRUCTURE AS A BASIS FOR CLASSIFICATION

(a) GENERAL PRINCIPLES

Ecologists give much attention to the variability of communities in space, especially in sampling populations. Sampling in turn brings into prominence the scale of movement of different sorts of animals, which decisively affects the usefulness of a particular sampling system. It is well known that one may sample the soil microfauna in units of a few cubic centimetres, though large carnivorous ground-beetles may be too scarce to be counted by a system even of square-metre quadrats, and a raptorial bird census may need a thousand acres or more. The purpose of the condensed discussion of dynamic population relationships in the foregoing section was to suggest that the differences found between one sample and another are partly, perhaps to quite a considerable extent, caused by fluctuations, by swayings one way or another of population balance either 'horizontally' by competition or 'vertically' between species in different consumer layers. That is to say, the local differences in conditions such as microclimate, soil, water and vegetation (alive or dead) can never by themselves wholly determine or explain the local differences in the composition of animal communities. Indeed, correlations between the numbers of a species and such conditions may be very misleading and even useless without consideration of the properties of the species network itself, and its past history. These local complexes of physical habitats and vegetation may be looked on rather as the *arenas** within which some temporary relation between the species of animals is arrived at, by a combination of mutual opposition and various degrees of symbiosis. Any measurement of the community composition on a very local basis is likely to be out-of-date quite soon, at any rate in some respects. It is because communities are never stable in time that the determination of their composition by sampling them in space is so perplexing. And in so far as the temporary or semi-permanent replacements of one species by another in a given

* The word 'arena' seems a handy one to denote a clearly recognizable structural unit defining the place where a mixed population of species is engaged in the struggle for survival. Not only human gladiators, but also wild animals, 'fought in the arena'; it must be admitted, however, that in these combats the element of symbiosis, widely found in nature, was somewhat lacking.

ecological niche are accepted as likely, the quantitative use of animal species as indicators of community types becomes questionable, or at any rate needs to be carefully established over a fairly long experience of the community.

The principles of organization and energy exchange that have been described in previous sections are generally subscribed to or are implied in most discussions of 'community', a term that in its practical application may mean any section of the species network chosen for study, whether arbitrarily carved from the general network or chosen for special characters. This empirical use of the word has the advantage of realism. It recognizes that the nature of most communities hitherto described is not fully known, at least, in so far as the boundaries between them and neighbouring parts of the species are not usually given a quantitative meaning. If they are quantitatively described, it is seldom in dynamic terms. Thus a community may be a convenient bit of nature selected because nature as a whole is too large to study, or it may be the community of a true ecosystem in the sense that it has some of the features of organization, integration, or comparative independence that the ecologist is especially seeking.

Regardless of the criteria used to prescribe habitat boundaries, lateral exchange of organic matter and energy is bound to take place between the habitats. Even between those with such obvious physical differences as terrestrial and aquatic, interchange occurs if only periodically. A species such as the dragonfly may pass some of its life history in water and some on land, finding its energy requirements in each environment and taking part, at different seasonal life stages, in the species networks of three or more relatively well-defined communities. Other species, such as some birds, may maintain a more frequent interchange by feeding both in water and on land, thereby playing important roles in two communities during short periods of time. On the whole, the finer the habitat divisions the more frequent will tend to be the interchange of activity across prescribed boundaries and the less self-sustaining the community living on the described area.

The first instinct of an ecological surveyor is to search for that elusive thing 'a uniform habitat', hoping to contrast it with other neighbouring 'uniform habitats'. Gleason (1926) with his 'individualistic concept' seriously questioned such comparisons at the plant sociological level; and it is soon found (Diver, 1938; Watt, 1947; Elton, 1949) that such uniformity as occurs is in recurrent patterns of small components like individual trees, parts of the herb carpet, or such widespread units as carrion. This patterning creates local concentrations of energy in organic form in characteristic forms of matter, closely followed by groupings of species into what we call *centres of action*. Examples from deciduous woodland are a log, a bed of nettles or a group of toadstools.

The process of subdivision, if carried to its logical conclusion, brings us to a single species living in its chosen and (from the behaviour and life history point of view) unique habitat. But it is also interspersed with other species, and such interspersion takes one back in a circle to the species network again. We therefore look on any major habitat as containing different kinds of repeated centres of action which interlock with one another in numerous ways, but in which the degree of integration and intensity of dynamic action are at a high level. This view does not just rest on theory, and can be substantiated by considering an oak tree, a log, a patch of water weed in a river or a dead animal. Such habitat components locally concentrate the flow of energy and the closeness of population relations. They not only achieve identity, but a broadly repeated identity.

In laying out a system of classifying habitats it is therefore desirable to choose sub-

divisions whose scale conforms with the probable grouping of such real centres of action, while at the same time looking for descriptive habitat characters capable of being used in a standard way. The chief intrinsic difficulties are seen to be: (1) the fact that any one bit of the whole community is seldom dynamically independent of the rest, so that any limits chosen must be partly arbitrary; (2) the nature of the pyramid of numbers which usually combines a large number of small-ranging animals with a smaller but dynamically powerful group of wider ranging forms, some of whose movements may indeed be on a continental scale; (3) the great variety of physical and vegetation complexes; (4) the fluctuating balance among animal species.

All these considerations point to the wisdom of choosing at present a rather broad scale of habitats, compiling lists of animal species living in them, and subsequently refining the community relationships and subdivisions in the light of further research on populations. This means that rather long species lists for communities will be obtained, from which one will expect to find in any one place a selection living together as a result of the processes already outlined. In making the classification described in the next subsection, we have also taken into account a number of purely practical matters connected with the indexing and assembly of the information, which in turn depend partly upon the way in which zoological information has hitherto been collected, and partly upon the ways in which we think improvements could be made in future methods of recording. The method of habitat recording suggested is not so much a novel one in itself as a common basis from which field data about both individual species, and groups of species in communities, could be assembled without the sort of hiatus in information that so often makes the former unusable for the latter. It does not in the least imply that more refined additional observations are not needed; these will ultimately be converted into generalizations on a smaller scale of subdivision for communities.

We begin by dividing habitats into six large *habitat systems*, subdividing some of these into *formation types*, qualifying them by stratification into *vertical layers*, and adding certain further qualifiers, at present rather restricted in numbers for the purpose of adaptation to the operation of punch-card records. Although these may appear somewhat simplified categories, they result in over 1200 combinations, from which it is still necessary to regroup a smaller number for the practical assembly of community-species lists. We have left marine categories virtually untouched, as the present paper is intended primarily for land and fresh-water research. But there is no reason why the ideas could not be adapted to marine habitats.

(b) HABITAT SYSTEMS

The present classification begins by recognizing three major natural habitat systems: (i) *Terrestrial*, (ii) *Aquatic*, (iii) *Aquatic-terrestrial Transition*. Three further systems of lesser rank, but with distinct and recognizable characteristics, are: (iv) *Subterranean*, (v) *Domestic*, (vi) *General*. The Subterranean system means such places as caves, not just the soil or upper subsoil layers. The Domestic system takes account of man's locally overwhelming influence in erasing or modifying natural habitats and setting up special structures (houses, stores, gardens, etc.). The General system is a category created for distinct, usually small, centres of action that are generally distributed through the other larger systems, e.g. dying and dead wood, dung, carrion. These systems will be discussed individually below.

(i) *The Terrestrial System*

Two general approaches are available for the classification of the land habitats of animals, either by way of habitat structure as seen in vegetation and life form of plants, or by way of lists of plant species and plant sociology. Previous sections have dealt with some limitations of the second approach, which arise from the realization that direct and limited connexions between animals that depend on particular plant species are not, as formerly supposed, the dominant situation determining the composition of the community, and from the great local variability within the plant association types described by botanists. Detailed studies of the floristic composition of an area are normally beyond the scope of the ordinary field naturalist and usually beyond the labour capacity of the animal ecologist studying populations. Even when such lists are compiled they apply only to one sample of the plants and can help to 'explain' only a segment of the total animal population. In other words, the animal ecologist who bases his habitats on phytosociology must confine his attention to areas which have been thoroughly worked by plant ecologists, and more especially by plant taxonomists, with little certainty that this description will be valid in following seasons or neighbouring localities. Direct and restricted associations between animal and plant species occur quite commonly; but even phytophagous animals often have such variable feeding habits that they can satisfy their requirements from a wide range of plant species, alive or dead. One is also left with all the species whose relations are above the primary consumer level.

Vegetation and life form, on the other hand, provide immediately recognizable features. With this approach, a method of classification can be devised by which the ordinary observer can fairly accurately record the time and place of ecological events without an intimate knowledge of plant ecology and its associated concepts and terms. In other words, a classification based on vegetation and life forms allows us to work from the general to the particular, even to the level of single-species situations, without violating the more general levels of classification.

Two Australian ecologists, Christian & Perry (1953), have devised an interesting field-recording method, expressed in short formulae or codes, by which both the species composition and the vegetation structure of plant communities may be noted. This is designed for rapid reconnaissance of large stretches of country in the course of regional surveys. Although it requires a reliable field knowledge of plant species, and the formulae for these are rather cumbersome, the method has some excellent features, especially the way it combines a statement of the ecological stratification within vegetation with notes of the actual heights of the layers (see below). They remark: 'Apart from being useful for this subsequent collation of floristic data, a precise description of a structure is a valuable record in itself, as it enables the broad differences in vegetation to be recognised and related to environment, irrespective of the species present.' We think that this corresponds to many of the requirements of animal ecologists; and also of many animals themselves, which after all recognize their habitats in a variety of ways that are very often related to structural features. The choice of song posts and nesting sites by bird species at different stages in the development of planted pinewoods in the Breckland affords a good example of the second point (Lack, 1939).

In a great many instances detailed plant studies must be undertaken, as determining the food and other resources available for particular herbivores, but these can easily be

accommodated within the broader framework of classification. It should perhaps be repeated that there are three difficulties about building up a community picture mainly upon rigid relationships between animals and plant species. One is that the relationships are not commonly so rigid as has been supposed, though there are a large number of monophagous herbivores, especially among insects. The second is that there are probably more species of invertebrates living upon dead and dying matter than upon live green plants (Elton, 1949). The third is that although an animal species may be closely tied to one species of plant, the latter may occur in a wide range of habitats, and its presence is not exactly predictable even within one of the botanist's single plant associations. And yet by far the greater number of statements about the food plants of insects (in text-books especially) give no indication of the habitat in larger terms. Most carnivores and a great many parasites are not monophagous at all, yet have clearly defined habitats.

Formation-types

The successional sequence from initial colonization of bare ground to the establishment of a climax woodland suggests the use of four major kinds of habitat, for which we propose to use the term 'formation-type', much as defined by Tansley (1939, pp. vi-vii). He says: 'Since eco-systems developed under essentially similar (though not of course identical) conditions, and dominated by the same life forms, are often widely separated geographically and may possess entirely different floras, it is convenient to consider them as separate formations, but belonging to the same *formation-type*.' He lays emphasis on the relative stability of many of these formation-types, even though they can be arranged in the order of a succession series, or may actually be changing along such a sere. He adds: 'Similarly, I regard pastured grassland as a formation-type, again marked by distinctive life forms, though here the stabilising factor is zoogenic and usually anthropogenic.' A great deal can always be said for and against the adoption of particular ecological terms for animal ecology, but we have found this one to conflict least with current usages.

(1) *Open-ground type.* Any habitat or plant formation in which the dominant life form of vegetation (if any) is not normally more than 6 in. high. It includes any seral stage from bare ground up to but not including the establishment of a field layer more than about 6 in. high, as well as some climax formation-types such as low tundra fjaeldmark, and some alpine habitats. The 6 in. limit was chosen in order to include conveniently the bryophyte layer, e.g. in woods, and such commonly met types as grass turf.

(2) *Field type.* Any formation or seral stage in which the dominant life form coincides with the field layer (see Tansley, 1939). Vegetation in this category will seldom exceed 6 ft. in height, but may be either annual or perennial.

(3) *Scrub type.* Any formation or seral stage in which the dominant life form does not exceed a shrub layer. Generally the vegetation will not be over 25 ft. high, and includes young or small trees below that height.

(4) *Woodland type.* Any formation of seral stage in which trees are the dominant vegetation.

For our immediate needs of describing a habitat recognizably, the question of whether or not a formation has reached a climax is only of historical interest—though that interest is great. It will not usually have a direct bearing on the recording of observations about animals. This follows partly from the greater mobility of animals than plants. With the present method it is not necessary for the observer to concern himself with such questions

as 'is this a climax or a seral sub-climax?' He need only classify the vegetation according to dominant life-form, using the vegetation height as the criterion of dominance. Likewise, he need not trouble, at the preliminary level of habitat classification, to speculate on the range of factors which might be responsible for a sere or its possible future development.

In adopting *major formation-types* as a preliminary basis of classification of animal habitats, we hope to avoid many of the obstacles presented by disagreement about terms and concepts within the field of plant ecology. We prefer to remain clear of the specialists' realm in so far as possible, short of imposing unnecessary additions on to an already unwieldy body of concepts. Although it is assumed that the field ecologist will add anything relevant to his description of the vegetation and of plant species in any particular instance, in the assembly of primary community lists we are avoiding the creation of a great many subdivisions based upon this information, for the reasons stated above. There are, however, four modifying terms that seem essential: Deciduous (broad-leaved) *v.* Conifer; Mixed Deciduous and Conifer; 'Edge'; and Rotation Arable. There is a sharp division between deciduous and conifer woods (and their analogues of early stages, in the other formation-types), both in the main herbivorous animals and in the structure of vegetation layers and soil development. Yet even here, when one comes to the higher consumer layers of animals, the differences begin to fade somewhat, as has been proved by woodland bird surveys (Elton, 1935; Lack & Venables, 1939). The term conifer here includes such deciduous conifers as the larch. The mixed category is a transitional type.

It is possible to destroy any classification by introducing transitional or exceptional categories in sufficient numbers. But the characteristics of the edge of a wood, seen also in glades and rides within woods, are so well known to be reflected in important differences between the fauna there and inside the closed woodland, that we have used the omnibus word 'edge' as a qualifier. It is applicable also to transitions between other formation types. Thus a hawthorn hedge between two fields would be scrub qualified by edge.

The most difficult question in practice is to place formation-types which contain taller vegetation scattered amongst lower formation types, e.g. a single birch tree standing in a five-acre field of rough grass, would hardly justify the classification of 'woodland formation-type', even though the vegetation at the base of the tree may show the effects of its presence. The difficulty can be overcome to a considerable extent by adopting the botanists' method of assessing cover mixtures by eye in a progressive scale with five classes in it (Braun-Blanquet, Fuller & Conard, 1932). Apart from such mixtures, if one takes a series of formation-types or stages from bare ground to climax oakwood, for example, our method of classification would suggest the study of seven representative stages: the four formation-types, and three transitional or 'edge' zones. The selection of field samples according to some such regular principle would greatly aid subsequent correlation with results from other areas and other series.

Rotation arable covers such a very large part of Britain that it requires to be separately denoted. It is essentially an extremely rapid sere from bare ground to field type, usually with a cycle of two or three years. The large spread of ley grassland farming makes it convenient to define ley grassland as 'arable' in its first year, but thereafter include it with other grasslands in the open ground and field formation-types.

It seemed justifiable, even at this stage of our knowledge, to introduce qualifiers for Acid and Non-acid, since the dominant plant indicators are easily recognizable, and for

Maritime, to apply to the open-ground and field formation-types. In such acid-soil vegetation as *Calluna*, *Molinia* or *Scirpus* moor, there is at any rate a relatively great poverty in number of animal species, compared with their non-acid equivalents such as roadside meadow or chalk grassland, with certainly a good many qualitative differences of other kinds. Maritime communities such as sand dune deserve separate treatment in community listing, yet even here it must be emphasized that they contain many plant species, and many animal species (e.g. moths and spiders) characteristic of grasslands of inland areas.

Vertical layers

Although the stratification of vegetation is the daily preoccupation of many plant ecologists, it has been the parameter of nature most neglected by zoologists, especially as regards making any exact measurements of the height from the ground at which animals live, or the ranges within which they move in relation to the habitat structure. Even at the stage of open-ground formation-type, there may be four recognizable layers: (1) subsoil and rock, (2) topsoil, (3) ground zone, with or without vegetation, (4) air above the ground or the vegetation. At each additional stage represented by the three other formation-types new layers are added, and previously established strata usually retained—in some form, even where the species alter. Finally, a woodland formation-type may develop, and in it we propose the standard recognition for practical descriptive purposes of the following layers: (1) subsoil and rock, (2) topsoil, (3) ground zone, (4) field layer, (5) low canopy or shrub layer, (6) high canopy or tree layer, (7) air above vegetation. Each addition to the stratification of a habitat will modify conditions for the vegetation and animals living below it, and will at the same time provide routes for a greater degree of vertical exchange of matter and energy. We may note that the complexity develops not only upwards but downwards from the ground surface, with the development of root systems and soil humus. However, certain characteristics will be common to equivalent layers in different formation-types.

(1) *Subsoil and rock.* This layer corresponds to the C and D horizons of soil-profile nomenclature, and except for deeper tree roots consists of inorganic material, including weathered parent material and the underlying substratum. As an arena for communities it is relatively unimportant, and except where burrowing animals have nests and galleries in the subsoil is seldom occupied. These nests may, however, contain rather specialized dependent invertebrate faunas. The main stratum for such nests below ground is, however, the topsoil.

(2) *Topsoil.* This layer presents a practical problem of definition that is not quite answered for our purposes by the current usages of soil science. Part of the difficulty comes from genuine differences among soil scientists themselves. We have tried to bring our own ideas as close to theirs as possible, without sacrificing the utility of simple structural criteria. If the organic litter is brushed off the surface of a mull soil, a true topsoil surface is usually exposed; but where raw humus is formed, as in the mor soils of a pine-wood or a moorland peat, decomposition and incorporation of leaf litter occur in such a way that the line between litter and topsoil can be difficult to ascertain. There will often be a continuous gradient or series of subzones down from fresh whole leaf litter to amorphous incorporated humus. Our methods must be practical enough for rapid use in the field, and we propose (a) to include as 'litter' all organic material that can easily be

brushed away from the surface by hand, (b) to treat such litter as part of the ground zone, (c) and so define 'topsoil' for the present purpose as mineral soil plus organic matter in it or compacted on it, but excluding the loose litter defined above. This litter corresponds more or less to the pedologists' F_0 or A_{00} horizon, the topsoil to their F_1 or A_0 (compacted raw humus retaining leaf structure) plus H or A_1 (soil with amorphous raw humus) plus lower soil horizons such as A_2 and B. It must be emphasized that these comparisons are approximate and must remain so until pedologists agree amongst themselves. Hesselman's 'förna' (or *foern*) layer seems to include both the F_0 , the F_1 and some or all of the H horizons. Our criterion for the litter is therefore likely to conflict slightly with any use of the term *foern*; and in practice one will be likely to brush away a portion of the compacted F_1 layer in a mor soil, say beech raw humus accumulated in a hollow.

(3) *Ground zone*. Included in this is all low-growing vegetation, less than about 6 in. (15 cm.) high; inorganic debris such as stones and smaller human artefacts included in the general system, that are lying on the ground; surface litter (as defined above); also all other surface organic debris, even if it projects into higher layers. The last point is taken for convenience, though it is strictly true that the ground zone does possess the axiomatic property that objects (such as dead branches, tree trunks, animals) falling on to it from above cannot fall any further. The organic litter in this stratum is always of a coarser texture than that incorporated into the topsoil, and the animals associated with its breakdown are characteristically different from those in soil, and normally larger in size individually, group for group. There are regular seasonal sequences in leaf litter, especially in deciduous woods. Not only does the quantity decrease after the autumn leaf fall has brought new supplies, at different rates in different species of tree-leaf (Lindquist, 1938); the quality also changes. On fresh deciduous leaves there may be only one dominant saprophytic micro-organism, the yeastlike *Pullularia pullulans*, replaced in importance by other forms later on (Smit & Wieringa, 1953).

In spite of its narrow vertical depth the ground zone is probably the most important and certainly the most complex of the strata. All the organisms in a formation-type must eventually in some way take part in the energy relationships of this layer, either by their activity in life which will bring many species to the ground if only as transients, e.g. some leaf-eating moths and their parasites to pupate; by excretory products added to the organic litter (it is well known that one can *hear* the excretory rain of oak-moth caterpillars when abundant); or by dying and falling to the ground. The ground is also practically a very important layer to the ecologist because it is the layer he walks on, and from which he makes most of his direct observations, with perhaps a rather distorted effect upon his notions of stratification in the community. Many animals have vertical day and night movements, analogous to those of plankton in the sea. Todd (1949), for example, ascertained that the large harvestman (*Leiobunum rotundatum*) spends the day on tree trunks at various heights, coming down at night to search for prey in the ground zone and the field layer. Conversely, Green (1950) found that the beetle (*Cylindronotus laevioctostriatus*) spends the day in the ground zone, but climbs tree trunks at night in order to feed on *Pleurococcus*. Some species of birds show strong seasonal differences in height at which they feed, coming down to the ground for the fallen tree seeds in autumn and winter (Hartley, 1953). The complete understanding of the ground zone community will require especial care in timing the observations, owing to the largely transient nature of many species.

(4) *Field layer.* We define this as vegetation above the ground zone but seldom over 6 ft. (1.8 m.) in height. The upper limit is chosen to conform with the natural limits of the taller herbs or forbs, and also because 6 ft. is about the height of a man. In many places one can distinguish between a low- and a high-field layer, e.g. the difference between a low layer of *Mercurialis perennis* or a high layer of well-developed bracken or *Heracleum*. These distinctions are usually easy to make both on the basis of life-form and actual height, and the punch-card used by the Bureau of Animal Population offers the space to record both.

Often this layer is one of erect, annual herbs with no woody structure; but it may also contain plants with more permanent structure, such as ericaceous shrubs or bramble. Some are completely annual, while others have quite long individual lives. There are usually far more species and always more individuals mixed together in this layer than in either the shrub or the tree layer. This is so with the plants ordinarily thought of by plant ecologists as belonging to the field layer; but it also follows from the method of structural treatment adopted by us. According to this, every part of each plant present in the given layer is counted in it, e.g. a tree is a member of every stratum through which it projects, from which it follows that the ground zone has the greatest number of species in it, even though a great many of them may be represented by stems or trunks passing up to higher strata. This approach is not only based on the true structure of the habitat layers, but has value for defining the vertical ranges of activity of species which may have to be taken by methods like sweep-netting. Good examples are the scorpion flies (*Panorpa*), which sit about on a wide variety of plants (e.g. nettles, bracken, shrubs, tree branches) in the field layer, and from there visit other parts of the layer, or the ground zone, to pick up dead insects. It is realized that the field layer is usually a mosaic of plant societies or local associations, rather than a uniform mixture of species, and that it has complex seasonal changes in structure. With the seasonal dying down of much of the herbaceous and forb vegetation, most of the animals have to find refuges in other parts of the habitat. Thus the peacock butterfly larva lives on nettles (*Urtica dioica*); the adult spends much time visiting flowers in the field layer, but may hibernate in hollows of trees; while a chrysomelid beetle may spend the winter in its larval stage on the roots of the plants it lived on in summer as an adult. The low height of the field layer also makes daily vertical exchange with the ground zone through animal activity more complete than with higher layers.

(5) *Low canopy.* This layer coincides with shrubs; its maximum height we have rather arbitrarily defined in this classification as about 25 ft. (7.6 m.). Whether formed by regenerating tree stages, or composed of true shrubs, this layer is in many ways similar to the high canopy. We have chosen the terms low and high canopy, rather than scrub and tree, because in most woodlands the branches of trees come out or down into the scrub zone, or even into the field layer, to such an extent as to make the simpler terms inadmissible for this purpose.

(6) *High canopy.* This may be any height from 25 ft. up to the limit of tree growth. Although we have certain generalizations about vegetation, seasonal changes and structural features, very little is known about the life of animals in this higher layer. In some ways it is unfortunate that the naturalist has lost most of the arboreal skill of his forebears, and there is much to be done by way of physical exploration of the canopy, just as recent diving exploits have revealed a great deal that is new about animals under the sea. Most collecting is done at heights below 10 ft. (3 m.), which is about the reach of

someone using a sweep net. Most observations above this height have been on larger forms like birds that can easily be seen or else deductions are made from movements of animals to and from lower levels. Paradoxically, we probably know more about the arboreal life of insects in high tropical forests than in our own.

(7) *Air above vegetation.* Here also collecting and observation are difficult, and our knowledge so far is confined mostly to studies of 'aeroplankton', often at great heights, and distant observations of birds and a few insects. It must be emphasized that this term 'air above vegetation' is intended to apply only to the air above the *tallest* vegetation in the habitat. It does not include the air spaces interspersed among plants or other structures. We would describe an Eristalid fly hovering 20 ft. up in a wood as 'in the low canopy layer', but a kestrel hovering over a field as in 'air above vegetation'.

(ii) *The Aquatic System*

This system includes everything up to the normal surface-water line on the landward edge, as well as vegetation or animals in the air above the water. To begin with it is convenient to split the aquatic system into Freshwater, Brackish and Marine, since these are groupings that can be easily recognized by the senses without special apparatus or chemical tests. The last two form qualifiers in the punch-card system, that can be added to the formation-types and layers to be described below. As limnology is already a mature branch of ecology, it was decided so far as possible to incorporate the main notions already in use, in so far as they provide any recognizable characters for describing habitats in a standard manner. These limnological subdivisions are especially applicable to lakes themselves and to the stratification of lakes. For the smaller water bodies it has been necessary to devise a special classification based upon size and speed. These are treated as formation-types.

Formation-types

The common division of standing (lentic) and flowing (lotic) waters needs to be expanded into a rather fuller series of types. By taking five sizes (A–E) and five speeds (1–5) it is possible to get a theoretical set of twenty-five combinations. A few of the largest do not occur in Britain. The rest are summarized in Fig. 1, which gives examples of the formation-types obtained by this method. It will be seen that the size ranges from very small water bodies like tree-holes or trickles up to large lakes, rivers, estuaries and the sea; and the speeds from still water to the steep gradients of torrents and weirs or the verticality of waterfalls. The arbitrary lines of division made between the categories ought not to present much difficulty in the field (and allowance is made in the punch-card for simultaneously registering transitional types by punching two neighbouring sizes or speeds).

It has not seemed advisable at this stage to introduce chemical criteria other than those for salinity, as the object of the present system is to arrive at the greatest common measure of agreement and recognizability both by the ecologist and the naturalist, before attempting further subdivisions. It cannot be said that there is yet general agreement among limnologists about the classification even of lake systems, although much useful information exists about their oligotrophic or eutrophic nature, the influence of peat or sediment on the lake chemistry, the temperature conditions, etc. One of the kind of problems that is met with is the existence under the wave conditions of littoral habitats

in large lakes of species (e.g. the water strider *Gerris najas*) that elsewhere occur in rivers. But a fact like this would emerge quite clearly from the community listing adopted here.

A decision had to be taken about water bodies that fall strictly within the Domestic system, e.g. reservoirs. It transpired that such a large number of water bodies in this country are either created by man or have their shape and channels and their speed of flow controlled to some extent by man, that it was convenient to assemble *all* water bodies under the aquatic system as used here. There are, in fact, very few species of animals in

	A Very small	B Small	C Medium	D Large	E Very large
1. Still	Tree-hole	Small pond <20 sq.yd. (17 sq.m.)	Pond <1 acre (0.4 hect.)	Large pool or tarn <100 acres (40 hect.)	Lake or sea
	Trickle, gutter	Ditch, field dyke	Canal, river back-water		
	Trickle	Lowland brook or small stream	Lowland river	Lowland large river	River estuary
	Spring	Upland small torrent stream	Large torrent stream		
	Water drip, pipe outlet	Small weir or waterfall	Larger weir, medium waterfall	Large waterfall	

Fig. 1. Formation-types of water bodies classified by size (A-E) and speed (1-5). Examples: a large lake is E 1, and all rivers in the Oxford district are in C 3. The scale ranges from a tree-hole (A 1) to Niagara Falls (E 5).

Britain that occur in domestically created waters and not wild, the chief exceptions being artificially heated tanks, etc., like those in tropical plant houses, and which are negligible in importance. However, just as with the qualifiers mentioned above, we can record domestic as well as aquatic, which enables the information to be segregated if desired.

Vertical layers

These are only completely developed in fairly deep lakes. The stratification given below is a combination of what can be seen at the surface in the form of lateral and vertical zones, with some of the usual limnological divisions for the deeper water zones.

(1) *Bottom*, qualified as *light* or *dark zone*, these being the equivalent of the littoral and profundal zones. The latter does not have green vegetation. The light zone of the bottom contains that portion of the benthos not living in submerged vegetation. The bottom zone corresponds to the whole vertical range of subsoil, topsoil and ground zone of the terrestrial system. Probably no lake or even marine animals live in the subsoil, and usually, in fresh waters at least, the soil plus bare ground zone is only a few inches deep. Since most of the collecting methods in use, like dredging, cannot distinguish between the bottom surface and the substratum layer, it seemed impracticable at present to compile separate community lists for them, though there must be many real differences.

(2) *Water mass*, i.e. free water not among vegetation, again divided into *light* and *dark*

zones. This is the realm of plankton. It will in practice mingle to a considerable extent with the submerged vegetation, and we have combined the two together in compiling community lists for ponds and some other smallish water bodies.

(3) *Submerged vegetation*, i.e. benthic vegetation, theoretically excluding phytoplankton, though there must be an intermixture of the two. This will occur only in the light zone. It is intended to mean the vegetation above the bottom surface but not including the latter. There will be some difficulty, however, in completely separating the two, since sweeping and dredging may 'scramble' both layers of the community, and the allocation of species will depend a good deal on knowing their habits, which fortunately have left a more recognizable morphological impress on aquatic than on terrestrial animals.

(4) *Water surface*. This is meant to include the under and upper sides of the surface film, both of which have certain characteristic inhabitants; animals swimming on the surface partly exposed; and the floating leaves of submerged plants like water lilies and *Potamogeton natans*. All emergent forms pass through this layer, but few of them remain long enough in it to colour the community very much. A good many land and transitional invertebrates fall on to the water surface, and form a substantial food supply for fish and insects.

(5) *Emergent vegetation*. This layer is formed by the emergent portions of reed-swamp and similar vegetation. It does not include the under-water portions of the same plants, which come under (3). Laterally the layer ends at the edge of surface water and land. Beyond that we are putting marshy vegetation without surface water into the aquatic-terrestrial system.

(6) *Air above*. This follows the same principles as in the terrestrial system. In the compilation of preliminary community lists we have found it convenient to combine (5) and (6).

(iii) *The Aquatic-terrestrial Transition System*

In setting up this we have taken account of the two main features of the zone between water and land. The first is just the gradient in water content of the soil, with the accompanying very sharp changes in soil and vegetation types. The second is the very large number of aquatic insects that have their early stages in water but emerge to pupate, or as adults already, and conduct their mating and an important part of their dispersal out of water. Some species (such as the dragonfly *Libellula depressa*) wander great distances from water, and may invade woods and towns. Others, probably the majority, do not stray very far from their original home, and characteristically inhabit a restricted zone between water and land. It is not suggested that such alternation of habitats does not occur in the life histories of animals in other habitats, but it is striking and especially characteristic of the aquatic-terrestrial transition zone that most of the invasion comes out of the water, the return traffic (except for oviposition) being relatively light. A decision had to be made about the definition of different kinds of transition zone, according to (a) the water body type or (b) the terrestrial habitats next to it. Since the same kind of water body such as a river may have on its margins many and complex terrestrial habitats, it was thought best to define the transition communities by the water body and not by the terrestrial habitat, though this will clearly exert an influence, as when certain emergent insects prefer to sit on branches of trees. There will, indeed, be tremendous complexity and variation in detail in this whole zone.

On one frontier, the transition zone is marked by the appearance of water above the surface of the ground. Fluctuations in this line, especially with entirely seasonal temporary waters, have to be realized and treated in a common-sense manner, which means in practice noting the normal water limits over the year, with an eye upon the general vegetation zones as well.

It is much more difficult to draw a *structural* line for the frontier between the transition and the terrestrial zones. The real line should be the limit of normally waterlogged ground, though this cannot always be determined by surface inspection, other than by using dominant vegetation indicators, as, for instance, certain *Juncus* species. In general terms, this inner frontier of the system is intended to correspond both with the change from marshy vegetation, and with the diminution of the often massive riparian emergent fauna like mayflies and other insects.

In marine and brackish habitats the transition zone is well-enough marked by tidal features, and emergent insect life is far less abundant.

(iv) *The Subterranean System*

Cave communities and those of underground waters are very interesting ecologically, but are not highly developed in this country, and are included here in one system for practical convenience of assembling information about them. They typically resemble the profundal zone of lakes and many of the specially constructed habitats of man, in that all the sources of organic energy come from outside the system, and are not manufactured by green plants on the spot.

(v) *The Domestic System*

The object of creating this as a separate system has been already explained. The communities in the semi-sterilized habitats that man has set up are partly impoverished samples of what would live in a richer mosaic of natural habitats, and partly peculiar in so far as man has introduced edible substances and created conditions (especially local high temperatures) that do not occur elsewhere in this country. Many of them are atypical in structure and composition. The system is not intended to include 'semi-natural' plant communities, i.e. managed pastures, arable land, woodland, etc., but man's buildings and other structures on a large scale, together with highly artificial communities like gardens and town parks. The present century has seen an extraordinary increase of partial sterilization in the management of crop weeds and pests, and the control of huge areas of rough pasture; but such communities, though changing and becoming poorer in species, still fall naturally under the terrestrial formation-types. As explained earlier, all the aquatic habitats found in the domestic system are included with the other aquatic ones.

(vi) *The General System*

Elton (1949) drew attention to the numerous small but rather concentrated and specialized centres of action formed not only by individual living plants like trees, but by various kinds of dead matter, either in a state of decay or else artefacts of animals or man. Since these may occur scattered through the four major systems (terrestrial, aquatic, terrestrial-aquatic and domestic), as well as to a lesser extent in subterranean habitats, it was thought convenient to group them together in one 'system'. They are as follows:

(1) *Dying and dead wood.* The main known differences within this community are between deciduous (broad-leaved) and conifer trees, and between natural logs, etc., and

those found in domestic structures. We have adopted qualifiers for the first two, while the third can be dealt with by simultaneously recording the domestic system.

(2) *Macrofungi*. These tend to form isolated centres of action, and have a series of insect communities often not confined to one species of fungus (Scheerpeltz & Höfler, 1948, for beetles). Part of the community is associated with dying and dead fungus, though some species also inhabit the living plants.

(3) *Dung*. The most important kind of dung forming habitats for animals comes from the excretion of waste plant matter by herbivorous animals, notably cattle, but also many other species like horses, sheep, deer and rabbits. The commonest thing is to find small accumulations of dung scattered about, but man's activities may produce large aggregations, as with farmyard manure heaps, and also the very special habitats found on sewage farms, which in turn support certain species of insects and worms commonly found on seaweed wrack on the seashore. The natural dung and the manure heaps can be conveniently treated as one general community; sewage farms require qualifying further by the term 'domestic', although this may sound a little odd in ordinary parlance. It needs to be stressed that where dung (or equally carrion, below) is simply a food source without being in the strict sense a habitat that the animal lives in or is attached to, we do not include it in the present category. Thus the scorpion flies mentioned earlier depend for food on insect carrion, but do not live in it; a dung-beetle in a cow-pat is in quite a different ecological position.

(4) *Carrion*. There is an even wider range of dead bodies than of excreta of ecological importance, the largest ones on land being mammals and birds, and in water fish and drowned mammals and birds. But even the bodies of small invertebrates can attract a special carrion fauna of animals like nematodes living inside them (information from Dr C. Overgaard Nielsen).

(5) *Animal artefacts*. These are included because they are small and scattered often in more or less repeated units. Among them nests of warm-blooded species are particularly important, as they contain quite a rich community of parasites, semi-parasites and associated predators and guests (inquilines). Most of these nests are made from dead plant or animal material. Some of them, as with the tawny owl, contain an appreciable quantity of carrion and attract some of the carrion species of insects. The other important class of nest is that of the social Hymenoptera which also partly get materials from vegetation, but with more chemical processing. They contain, especially those of ants, some specialized inhabitants not found anywhere else. The category can be extended to include a number of other animal-made structures or alterations of the natural environment, such as burrows, earths, or the bore-holes of the goat-moth (*Cossus*) in live trees.

(6) *Human artefacts*. It was found convenient to set up a rather vague category to include the smaller structures made by man that are found dispersed throughout natural or semi-natural habitats. They include such things as stacks of field crops (of which the plant constituents are alive but dormant); fence-posts, which may simulate tree-trunks in so far as they carry lichens and associated microlepidoptera, etc.; stone-walls, with their special cover and climatic features; and many more which cannot possibly be catalogued here. Their communities may often be rather atypical and limited in numbers of species.

Besides being usually in rather small units and distributed rather thinly but widely in major habitats, the general system is characterized by the temporary nature of many of its components. Dead and decaying matter, unlike the living plant or animal, does not

renew itself by growth or reproduction, but is fairly rapidly used up. As a result one can observe in a small piece of fungus, dung or carrion extremely quick succession stages, which have been very well particularized by Mohr (1943) in the case of cattle droppings. Dead wood often lasts a good deal longer, but it eventually disappears as the result of biotic action. We must suppose that the animals that depend upon such temporary habitats must have remarkably well-developed senses adapted to finding each new unit as it is produced. Perhaps the most striking example of a simple piece of behaviour directed to this end, is the blood-sucking fly, *Lyperosia irritans*. The female sits on cattle, and may fly down and lay its eggs within a minute of the production of fresh dung (Hammer, 1941).

(c) **OPERATION OF THE HABITAT CLASSIFICATION**

A brief discussion of the problem of recording habitats and other field information about 'species events' was given by Elton (1949). A number of new recording and indexing methods have since been developed and are now in use for ecological survey by the Bureau of Animal Population. It is proposed to publish details about these in a separate paper. We mentioned above that over 1200 combinations can be made, using only the categories of system, formation-type, vertical layer, and the few qualifiers so far adopted. Some of these do not exist, however, or are for practical purposes of no importance for the job. But even the large number remaining is too large to work with, when one is compiling community lists, though many of the subdivisions are useful for individual species. We have therefore grouped the combinations into about 127 habitats.

The assembly of information for the compilation of community lists includes the following main items or operations: (1) The field records, which, provided they supply the type of habitat data required subsequently, can be made in any form of notes or indexes that suits the observer. (2) A standard punch-card, on which such data are transferred, or abstracted, half the card being devoted to the habitat groupings described above. The card also accommodates information about species of plant and parts of the plant concerned, locality, date and time, absolute vertical height, and certain categories of biological information such as breeding, behaviour, parasites, etc. (3) A standard check-list for each taxonomic group, and abstract books dealing with the key ecological and recent taxonomic literature under species. (4) A card with abbreviated coding for the habitat combinations, for each species, from which its known habitats can be ascertained at a glance. (5) Community lists for each habitat combination. (6) Collections of specimens in the form of community groups, and as evidence for the validity of species records.

In regard to the very vital question of the criteria used to 'admit' a species into a community list, it will only be said here that we are trying to find answers to three questions. First, does it occur or has it occurred at all in a given habitat and if so how exclusively and frequently? Secondly, are there any known biological attributes of the species (its 'niche') which make its occurrence there functionally significant to itself, to other species or the ecosystem generally? Thirdly, is there evidence either that its population size or biological influences make it quantitatively important in that habitat? On the last point, a species might be quite rare in a habitat and yet have some strong 'trigger' influence, as by pollinating a plant; or it might be quite numerous at certain times, and yet have only a transient influence.

One of the special reasons for adopting the punch-card system, in spite of the labour it involves, is that once the records are in this state information about species can be

fairly quickly assembled, and the assembled information can be fairly quickly broken down and analysed again. Without this flexibility, and especially the power to retrace the evidence in community research, it is extremely difficult to revise conclusions arrived at, e.g. supposing that changes are discovered in the taxonomy of a species, making it now into two distinct forms; or that a certain person's records are found to be doubtfully valid; or that one wishes after the accumulation of further data to regroup by date, time of day, plant species or some other variable. So far, the system has operated successfully, and is producing basic community lists for species of the Wytham area, that will have some ecological interpretation attached to them, and be backed by permanent records and voucher specimens. Since the Oxford district probably contains something like half the British species of animals, these lists ought to give some idea of the nature of animal communities in Britain. From them an ecologist could begin to know what species are or may be associated with the ones he is especially studying and some of their ecological interrelations.

Finally, we would like to say clearly that a purely mechanical system of building up community lists is not the object of this survey. The indexing and the habitat classification are essential, but strictly subordinate to an intelligent study of the ecological nature of the communities, with the aid of biological observation and measurements.

5. SUMMARY AND CONCLUSIONS

The central problem in animal ecology is natural control of populations in nature. It is generally believed that natural control is usually dependent upon density-dependent population pressures, either within the same species or between different ones. Therefore, to understand population processes properly we require to know something about the species network in nature. Although there are certain species whose numbers are predominantly regulated by intraspecific relationships alone (though often with strong fluctuations), it is usually necessary to take into account also other kinds of density-dependent pressures resulting from interspecific competition, herbivore-plant, enemy-prey or host-parasite relationships. The ecological survey at Oxford for which this paper provides a theoretical and practical background, is partly a fact-finding survey on a particular area (Wytham Woods), but equally a research on how to improve the methods of recording and relating ecological events, so as to provide a general basis of knowledge about natural grouping (communities) within the species network.

Ecological survey deals with three aspects of the situations found in nature. First, the presence and absence, habits, life histories and tolerance limits of species, from which a more or less qualitative picture of the species network can be established. This can be extended by counting numbers and analyzing population structure, to reach a more exact description. This we call the natural history and statistical stage of survey. Secondly, studies of population processes and balance in particular species can be undertaken. Here we have emphasized the intrinsic properties of the species network as a system of interconnected populations which give the community a dynamic as well as a statistical meaning. Thirdly, the productivity of the community or the whole ecosystem, or parts of them, can be measured in terms of energy paths and energy flow, adding a physiological and physico-chemical interpretation of the demographic picture, which has so far been little done.

As a setting for ecological survey the following practical requirements are needed: taxonomic soundness in the sense that ecologists shall speak a common language when referring to species; continuity of the survey in one place over a fairly long time; a generally agreed system of classifying and noting habitats; and a system of processing records and specimens, and assembling them into community lists. In making any such synthesis, even for a limited area, it is necessary to be clear about the limitations inherent in ecological surveys, arising from the degree of indeterminacy that exists in the prediction of population relationships and trends. Interspecific competition is taken as one example to illustrate that the distribution of species within interspersed community groups is not to be explained only by the set features of the physical environment or vegetation, interacting with set characteristics of the species. The interaction of animal populations amongst themselves introduces other features, of which fluctuations and temporary replacement of one species by another are especially important. We need to know not only how many different ecological niches may occur in a community, but within each of them how many species may be in dynamic balance and how this balance may change. One result of the widespread occurrence of fluctuations in populations (probably in a great degree caused by biotic relationships) is that the composition of communities fluctuates also. The community list for a particular habitat will therefore be a list from which only a particular selection of species will be present in any one year. The proportions will vary, so that the nature of a community can only be understood by following its history as well as by knowing the biological potentialities of each species.

The ecological survey in the Wytham Woods area near Oxford is being partly supported by the Nature Conservancy as a pilot project for studying the methods applicable to any nature reserve. This area is fairly representative of calcareous soil ecosystems in the midlands region of England, which means that the conclusions from it should be applicable in general to much of the British fauna. The methods of collecting, indexing and analysing records, to make a series of community lists, will be described elsewhere. One essential feature underlying them is, however, outlined in the present paper: the use of habitat structure as a basis for a simple general classification of habitats. We have chosen habitat subdivisions whose scale is likely to correspond with real centres of dynamic action among populations, while at the same time using descriptive characters capable of being used in the field in a standard way. A rather broad scale of divisions was adopted, for various reasons. These divisions are described in §4, in a series of six habitat systems, some of which are further divided into formation-types, and vertical layers, with a few further special distinctions. The classification has been especially designed to be applicable to punch-cards.

We emphasize, however, that any purely mechanical or statistical method of building up community lists of animals must be subordinate to study of the ecology, physiology and behaviour of individual species, of population processes, and of whole sections of the species network treated as dynamic entities.

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