POPULATION INTERSPERSION: AN ESSAY ON ANIMAL COMMUNITY PATTERNS*

BY CHARLES ELTON
Bureau of Animal Population, Department of Zoological Field Studies, Oxford

(With one Figure in the Text)

Most of the great advances in ecology during the last quarter century have taken place either within the field peculiar to plant ecology, or in the demology or population problems of animals. On the one hand we have seen much progress in the general classification and nature of plant communities, their succession relations, the physiological reactions and symbionts of particular plants, soil organization, ecological genetics, and Holocene vegetation history. On the other hand, there has been an outburst of field research on the density of animal numbers, and on the age and sex structure, movements and fluctuations of animal populations, accompanied by some rather exciting experiments in the laboratory on self-limitation, competition, parasite-host and predator-prey relationships, backed by ambitious mathematical theories of various kinds.

These main fields of research have brought into clear relief some of the intrinsic differences between plant and animal ecology, and especially the manifold consequences of animals' power of movement. But between these two fields lies a tremendous region in which plant and animal ecology join, and where all the discoveries made in either should logically be synthesized to give us at least a working model of how whole ecosystems are arranged in nature, and how they work and interact. In this region lie studies of animal community structure and pattern and energetics, the description of animal habitats, relationships between plants and animals in respect to food, cover, pollination, dispersal of fruits and seeds, and other reactions of animals on vegetation and plants on animals. It includes a huge range of facts about animal behaviour and distribution and many problems involving the general equilibrium in nature. For it must be remembered that such general equilibrium does exist, even though it is subject to recurring fluctuations of all sorts, and even to complete local breakdowns of the ecosystem such as the poisoning of lake faunas by outbreaks of blue-green algae (Prescott, 1939), and the desolation of vegetation by field mice, locusts or caterpillars. I shall attempt to explore a few general laws regulating the distribution and balance of communities that do not seem to me to have been looked at as a whole. I am quite aware of the depth of our ignorance of many matters that take part in the completion of such a picture. It would be absurd at the present time to hope for completeness. Nevertheless, I am absolutely convinced that we are on the threshold of a period when synthesis of animal and plant community facts and concepts will not only be possible but necessary, if we are to interpret ecological phenomena fully, and see them in the proper contexts. I think that the ocean of ecological facts has reached a dangerous tide level, and the ideas I wish to develop here may have a certain value as a raft to float on. The general ecologist needs a raft from which to cast his sampling plankton net. The plankton may be patchy and the work of collection and synthesis very laborious,

* The substance of this paper was read as Presidential Address to the British Ecological Society on 7 January 1949.

J. Ecol. 37
Population interspersion: an essay on animal community patterns

but if he has some clear principles by which to sort out the material, great advances are possible. But one should bear in mind the excellent remark of Thoreau that 'The volatile truth of our words should continually betray the inadequacy of the residual statement'. In case this paper comes to the attention of naturalists as well as ecologists, I would like to add that the ideas in it were largely obtained while pottering about in the woods and elsewhere in the country, and during the necessary period of rumination entailed by setting and labelling specimens and processing the records of some thousands of 'ecological incidents'.

I have sat through a great many papers at meetings of the British Ecological Society during the last 25 years, and the dominant impression retained is of the extreme range and fragmentation of ecological knowledge. At times one's mind has almost seemed to crack in the effort to understand the relevance to the main purpose of the Society of some specialized piece of discovery about plant or animal life. Synthesis is still rather limited, owing to this enormous area and variety of research. There is, of course, no doubt that the quality of research can only be kept high by some specialization, by focusing deeply on limited fields. But what is the ultimate goal and purpose of all this ecological research? Why do we continue to meet at all and listen to each other's fragments of discovery? Not, I feel sure, just to understand about root fungi or the zones of salt-marsh vegetation or the bee visitors to fruit trees or the changes in numbers of arctic foxes or gall-flies, however fascinating these are in themselves.

I have roughly analysed the first 16 years of the Journal of Animal Ecology, i.e. 1932–47. Of 312 papers, only 40, or 13%, were concerned with ecological surveys of whole animal communities. By this I mean surveys attempting to describe a large sample of the different taxonomic groups present in habitats, not those dealing say only with birds or amphipods. But only 8% of the whole were concerned with British communities. These twenty-five surveys included six terrestrial, nine fresh-water and six marine habitats or complexes; two were general, and two marine Holocene. Of these the terrestrial ones were the least complete. There were only four papers that discussed community composition in general, i.e. about 1.3%, and two of these were in flat contradiction to one another.

During the same 16 years the Journal of Ecology published 268 papers, rather fewer than the other Journal, though some made up for this by their majestic size, and 253 dealt with plant ecology primarily. Of these no fewer than 68% were studies of plant communities, 35% referring to this country, 25% to other countries (mostly Tropical). And twenty-one (or 8% of the total plant papers) dealt, often in a highly philosophical way, with theories and methods of community analysis, and there was some measure of common agreement resulting from them. (I omit five animal community surveys. If they are added to those in the Journal of Animal Ecology, they only slightly increase the percentage of community papers.)

So it would seem that plant ecologists have made considerable headway in the organization of their part of the whole subject, and that a great deal of their information is already in a partly integrated form. They have not solved many problems finally, but they do begin to know what shape the problems are. Animal ecologists, on the other hand, have been concerned so far with fragments, sometimes quite large ones, but nevertheless fragments, and the split between the plant and animal ecologists' outlook is quite considerable, and is reinforced by a great degree of separate training in universities. It must be pointed out here that none of these surveys analysed above was or claimed to be describing completely
all the forms of plant or animal life even on a sample area of a habitat, or to represent more than one local variant of a complex system or formation. Animal ecologists have usually had to leave out the parasites, which are a legion, and many free-living microscopic animals; plant ecologists also omit most of the parasites such as fungi, bacteria and viruses. They omit even the very numerous macroscopic fungi, and not infrequently the cryptogams, or at any rate the lichens, and the microscopic algae. The plant ecologist also usually leaves out the animals, and the animal ecologist usually makes an exceedingly sketchy record of the plant background.

In making these preliminary remarks, I do not wish to seem critical. There are perfectly good reasons why this situation exists in ecology. There are more species of animals than of plants, even if we include the fungi and other lower forms. Animals usually have complex life histories, of which the earlier stages may be ecologically the most important though harder to find and to identify. Animals have activity rhythms, and are often inconspicuous or invisible while resting, either by taking refuge under cover or by camouflage. Their seasonal occurrence in an easily identifiable or observable form may be brief and complicated by weather affecting activity. All animals move about to some extent; amongst other things, this makes many of them hard to catch, or hard to follow and observe. Furthermore, animals live in a number of habitats, like carrion or caves or lake bottoms or the abysses of the sea, from which green plants are absent, i.e. animals inhabit a more complex range of habitats.

Take one simple example of the problems the ecological surveyor of animals may encounter. In Wytham Woods, on the afternoon of 14 August 1948, I visited a wide grassy and rushy ride through oak-ash-sycamore woodland, which had a magnificent population of tall teasels in flower. The plant ecologist could note down 'Dipsacus fullonum ab. fl.' On these flowers were scores of fresh peacock butterflies (Vanessa io), also seen sunning themselves on the bracken of the woodland edge. With them were a dozen commas (Polygonia c-album), several fresh brimstones (Gonopteryx rhamni), and a few elderly silver-washed fritillaries (Argynnis paphia), also one or two gatekeepers (Maniola thalassa), green-veined and large cabbage whites (Pieris napi and brassicae), a brown argus (Aricia agestis) and some bumble bees. The day was dead calm, warm and sunny. Next day at the same hour, Dipsacus fullonum was still ab. and fl., but there were no butterflies on them except a few peacocks, and these were hanging on with difficulty against a strong west wind, though the weather was still sunny. Only by repeated and frequent visits would even an apparent relative abundance of butterflies be established, and this would need to be interpreted very cautiously, because absence could be due to four things: inactivity, death, emigration, or inefficient observation (as on a small number moving over a large area of habitat).

Then, if we want to know where the peacock butterfly had bred, we are at a loss unless we know its food plant (in this case nettles), whether its caterpillars bred on nettles within the woodland canopy or at the edges of surrounding fields—or still farther away. The large white might even have spent its early life in some Baltic farmer's cabbage patch.

Annual fluctuations in numbers add another problem; in 1947 hornets (Vespa crabro) were commonly seen cruising about this teasel patch. In 1948 there was none. This could be due either to the accidental proximity of a hornet's nest in the first year, or to a general scarcity of hornets in the second year (which was indeed observed), or to both. From this we see that a survey of animal communities is a long and tricky task.
Population interspersion: an essay on animal community patterns

The ultimate goal of an ecological survey I would suggest is: ‘An attempt to discover the main dynamic relations between populations living on an area.’ This area has usually been taken as one of the major ecosystems such as a lake or a river or a wood or a salt-marsh or a sand-dune complex, i.e. a system that is strongly interlocked in its parts but shows some fairly well-marked boundary with neighbouring ones. I want to suggest that the unit we should choose for detailed study could be much smaller than this, and yet should be known in such a way that it can be related to the system as a whole.

This introduces the main subject of this paper: habitat patterns as they affect animals. We have had previously two distinguished presidential papers bearing on this subject, one in 1941 by Captain C. Diver, who dealt with micro-topography and habitat loci, as he had studied them in his great Studland Heath survey,* the other by Dr A. S. Watt (1947), on ‘Pattern and process in the plant community’. These earlier contributions encourage me in the belief that there is here an important and somewhat undeveloped aspect of ecology in which different specialists may find great common interest, and which may give both them and the naturalist some help in overcoming the obstacles of building up survey of ecosystems.

Ecologists are going to have to do a great deal of hard thinking if they are to achieve even one of the scientific recommendations mentioned in the White Paper on conservation (Ministry of Town and Country Planning, 1947, p. 70): ‘The biological survey of National Reserves and the conduct of wider surveys with the ultimate aim of carrying out a thorough survey of wild plant and animal life throughout the country as a continuing process.’

Imagine, for a moment, a potential habitat in which no organic life has yet appeared at all: a bare dune, mudflat, hill slope, river bed. When we set out to describe any spot on such a potential habitat, the first thing we do is to determine its position in space and time. We give it geographical location, usually a place name, from which by implication we can derive its position on a grid of geographical co-ordinates (now added to the modern 1 in. map), its height above the sea, nearness to salt or fresh water, and to a limited extent consequentially the aspect and main gradient.

These and the date have for a long time been the only things that the taxonomist put on his labels, though that is changing greatly under the impact of ecology. When we come to the detail of minor topography, we find it difficult or impossible to describe it quantitatively, because it is mostly arranged in quite irregular patterns of hollows, hillocks, ravines, etc. It is exceptional to find any fundamentally periodic arrangements of such minor topography, such as occur in Arctic soil polygons, or between cracks from drought. The habitat is in a state of ‘undiluted geography’ formed from local differences in shape of ground, water table, water quality, aspect, soil texture, and rates of erosion and deposition and comminution. It has been necessary to mention these rather obvious primary features, in order to contrast them with the next stage when definite periodic patterns in space begin to appear.

Let us next imagine vegetation colonizing and modifying this surface, through succession phases perhaps up to something like a stable climax, or perhaps lodging at some transitional stage. As soon as you have populations of plants mixed together, an orderly pattern begins to be laid down. The interspersion of one population with that of another species necessarily means that the individuals of the first are partly separated from neighbours of their own

* This paper has not so far been published, but some cognate ideas about the plant carpet as a mosaic of animal habitats are discussed by Diver (1938). These have a close bearing on topics discussed in the present paper.
species by those of other species. And this leads in turn to several types of periodic arrangement in space, of more or less regularity: in other words, to a habitat pattern, with many small components repeated at spaced intervals. It is these small components that form the primary habitat units for animal communities. First, the dominant plants, especially where they are trees or shrubs, tend to have equal spacing, such as we may see in a developed elder scrub or beechwood. That is brought about, as we know, by root and canopy competition. Secondly, the original minor differences in the ground, which were irregular, may in time and with the development of vegetation and other processes gradually tend to be smoothed over. This happens with humus formation in a wood, and we might expect to find increasing regularity of the spacing between say dominant trees, resulting from the modification of the primary habitat by plant activity. Where this does not happen completely, we would find the original irregularities of the primary topography and soil still appearing, though greatly modified by the vegetation, e.g. in such things as deep hollow, ravine, water catchment, and so on. Although these do not provide a regular periodic spacing of minor habitats, they add variety to the habitat. Thirdly, there are various minor successions set up, mostly through the dying of individuals. The most imposing of these is the falling of old trees and the formation of glades which become filled up anew by saplings. Jones (1945) has pointed out how such gaps fill up and tend to maintain a general canopy even though the trees are not all of the same maturity. The openings that occur through such minor successions will normally be distributed somewhat at random, though they must in turn be based upon the basic vegetation pattern that gives rise to them.

Another point about the general vegetation pattern needs mentioning. The dominant plants, say a beech tree, or a grass tussock, will tend to have the greatest regularity of pattern, and at the same time the greatest contact between their canopy. But they will always create around them a periodic centre represented by the tree trunk or tussock, and a concentration of leaf and leaf fall. Those species that are less abundant, i.e. the majority, will be dispersed in either of two ways. If they are directly dependent upon the dominant, as with moss on a tree trunk, or a saprophytic orchid on beech humus, they will or will tend to follow the regular distribution of their dominant. Conversely, those that can only live outside the influence of the dominant, like bracken in a wood, will tend towards some inverse periodic distribution in the interspaces. The second type of distribution is of the less abundant plants that are not geared on to the primary vegetation pattern, but occur in a random manner throughout the community. Not only will these be less regularly or quite irregularly spaced, but the distances between each plant or patch or society will tend to be greater than between the dominants.

I get the impression that although plant ecologists are quite aware at any rate in some level of their minds, of the patterns I have been talking about, they have nevertheless rather taken them in their stride, and have devoted comparatively little quantitative research to the subject, other than the excellent kind of micro-succession studies illustrated by Watt’s Breckland work. There are few data, except for certain types of trees dealt with in siliculture, for the minimum or mean distances between plant units, i.e. components of patterns in a community, the frequency of glades of a given size in a forest area, the random or non-random distribution of different species in space, or the areal size of each component like a tree with its canopy. Nor do we have a picture of the leaf litter or soil patterns associated with such vegetation.
Population interspersion: an essay on animal community patterns

So far we have arrived at an idea of the habitat being a mosaic of centres of different kinds, really centres of action in which interspersion between populations tends to be complete and ecological dynamic relations (at any rate among invertebrates) at their strongest. These centres I shall call minor habitats: single trees, homogeneous clumps of saplings, societies of herbs, grass tussocks, units of aquatic plants on a particular patch of river silt, patches of reed swamp along a river. Although they may be so close and homogeneous (as with a Phragmites swamp or a crop plant) as to lose the qualities of obvious patterning, usually they are spaced out and repeated more or less in the same form, partly regularly and partly irregularly. There are two main kinds of pattern. I will call them area patterns and boundary patterns. The first is what you see in an air photo of a wood or scrub or in the pools on a salt-marsh or on hillocks in a dune system. The second is seen along the seashore or the margin of a pond, lake or river, in field and road boundaries of hedge or wall or grass verge, and in small streams. In the vertical dimension, a tree trunk presents a boundary pattern. In the boundary type, there is broadly speaking the width of one minor habitat, and this is strung out in two instead of three dimensions. For example, compare the occurrence of buckthorn or elder in a chalk hawthorn hedge with their distribution in a reverting field or a wood.

Let us now consider the interspersion and patterning of animal populations. They partly follow the arrangements of the terrain and the vegetation, but they also impose new patterns of their own making; these may be quite independent of the others, and of each other, but are often periodic in space. Take first the groupings around minor physiographical habitats. In this category we may place the faunas of woodland or other springs, which are restricted to the head-springs of a stream. These springs are determined by the geological strata, and there is no regularity in their spacing. Nevertheless, they form small loci separated by some distance from the next. In a similar category are the patches of fine mud, coarse silt, and gravel that occur in a river, according to the contours and speed of the currents. Mud-living forms of mayflies, chironomid flies and Mollusca often have a patchy distribution according to the distribution of the substratum. But such arrangements are so irregular and their texture and scale vary so greatly that we are hardly justified in calling them regular patterns at all. It is when we come to vegetation that the influence of regularity is felt, as in the grouping round minor habitats formed by plant individuals or societies, e.g. an oak tree, a patch of sycamore saplings, or a Juncus tussock. Here it should be noted that I shall use the phrase 'minor habitat' in a relative sense, not to describe absolute size. Microhabitat I shall reserve for the detailed parts of a minor habitat, as 'twig', 'under-side of leaf', 'flowers', 'under bark', 'bones', etc.

Each plant species usually has a nucleus community of herbivorous animals, almost entirely insects, confined to it for food, or at any rate very characteristic of it. They do not always necessarily dwell on the plant or near it; indeed, life histories completely on one plant are not the commonest thing to find. Most herbivorous insects spend a substantial part of their life associated with the plant, but the other part in the soil, moving about, lodged in some refuge, or even on another plant. These monophagous and characteristic herbivores are being indexed by Dr O. W. Richards, and gradually published through the Society's Biological Flora. This requires enormous labour and discrimination, and will give a most valuable basis for studying the minor communities on plants.

In the selection of plant faunas already issued, the number of specific and characteristic herbivores for the British Isles varies from none in Cladium mariscus and Allium
vineale to thirty-eight in the common maple (not counting flower visitors, which can in some cases also be specific, or at any rate highly characteristic). In between we find numbers like four on Tamus communis and Atropa bella-donna, ten on Glyceria maxima, twenty on Rhamnus cathartica, while the genus Polygonum has twenty-nine and the genus Juncus thirty-three. These figures cannot have a precise meaning in detail; but they do indicate the sort of scale we may expect to find, although on some large, ancient and complex trees like the oak, the numbers will be very much larger.

Such herbivorous animals belong almost entirely to the insects, and to the five largest orders: bugs, butterflies and moths, beetles, flies, and the Hymenoptera (and of these substantially the sawflies and gall-wasps). Flower visitors could be added to these other herbivores, and will be referred to later on. For instance, although the black nightshade (Tamus) has a very small number of insects feeding on its leaves or stems, it possesses flowers that are extremely attractive to flies and some other insects.

Besides these restricted forms, there is a large number of more polyphagous herbivores that may be equally or more important and abundant, and when we come to carnivores, this is still more the case. Nevertheless, the periodic spacing of the minor plant habitats or components of the pattern must bring about a periodic distribution of density of all these forms, whether they are specific to the plants or not. This can be illustrated by a diagram, for any given herbivore. First take the imaginary instance of population density of a specific birch-tree aphid, the trees being scattered about in a developing oakwood. The vertical co-ordinate is population density, the horizontal one lateral distance (Fig. 1a). The flat-topped peak represents a group of birches, the others individuals.

If we were plotting the density of a parasite which attacks only this host, there would be a similar grouping (Fig. 1b), that is, if the parasite succeeds in finding all the minor centres. If, however, we are plotting the distribution and density of a carnivore such as a lacewing, whose larva and adult are attacking various arboreal aphids, its distribution, though still in patches, would be contoured in some such way as in Fig. 1c. The important point at the moment is the discontinuity or contouring of the population distribution. As far as I know, real examples of such distributions have not been measured; nevertheless, the situation must tend towards something like what I have drawn.

When one works for some time in a deciduous wood, it begins to dawn on one that these minor habitat centres have very characteristic community compositions. Thus one soon learns to expect caterpillar abundance on oak, aphid abundance on sycamore, leafhoppers on ash, chrysomelid beetle abundance on Mercurialis, and butterfly-caterpillar colonies on nettles. I mean that not only is the species composition of the herbivores different, but also the dominance of different types of herbivore, or as one may say, there is a spatial separation of the chief key industries.

There are, however, some forms that do range very widely; for example, the tree long-horned grasshopper (Mecohema thalassinum) is found on oak and ash and sycamore. Carnivorous insects are not usually very restricted; some, like the common green lacewing (Chrysopa carnea), are widespread on trees and shrubs that carry aphids; but the snake-flies (Raphidia), though not infrequent on oak, where they find excellent crevices to lay their eggs, are seldom found on young sycamores which have very smooth trunks and twigs. Furthermore, I have formed a strong impression that except for certain animals like spiders that broadcast their young, and are often fairly wide in their feeding tastes, these minor plant centres tend to keep their integrity, and that such random searching by
animals as occurs results either in finding the right habitat or in death. In other words, the complications introduced into ecological survey by purely accidental visitors are not very serious so far as herbivorous forms are concerned. Many of the accidental visitors come from other minor communities that I shall mention. This conclusion is a natural one, since arthropod herbivores are, after all, adapted in their responses to finding the plant they breed on.

Now we come to further population patterns superimposed by the activities of animals that range beyond a single minor vegetation unit. This usually arises from the way that birds

![Graph](image)

**Fig. 1.** Theoretical diagram representing a transect through some major habitat such as a wood, at a time when the animals concerned are confined to their minor habitat centres, and not undertaking lateral migration.

The vertical ordinate is population density, the horizontal ordinate is lateral distance. (a) A monophagous herbivorous insect, (b) a monophagous hymenopterous parasite attached to it, (c) a polyphagous predator.

and mammals, and some social insects, establish refuge centres from which they move over a foraging area, which are not infrequently territorial, i.e. the boundaries are not merely determined by the distance from home, but by active competition between neighbours. Such territorial spacing is well known among many birds during the breeding season (e.g. willow-wren, kingfisher, tawny owl, oyster-catcher), and it frequently occurs among rodents such as mice and voles, and in some predators like the badger. Ants sometimes produce similar periodic arrangements, and in the wood-ant (*Formica rufa*) they are certainly in part territorial. In dense conifer woodland the nests may be spaced out in a boundary pattern or chain of beads; in more open woodland they may form an area.
pattern, a sort of Balkans among ants. The yellow ant (*Lasius flavus*) that forms mounds in pastures is really an aphid farmer, keeping its flocks on the roots of grass, and these mounds impart a clearly periodic pattern to some fields.

Let us note two general dynamic consequences of the patterns so far mentioned. In all of them, the population of each species of animal tends to a periodic contouring, not to a general distribution of density at random. This means that theories about population changes and interaction, which are nearly all based upon conceptions of mean density, must learn to take account of the fact that populations are split up into groups or centres of action. A. J. Nicholson has explored this point a little, but it needs far wider recognition, and its full consequences still have hardly been touched by mathematicians. The unit to which we can attach the idea of complete dynamic population interspersion is frequently this small minor centre of pattern component, i.e. an oak, a group of aspens, a patch of water *Ranunculus*, a small spring, or a glade in a wood with a population of red campion in turn forming patches within it.

The second consequence is the lateral movements from and between centres, discussed later on.

The distribution of density will usually vary between day and night, where these larger ranging species are concerned, so that during the daytime we might find wood-ant density and activity distributed in decreasing amount with a high concentration near to and in the nests, and at night entirely confined to the nest centres. A tawny owl population would have the reverse alternation. The population pattern therefore has diurnal cycles in contouring, on which will be superimposed seasonal degrees of territorial or social activity, as well as year to year fluctuations in total density.

Man has imposed some of the most regular periodic patterns of all upon soil and vegetation, by his system of crop cultivation, which incidentally tends to produce a more complete canopy of unspecific dominant vegetation than much natural vegetation, at any rate at maturity. In simplifying, or as some would think over-simplifying, his crop stands, man has nevertheless been compelled to adopt a rotation system that is a crude substitute for the simultaneous processes of soil renewal that went on in the original vegetation. This has brought about a very marked major habitat interspersion, e.g. of cereal, grass or clover or roots, and fallow.

At this point, I would like to put in a suggestion, for it is nothing more, that the charm that we feel about natural ecosystems, which forms part of the driving force behind conservation, is based partly upon the mixture of order and disorder that I have been trying to analyse. It is probably a deeply instinctive satisfaction, and it undoubtedly comes out also in the field of art, both in music and poetry, and even in architecture. How often one has been grateful to find an irregular garden associated with the formal lines of a building, or a tree whose seed was blown or perhaps brought accidentally by a bird, breaking the regular alinement of a street.

Let us now continue with the survey of minor habitats, for by doing so we shall find it possible to split up our faunal lists into more easily handled units for field study, and at the same time build up a general picture of how major habitats are patterned and their populations distributed. These habitats can be taken in a fairly logical order.

There are first of all a number of detached parts of living plants: resting stages like nuts and seeds, and pollen. In nature the former do not usually form aggregations sufficiently large to merit the term of minor habitats in the sense I have been using it—they would be
better described as microhabitats. These frequently contain stages of herbivorous invertebrates. But man by his mechanical skill in assembling large quantities of seeds, nuts, roots and other living parts of plants, has created not only minor habitats like corn-ricks and potato clamps, but much larger ones in the form of grain stores and so forth, with all the consequent problems of stored product insect pests. These need not be analysed here, except to draw attention to the curious fact that the great bulk of the fauna of stored products consists of small beetles, moths and mites, and that the communities are, apart from a few parasites, composed of herbivores or scavengers that often also practise cannibalism on their own and other species. We have, in fact, the extraordinary phenomenon of an almost one-consumer-layer community combining within itself the herbivore and carnivore role, and also practising self-limitation. And as far as I know it is the only type of community that has ever succeeded in heating itself out of existence by ordinary metabolic activity, as occurs sometimes among grain weevils (Calandra).

Such aggregation by man, of what are normally small units, also occurs in sewage farms, timber yards, meat and skin stores.

Another aspect of these small detached living parts of plants is dispersal. The interspersion and movement of animals among plants has made possible the development of special seed and fruit dispersal and of pollination mechanisms, the animal acting as a minor habitat, or more frequently quite a microhabitat, and the detached part of the plant becoming a temporary parasite upon the animal. With seeds it may be ectoparasite (as with the enchanter’s nightshade on man’s clothes), or endoparasite (as with guelder rose fruits inside a blackbird); pollen is, as far as I know, always an ectoparasite. These reproductive products are here termed temporary parasites because they do depend upon the energy of animals moving about, and although the amount exploited may be often quite unmeasurable, the principle remains. When an insect carries honey away as well as pollen, it may be said that the parasitic activity is paid for, and this would undoubtedly be an interesting budget to work out! These consequences of the interspersion of animal and plant populations are mentioned here because they are essential for the continued existence of the community; because they bring the dispersal of female and male reproductive products of plants into a correct alignment with fungal and animal parasites that live on animals as minor or microhabitats; and because pollination by insects has made possible the development of some of the more important social insects, which themselves form further minor habitats for other animals.

The bodies of living animals are themselves the habitats of special communities of parasites, which have been surveyed to a limited extent, and which form part of the field of epidemiology. The principles of population interspersion are deeply involved in this field, but here it will only be mentioned as a vital secondary consequence of the community pattern shown by the host species.

Animal artefacts form important minor habitats. These are of a great many different kinds. First of all various burrows in the ground made by mammals like rabbits, foxes, badgers, moles and mice. In the nests of these mammals there is a considerable special fauna, some of it (especially with moles) confined to that species and not breeding elsewhere. Other mammal nests on or nearer the surface, as those of hedgehogs, bank voles and of ground nesting birds also, contain special assemblages of insects, including beetles, flies, parasitic Hymenoptera, Collembola, ticks, mites and fleas. Some are bloodsuckers, and therefore depend directly on the host, others are saprophagous, others carnivorous on the
previous species. The conditions are quite peculiar, especially in being highly sheltered and kept warm.

Nests of squirrels in trees, of bats in tree holes and buildings and rock holes and of various birds in trees and tree holes provide further special habitats. A tawny owl's nest is quite a startling special environment to collect in, owing to the extremely strong smell of ammonia that it gives off. We have not yet got a complete picture of the faunas of bird and mammal nests, though a great deal of scattered work has been done, and several important studies still remain to be published. They are enough to indicate that there is a strong difference between ground and arboreal nests, and between those of some of the species, and that they contain a considerable number of arthropods, either not found in other habitats, or else shared with decaying plant or animal matter.

Ant, bee and wasp nests have received a great deal of attention from entomologists. Well over a hundred kinds of insects have been found exclusively dependent upon the nests of British ants, and Donisthorpe's book on them (1927) should be consulted, for it is fascinating and also shows how much more work there is for naturalists to do in this field. During a rather complete ecological study of nests of the thatching ant (a close subspecies of our wood-ant, Formica rufa) in North Dakota, Weber (1935) found about thirty species of animals in one nest. Donisthorpe (1930) found twenty-four true myrmecophiles on this species' nests in Windsor Forest, the same number with Lasius fuliginosus and thirty-six with L. brunneus.

Wasp and hornet and bumble bee nests also contain a number of parasites and guests and carnivores.

If we were to list all the much smaller artefacts of animals, such as nests, burrows, food stores, etc., we should find a great number of other species dependent upon their activities, and therefore grouped around them in minor or microcommunities. This leads on to another large sector of the subject: secretions and excretions.

Of plant secretions the most important are honey and honeydew. The distribution of these on different plants plays a clearly defined part in the patterning of any community. Although there has been a great deal of general observation and some experiment upon pollination, the listing of species attached to particular plants is very incomplete except for the hive bee, and here the results are mostly averages of day's work, and we have not a very exact picture of how different insects move about and visit the minor plant units. Here is an attractive and productive field for exact ecological work. It is particularly necessary in such study to separate the casual visitor from the frequent and important pollinator or even the important robber, and to dovetail the data into a seasonal history of visiting species.

Honeydew secreted either by leaves themselves or by aphids sucking the leaves determines the local aggregation of visiting insects to certain trees, e.g. the sycamore or the lime. One would like to know much more clearly what honeydew actually is, or in what senses the term is used, and whether it is the same stuff on different plants, and how the collecting insects react to its presence on various plants. But such secretions and also sometimes sap flows (as from the elm) form an additional unit in the total habitat pattern.

The secretions of animals are especially important in the manufacture of the wax combs of bees' nests and the papery structure of wasps' nests; and they play a big part in some of the food chains we find both there and elsewhere, e.g. secretions from guest insects that enable them to become tolerated in ants' nests, and the direct collection of honeydew by
ants from aphids. But animal secretions do not seem otherwise to be important in this country as a source of minor habitats.

With excretion the situation is different. Mammals and birds produce large quantities of dung daily, especially the larger herbivores. American workers (Mohr, 1943) state that beef cattle produce about half a hundredweight of dung daily per 1000 lb. of animal live weight. That is to say that a cow weighing 1500 lb. might easily produce over 12 tons of dung a year, or say 6 tons on an acre. It is not surprising that dung is therefore an important minor habitat for animals, and essentially one that occurs scattered over the foraging area of the animals that produce it. Mohr has made a really intensive study of this community in Illinois, many of the genera of insects being the same as ours, and no doubt the principles he worked out would apply here. There were altogether about eighty species concerned, mostly flies and beetles. As a community it operates only in the warmer times of the year, and as here there is quiescence in winter. Mohr observed several seral stages, and there were parasites and predators. For instance, the staphylinid or rove beetles entered as soon as the pioneer flies and beetles had made galleries in the gradually drying dung. Later on other beetles arrived, some of them carrying mites on their bodies. The species taking part also differed according to the season, a thing we shall note for carrion also. The fauna also differed somewhat if the dung was dropped in the shade instead of the open. In various types of mammal dung, including manure heaps, in the Windsor Forest area (see p. 14) Donisthorpe (1939) found 100 species of beetles.

Hammer's study (1941) of the flies in cattle dung in Denmark, though confined to that group and admittedly not including all the families of flies with equal completeness, nevertheless shows the importance of this animal community, and the great complexity even within such a minor habitat. Sixty-four species of flies were studied, and most of these had coprophagous larvae, the rest being carnivorous. The former were mostly confined to dung, the latter sometimes occurring more widely, as in carrion also. The habits of the adults varied greatly, some being liquid dung-suckers, some blood-suckers, others predatory on insects, or flower visitors. The seasonal life histories also varied a great deal. Similar coprophagous communities are known, but have not been completely studied, wherever smaller mammals or birds have concentrations of dung, and part of the nest fauna is formed by such species.

We now come to decaying plants and animals. Since plants and animals are not immortal, and since they survive the hazards of attack by adverse influences sufficiently to be extremely numerous on the earth, it follows that their excretions and their dead bodies or parts of them are important minor habitats in themselves. This can be illustrated by reference to the examples of tree holes, logs and other dead wood, leaf litter, fungi, sea wrack and carrion.

Here something may be said about the relation of vegetation to animal life in general. It is well known from general observation that vegetation bulks much larger than animal life, in other words, that animals do not succeed normally in eating the vegetation at all completely. As A. H. Church wrote in 1922: ‘Trees or grass clothe the visible surface of the land, in close canopy or as thick undergrowth; animal life, beyond a few birds and the animals maintained by man, is conspicuously inconspicuous.... The living plant.... is dominant in aggregate mass and volume of living material....’ There are occasional or even recurrent instances where the balance of a community is so completely upset, or fluctuates so far outside its normal range, that vegetation is destroyed. Two rather common
ones are the defoliation of oak in this country by caterpillars, and similarly of conifers in Europe. How far this is a natural event, or is due to human alteration of primeval conditions, we cannot be certain. We do know, however, that the interference of man with predator populations and other means of protection of wild deer have brought about a series of large-scale crises in forestry, especially in the United States (Rasmussen, 1941; Leopold, Sowls & Spencer, 1947). I think we may suppose, for a working theory, that the interrelations of animals in a community impose checks and controls which normally prevent the herbivores from reaching a starvation level and destroying vegetation, though their fluctuation may cause considerable periodic starvation among predators. These controls may be both intraspecific and interspecific. Anyhow, the great surviving predominance of vegetation and the mortality of plants means that a very large production of dead plant matter in various forms is going on everywhere. This is partly produced seasonally, as with leaf litter, partly all the year round, as with wind-blown branches and fallen trees. Some whole great ecosystems, like lake and sea abyssal zones, depend on dead plant (and animal) matter.

One interesting minor habitat, widely developed in all forest regions, is the small tree hole full of water. It depends primarily on tree structure, but usually also on decay, which proceeds in damp conditions. The tree-hole mosquitoes are the most interesting members of this fauna. There are three British species. Other insects also occur, and Keilin (1927, 1932) has made some study of them. The most complete ecological survey is an American one, by Jenkins & Carpenter (1946), who found the same three genera of mosquito, as well as a fourth, that has turned carnivore on the others. They noted also a midge larva and two other species of flies and several beetle larvae, together with a microfauna formed by Cyclops, a nematode worm, rotifers, and several Protozoa. Tree-hole mosquitoes are extremely important in the Tropics in connexion with several diseases, including yellow fever.

Log succession, which is a very large subject in itself, can only be dealt with briefly. In a forest glade log formation often results from the death of a tree, and perhaps later of other marginal trees which become exposed to wind forces they were not bred to resist. If the logs and fallen branches come down fresh at the right season, they form the focus for an intense activity of animals specially adapted to invade and exploit this minor habitat at different stages of its decay. At the same time, stumps or broken trunks, sometimes whole dead trees, may remain standing for some years, and these have a rather different invertebrate faunal composition from logs, and such dead trunks are also used both for feeding and nesting by such birds as woodpeckers. Here is a very important element, not only in the woodland life pattern, but in the cycle of decay and humus formation. The most thorough ecological study of logs from a modern point of view is by Savely (1939), in North Carolina, where he made exhaustive collections of insects from oak and pine logs, over some years, and worked out also part of the story of their food habits as well as the microclimates of the logs. In the pine logs he found ninety-five species during the first year, i.e. on fresh logs. First came twenty-two species of phloem-feeders, like bark-beetles, and their galleries were invaded by thirty-seven kinds of saprophagous and fungus-eating forms. There were twenty-nine kinds of predators, nine parasite species, but only four sapwood-feeders. By the second year the phloem-eaters had gone, indeed, they were only present for the first few months. The total numbers of all insect species in the second to fourth years, were sixty-seven, fifty and thirty-five. After that the logs began to drop to bits. The oak species were rather fewer, and to a large extent different.
Hanson (1937) gives a full description of the animal community around the pine bark-beetle (*Myelophilus piniperda*) in this country. These included parasitic nematodes, eleven species of parasitic Hymenoptera, twenty-seven predatory beetles or their larvae, *Rhaphidia* (a predatory Megaloptera), five predatory fly larvae, and birds (though the last were not quantitatively important). I have (1948) been breeding out the fauna linked with the ash bark-beetle (*Hylesinus fraxinii*). In only one 8 ft. length of log, I have found, besides thousands of the bark-beetles, one or two species of other larval beetles, a gall-fly, several kinds of Anthocorid bug predators, more than six parasites, mostly Chalcids (including a small hyperparasite), and a very abundant population of Uropodid mite that arrives attached to the parent beetles, and leaves in a similar manner.

Another group of beetles, the longicorns, is important in penetrating wood. Some excellent work has been done by Kaufmann (1948) in putting together and adding to information about the kinds of dead wood that various British species of this group occur in. It appears that their range is fairly wide and that, while bark-beetles are highly specific to particular kinds of tree, longicorn beetles are often much less so. It remains to be determined how restricted are the fungi in decaying wood and the insects that live on them. I would like here to make a plea to foresters and to conservation people for dead wood to be allowed to follow its fate and lie about. It has been noted that natural forest has an enormous amount of dying and dead wood on the floor, and Jones (1945) has cited interesting figures for the amount of natural dead standing and fallen timber. It would be a great pity if ideas of tidiness derived from farm management, from purely traditional silvicultural ideas, or from town life, should lead to the constant removal of dead and dying wood from forests. There is undoubtedly a very large number of insects that depend for their survival directly on this minor habitat of dead and dying wood either on the tree or lying on the ground. Among them are some of the most exciting, large and beautiful or rare members of the British fauna. One need only mention the stag-beetle, the longicorns, a good many click-beetles, and several ants (like *Lasius brunneus*) that in turn have attached to them rare species of myrmecophiles. There are many more. Furthermore, logs and dead branches form the night or day or seasonal refuges for some woodland animals. In a short day's collecting on logs of various ages with a class of students last year, we found queens of two species of wasp, queen bumble bees, large Carabid beetles, ichneumons, and, in addition, found that some of the larger slugs and snails take refuge under logs, from which they forage over the litter when conditions are favourable. Can any forest entomologist or ecologist prove that the clearing away of at any rate fallen deciduous dead wood is necessary in the interests of forest health?

To emphasize at this point the large role played by minor secondary habitats in the animal community, the remarkable survey that Donisthorpe (1939) did over many years, in the Windsor Forest area, should again be mentioned. He collected about 1870 species of beetles (almost exactly half of the British beetle fauna), many of them again and again, and in every case he noted the exact minor habitat. This report forms the most important body of raw facts about this phase of ecology for Britain, although it has limitations from inevitable lack of quantitative data, and from the absence very often of any indication of the major habitat, except in so far as it can be inferred. About 285 species were collected under bark, in decaying wood, and in wood frass, and similar minor habitats, and most of these are species known to live there normally; about 270 species (some the same as those in rotten wood) occurred in fungi, some of which (mostly the conspicuous tree or log
succession

A

restricted

animals

(whose

variety

cultured

microscopic
tipation

animals

important

there

partly

it.

Indeed,

example,

bracket

a

There

Mycetophilid

sixteen.

example,

bracket

a

There

Dead

Baltic.

a

There

wood

is

108

one

fauna,

leaves

beech,

wood,

oak

beetles,

together

with

records

of

their

host

species.

For

e.g.,

Polyergus

squamosus

(‘Dryad’s

saddle’) has

thirty-five

species,

P. sulphureus

(‘Sulphur

bracket’) thirty-nine,

P. betulinus

(‘Birch

bracket’) thirty-six,

Pleurotus

ostreatus

(‘Oyster

mushrooms’) nineteen and

Fomes

fomentarius

(‘Tinder

bracket’) sixteen. But by no means all these were exclusive to any one species of fungus. One

family, the

Cissidae, is practically confined to toadstools growing on tree stumps, etc.

He lists also a further thirty-three beetle species that have been commonly found in fungi,

though their habitat range is much wider.

There is no doubt that a very substantial part of our British beetles occur in decaying

matter or in fungi associated with it, and less than a third are herbivorous on green plants.

There is a similar division inside the flies, though one cannot say exactly what the ratio is;

but the number of saprophagous forms is very large, including such groups as mosquitoes,

Mycetophilid flies and many small families. A substantial number of Collembola, Thysanura

and aquatic insect larvae, many of the Mollusca, the earthworms, most of the woodlice,

some aquatic Crustacea, and many millipedes, mites and nematodes are in the same cate-

gory. And their habitats are frequently discrete units scattered over an area, though it

still remains a major query how far soil animals are distributed in a patchy or discontinuous

manner. The same query applies to leaf litter, though anyone who has observed the floor

of a mixed wood in autumn cannot fail to note the patchiness of different leaf litters as

from beech, oak and other trees and shrubs, as well as from herbs and grasses. The patchy

distribution of ground mosses is to some extent the mirror image of the pattern of the

heavier leaf litter areas.

It is at present impossible to give a clear distinction between those dead wood species of

animals that actually eat wood, and those that depend on fungi. The same thing applies

partly with nest species. But when we consider Donisthorpe’s records, and the fact that

there are several thousand species of macroscopic fungi that may serve as habitats—

indeed, one can find beetles of fly larvae frequently in almost any ageing toadstool popula-
	
tion that one slits open at the right season—it is clear that they also form one of the most

important minor habitats. A beginning has been made in studying the animal relations to

microscopic fungi, as in the family Lathridiidae among the beetles, some of which have been

cultured successfully on Penicillium moulds (Hinton, 1945), and which are frequently

found in odd places like under bark and in old wasp nests. Perhaps we may eventually

have ecological survey lists that give all the fungi in detail by species, and mention at the

bottom just ‘Phanerogams and mosses also present’.

There are other minor habitat centres in decaying plants, for instance, dead bramble

(whose stems are famous nest sites for small wasps); and also on the seashore, where there

is a specific wrack fauna, that has been worked out in great detail by Backlund (1945) for

the Baltic. He found 108 species as regular inhabitants, of which about a third were

restricted to wrack.

Dead wood and leaves are ‘plant carrion’. Animal carrion adds a still further note of

variety to every community. Donisthorpe (1939) recorded ninety-five species from dead

animals and birds and from old bones in Windsor Forest area—that is, of course, only

a sample of the British carrion fauna. The only published attempt to describe a carrion

community in full ecological terms is that of Fuller (1934) in Australia. She examined the

succession communities of insects invading carcasses of sheep. This survey disclosed
Population interspersion: an essay on animal community patterns

forty-one species of flies, belonging to fourteen families, the most important ones being the bluebottles. Of beetles there were twenty-eight species belonging to ten families, and in addition seven parasitic Hymenoptera—a total of seventy-nine species, of which twenty-three were quantitatively or ecologically important. There was succession according to the state of the carcass, and the seasonal temperature, and some remarkable competition phenomena were observed, in which saprophytic fly populations of different species were also predatory upon one another.

Some of the chief minor habitats which form the focusing points for special animal communities have now been mentioned. In doing so I have emphasized the frequency of discontinuity, and the relatively small sizes of the populations. This really needs qualifying in several ways. There must exist a number of populations which are spread out less discontinuously, either because the basic habitat that I have been calling ‘minor’ is major in extent, or because the range and type of activity and movements of some species is not limited very much by the minor patterning. And it is clear that exact regularity of pattern, though interesting where it occurs, and convenient in certain ways for study, is of less fundamental significance than the occurrence of discontinuity as such.

So far, except for mentioning some of the ecological succession that occurs in minor habitats, the whole pattern had been described as though it were a static arrangement, or at any rate an instantaneous picture of a moving one. It has been noted that mathematical theories about populations have mostly treated them as if they were randomly interspersed over the area of some major habitat (imagined to be in some sense uniform), whereas we have seen that there are groupings of populations around small centres dispersed through the habitat, partly in regular patterns, and partly not; some related in their distribution—as might be logs and the occurrence of glade-living herbs and shrubs in a wood—and some quite independent, as with the territorial arrangements of owls relative, say, to the distribution of societies of Adoxa or clumps of wayfaring tree in a wood. Or again there may be a relation between the centre of an animal or bird’s territory (as with squirrels’ or sparrow hawks’ nests in trees), but little or none to the frequency distribution of plant species in the territory chosen for hunting.

Until we know more about the type and scale and distribution and relationships of these minor communities, we can hardly expect to understand very much about the dynamic relations. But one may with advantage explore a few general ideas. These come under the headings of population control within any one minor community; vertical and lateral movements of populations; the dynamic relations between minor community units of the same kind; those between minor communities of different kinds; and oscillations in numbers.

The dynamic balance within small communities like dung and carrion has been studied, but not with such quantitative care as to throw much light on the exact mechanisms of control. As regards control, we must distinguish very sharply between communities of animals depending upon living plants, or other animals and those depending upon dying or dead plants and animals. We already know as a general fact of observation that plant populations usually maintain themselves in spite of the inroads upon their biomass made by animal populations. Indeed, so apparent is this that it has been for many years a convention among botanists to treat dynamic vegetation systems as though the animals were not having any influence upon the energetics of the plants at all; or only to bring this idea in where the inroads are of a very conspicuous kind, as with rabbit or stock or deer grazing. But a little reflection will show that every plant population (except those few that
are, like many of our alien garden forms, free from attack) must be losing a definite and ascertainable amount of energy to the animals they support. For some curious reason, this is usually only studied when the plant is of economic importance, and often then only when attacks are severe and noticeable. Of course, exactly the same reasoning applies to animals, which are liable to attack or some energy drain from parasites. Thomas Park's recent experiments (1948) with the flour beetles *Tribolium confusum* and *castaneum* afford one of the most convincing demonstrations of this principle. In laboratory cultures, he was able so to control conditions that competition between the two species could be measured, and the results determined within a certain rather broad degree of probability. When both species were infested, as they usually are, with a Sporozoan parasite, *Adelina*, species A usually (though not always) replaced species B in competition experiments, but when the parasite was eliminated from cultures of the beetle, species B usually (but not always) eliminated species A. Has anyone yet measured the loss of potential energy to a plant species, from the operations of its herbivorous fauna, and the possible effects of this upon competition? I think the principle has been shown with differential rabbit grazing; but it must apply almost universally. This is to say, that competition hardly ever takes place between 'pure cultures' of plant species, uninfluenced by the animal community dependent upon them. But we may reasonably suppose that only those species or associations of plants will survive in evolution which carry animal communities that do not, either through the resistance or vitality of the plants themselves or by the internal controlling factors in the animal community, get completely devoured, or at any rate so weakened that they cannot compete successfully.

But with waste material like dead wood, litter and carrion, there is no reason at all why the animal community should not devour and destroy its habitat or the resources in it completely, provided enough of these temporary supplies are being produced (as with cattle dung) in relation to the life length and other properties of the animals living in them.

Varley's quantitative study (1947) of the insect fauna (nine herbivores, fifteen parasitic Hymenoptera and one predatory fly) living in a population of knapweed (*Centaurea nemoralis*) flower and seed heads, is the only one done so far that throws much light on the inner workings of a small community dependent on plants, of which the different micro-units are in dynamic relationship. His work was directed to some very interesting questions about host-parasite balance. But I think the other important conclusion coming out of it, apart from showing the inherent complexity of even a small fragment of the animal community, was his demonstration that among an apparently complex network of food relationships only five were really significant in controlling the numbers of the central species, the knapweed gall-fly (*Urophora jaceana*). May we pray that similar simplification will emerge from other studies of the sort!

The degree of interchange between minor communities is obviously a very fruitful subject for study, because it will greatly influence the behaviour of the whole population, and also has a bearing upon modern theories of evolution, such as those of Sewall Wright. It is, however, linked up with the wider question of patchiness in populations, which can be brought about in several ways: (1) patchiness may be due to the separation of minor habitats in a more or less repeated pattern throughout some major habitat; (2) patchiness may also occur entirely through the interaction of plants and animals on their habitat and on each other: this seems to happen in marine and perhaps in fresh-water plankton;
Population interspersion: an essay on animal community patterns

(3) it can also be caused by the short-term oscillations, or (4) by long-term scarcity of a species. I realize that the populations of any minor unit are never exactly the same as the others; this point has forcibly been brought out by Diver (1934, 1938), in his Studland Heath survey. Nevertheless, we must admit that there is a substantial amount of general basic resemblance between one dead rabbit and another, or between different oak trees or wood-ant nests. The differences arise more often through the varying species composition of the communities, and these may be due not so much to basic differences in the habitats (apart from seasonal ones) as to the improbability of all the species that could live there finding that patch, or arriving in time to colonize it at the right stage, or succeeding in establishing a population there. This part of the subject has been discussed and analysed a great deal by botanists, but I do not know of any very relevant work on animals. But once we admit that the composition of the colonists will vary greatly with chance, we must see that the resulting species interactions (e.g. through competition or predation) will work themselves out in a number of different solutions. In other words, we shall expect to find minor habitat centres differing rather strikingly in their faunas, and seldom to be able to do more than express a probability or possibility that a given list of species will occur. I think it is even conceivable that the existence of certain scarcer species in such minor community units depends partly on stronger competitors being absent by chance. These considerations make it even more difficult to attach very real meanings to the mean densities of populations spread over wide areas, since they will always tend to be split into numerous small components that are living in different biotic environments. The whole subject of interchange by population movements between isolated minor habitats requires extensive study by marking methods.

One of the very interesting features of these small habitat units is that many species spend alternate parts of their lives in more than one of them. Thus longicorn beetles live in dying or dead wood, and many of them as adults visit flowers of herbs or shrubs or trees and presumably feed on pollen. Strangalia (Leptura) maculata, that breeds chiefly in dead birch wood, but also in that of several other broad-leaved trees, is commonly seen on such flowers as the meadow-sweet (Spiraea ulmaria), and the blossoms of bramble, again, with a fairly wide range of choice in species of plant. The chief thing uniting larval and adult host-plants is that they are mostly species of woodland openings. Blackman (1918) gives a long list of Leptura species and other longicorns visiting Spiraea and blackberry flowers in an American locality. About half the British longicorn species are known to have a flower-visited habit (Fowler, 1890).

Similarly, some dung-feeding flies haunt other habitats. The predacious fly (Scatophaga stercoraria) so abundantly seen on cowpats, does much of its hunting on hedgerows and scrub (Dr B. M. Hobby, personal communication). Hydrotea irritans, that fly that is such a nuisance to us in the summer woods, is common in cattle dung, and it may originally perhaps have bred on wild cattle when glades were a small feature in a woodland landscape; whereas now the glades have become huge pasture-field areas with scattered woods between. But it still enters woods in large numbers.

I have similarly observed green-bottles of the genus Orthellia, that breed partly in cowpats in the fields, entering neighbouring woods and haunting sallow blossoms in the spring.

I think it stands to reason that the inhabitants of minor habitats that are separated from one another by some distance should wander in search of new patches, especially as so
many of these are temporary. It is also natural that we should find them feeding on flowers or honeydew of trees, or congregating at certain points for mating. And evidently in many cases this alternation of minor habitat during the life history has become obligatory. Among insects, e.g. some aphids, there are instances of alternation between two plant hosts during the life cycle which involve similar migrations. And we may consider that the tree canopy or trunk, and the soil beneath, are similarly different minor habitat units separated in the vertical plane.

In order to make such migrations in search of new places or resources, an animal must have sufficient energy stored up to make the journey, unless it can find refuelling stations en route. Williams, Barnes & Sawyer (1943) did an ingenious experiment on Drosophila funebris that illustrates this point. They attached each fly by wax at its tail end to a wire in such a way that it could use its wings as if in flight, but could not escape. They found that a week-old fly died on the average after 110 min., during which time it had made over a million wing-beats, and that it had used up all the available glycogen in its body. Very young and old flies died in about 20 min. We should expect therefore to find some relation between the migrating power of animals and the distance between minor habitat units. We shall not be surprised to find in the records of a single species, a great deal of apparent mingling of minor habitats, though further analysis might explain them quite simply.

I have only alluded in a very slight way to some of the dynamic implications of the types of population interspersion pattern that occur in nature. These small patterns are in turn built up into larger ones, such as one sees between wood and field and river, and there is much interchange of fauna between these. And on a still larger scale we have the alternation of bird life between England and Africa, or Norway and England, which expresses the same principle.

The patchiness of habitats affects oscillations in numbers. It is becoming increasingly understood by population ecologists that the control of populations, i.e. ultimate upper and lower limits set to increase, is brought about by density-dependent factors, either within the species or between species (see Solomon, 1949). The chief density-dependent factors are intraspecific competition for resources, space or prestige; and interspecific competition, predators or parasites; with other factors affecting the exact intensity and level of operation of these processes. This is another way of saying that control of numbers, and therefore of much of the oscillation that takes place in populations, depends on community relationships. It is therefore interesting to inquire how the splitting up of populations into partly isolated units affects these mechanisms. A good deal is beginning to be written about this, more especially in connexion with the development and natural control of insect outbreaks. Nicholson & Bailey (1935), whose main theory deduces that under certain conditions predator-prey or host-parasite population oscillations will tend to get more and more violent until they result in local extinction, have suggested that this might occur in nature, but that because it is happening in different population units, and not necessarily simultaneously, lateral migration is always replacing the extinguished or shortly to be extinguished nuclei. I find this theory, which has also been discussed by Smith (1939), rather difficult to believe in its entirety. But it is at any rate well known, and can be seen in the field, that outbreaks such as those of the oak moths do not affect every tree equally, and one may see immune trees in a devastated wood, and such trees form a reservoir of populations that have been almost
20 Population interspersion: an essay on animal community patterns

wiped out elsewhere—a consideration applying both to the moths and their complex, but also to the rest of the fauna which suffers from the defoliation.

From this analysis there begins to be seen an ecosystem on any area composed of comparatively limited minor centres of action, each having certain distinctive characteristics as habitat that are reflected in their communities, and which have a considerable amount of interchange by lateral and vertical movements. One would like to see a large number of studies by ecologists and by naturalists on these small component communities, but carried out in such a way that the data can eventually be linked with similar studies. In this way there might emerge some more clear-cut general picture of the workings of different major ecosystems. It has often been said to me by specialists that the time is not ripe for integration of ecological data into community form, with the implication, rather comfortable for the specialist, that there is no need to do anything about the synecology of animals or of animals plus plants in our lifetimes. I disagree with this outlook. Suppose you were in an engineering department that was faced with wiring for telephones a city with half a million houses. You would not say that because there is not enough wire and instruments to do the whole lot at once that you would have to wait ten years until they were all available. You would start a few centres and fit up as much as possible, but leave a great many terminals and some whole exchanges unconnected, and many houses without communication to the centre, but link them up as material came along later.

The analogy with community research on animals is very close. What has been deficient so far in most of the smaller detailed records, or surveys of minor groupings, is that they have not been recorded in a way which would permit of later linking with other surveys; the habitat data have often been ludicrously sparse, the context lacking, and the information incapable of full use by ecologists. This is shown almost wherever one looks for habitat data for animals. Even a first-rate survey for one animal group of minor and microhabitats like Donisthorpe’s usually lacks any definition of the major habitat. ‘In fungi’ by itself is a small part of what we need. Similarly, ‘the white admiral butterfly lays its eggs on the honeysuckle’ does not tell one the additional vital fact that this occurs usually in glade or ride conditions and not under thick canopy. Nor for that matter does ‘honesuckle f.’ in an oakwood necessarily tell one that part of its population is non-flowering and has probably been brought there by birds eating berries on the more open parts of the wood.

We require, therefore, two things to improve the recording and use of the vast detailed knowledge that is being collected all the time about wild animals (and plants). First some general notions about patterns of habitat and population interspersion, i.e. the context into which such observations fit. That I have tried to indicate in this paper in a very condensed form, but it really needs an enormous amount of further study and thought. Ecologists, and especially animal ecologists, need some comprehensive principles for classifying habitats, based on these patterns and their component parts. We need a Systema Naturae for habitats of all sizes, and we have arrived at a stage of knowledge where the outline of such a system might be drawn up. This time it cannot be done by one man—it would require a great deal of co-operative effort. The British Ecological Society might very well consider it worth while to spend some effort in trying to draft one, so that the present fragmented records could fit into a general synthesis of data, even though that synthesis may take many years to accomplish. But it might help to do for ecology what Linnaeus did for taxonomy. As with taxonomy, the categories set up would often be only approximations to reality, but they would if properly designed in the light of general dynamic
principles, provide a much better method of organizing field data than we have at present. And it might form an extra sheet anchor for naturalists, who may feel that much of ecology is becoming purely quantitative, abstract and mysterious. I hope, however, that we shall not invent fantastic Greek names for these categories, but use good old English terms like tree, tussock, dung and carrion. Later, when we begin to feel some assurance that the classification has been compared with ideas from other countries and begins to have a general validity, it might be necessary to invent more of an international lingo for the component parts.

As a first and very simple approach towards this ideal, I would mention the type of record card that has been in use for several years at Oxford, in connexion with ecological surveys, and which has begun to provide valuable habitat data for animals.

Species:
Place: Wytham Woods, Berks.
Date: 19
Habitat: Major:
   Minor (e.g. plant):
   Micro:
   Vertical:
Observer: Specimen code letter:

Please label specimens with your Initials, Date and Code Letter, e.g. C.D. 1. 5. 47 (A).

The record on any one card is meant to cover what may be called a single ecological ‘incident’ or significance. Such molecular information does not compete with intensive studies by research ecologists or naturalists, but supplements them. Here I would just say a word about the terms ‘professional’ and ‘amateur’ which one frequently hears used in a contrasted manner. Those who study ecology are not all professional ecologists, because that does imply certain special critical standards and experiences of methods; but are we not all amateurs in some respect? Our subject-matter is so wide that it includes vast outer fringes with which we have only an amateur acquaintance. This is true of nearly all scientific research, but of ecology par excellence. I would illustrate the point by a story. Several years ago I happened to find a live population of the pointed snail (Clausilia rophii), a species thought to be quite extinct in the Oxford region. I took it for confirmation to a friend who is naturalist and taxonomist of very considerable skill. He said: ‘You know, you amateurs have all the luck.’ And, observing a faint surprise on my face, added, ‘If you know what I mean.’ I did know what he meant, and the point of the story is emphasized when I add that the professional in this instance is a professor of theology.

There is no doubt that all ecologists are seeing things, and quite often recording them, if only in their notebooks, that could be valuable additions to our general accumulating knowledge of communities, if they were made in the form I suggest. This suggestion, of course, does imply the existence of active centres at which the data will be accumulated and eventually used scientifically. What better one can be imagined than the new Nature Conservancy, and any associated research institutes that it may develop?

The relation of such recording work to a real appreciation of the dynamic implications of habitat patterning may be illustrated by an example. Suppose one records, with date
Population interspersion: an essay on animal community patterns

and time and place, the Chrysomelid beetle Galerucella viburni feeding, at a height of 3–5 ft., upon the upper side of leaves of the wayfaring tree, Viburnum opulus, in a ride in an oak-ash-sycamore woodland on limestone. That is a reasonably good primary record of an ecological incident. But suppose I put it in more general terms, for interpretation. ‘I have observed an unknown number of active parcels of potential energy of unknown size, moving about in a manner that may be random or not, in a habitat that I can only describe by some rough indicator species of plants and the underlying rock. I assume that because these parcels are probably morphologically similar they are also more or less genetically similar. The patch of habitat in which they were operating was one of an unknown number of similar and some quite dissimilar ones situated at an unknown distance from this one. The operations of these parcels of potential energy is likely to be interrupted or reduced by the activities of others: I do not know what these are in Britain, but I can cite some suggestive data from Europe.’ In this way one may arrive at a constructive ignorance—insight not too damped by caution.

It can be seen that population interspersion is a subject that involves equally all the present theories of demology as well as the arrangement of communities, because it is of the nature of animal communities and therefore of their populations not to be evenly distributed, though the unevenness of density is itself subject to ecological laws.

Dr Watt ended his Presidential Address with a quotation from Shakespeare about the relation of the part to the whole. I will venture to end also with a quotation, from a little-known sonnet-writer (J. B. White), which might be applied to minor communities and habitats:

Or who could find,
Whilst fly and leaf and insect stood revealed,
That to such countless orbs that mad’st us blind?

REFERENCES


Donisthorpe, H. (1930). The ants (Formicidae) and guests (myrmecophiles) of Windsor Forest and District. Ent. Rec. 42 (Suppl.), (1)–(18).


