

THE RELATION OF POPULATION DYNAMICS SOME OTHER AREAS OF ECOLOGY*

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Near where I live in Northern Ireland there is a large circular "temple" built on the very edge of a cliff in classical style of the late eighteenth century by Frederick Augustus Hervey, Earl of Bristol and Bishop of Derry. Around the lower edge of the domed roof is a Latin inscription which can be roughly translated: "It is a pleasure to stand upon the shore and to see ships tossed upon the sea".

To most visitors this seems a cynical and heartless sentiment not uncharacteristic of a particularly worldly prelate. In fact you will find in Bacon's essay on "Truth" that this is only part of a quotation, which continues. . . "a pleasure to stand in the window of a castle and to see a battle. . . below, but no pleasure is comparable to standing upon the vantage ground of Truth. . . and to see the errors and wanderings and mists and tempests in the vale below".

I have a feeling that this might appear to some of you to sum up the academic ecologist's attitude to the problems encountered by the practical agriculturalists, wildlife managers and horticulturalists. I recognise that the history of ecology has been far too often dominated by academic disputes about theory and terminology which bear little relation to problems of population management, and that there are still many practices which work empirically but for which we have little theoretical foundation. I am in a particularly vulnerable situation just now because, for the last five years, I have mainly been involved with university administration and teaching and have had limited time for practical work. I need to take special note of Bacon's final addition to the above quotation "so always that this prospect be with pity and not with swelling or pride". My intermittent involvement with the ecological literature certainly means that you will be able to augment and correct the examples on which I shall rely. But possibly, too, from my more distant vantage point, I can suggest some of the broader problems which worry me about the present state of ecology

and which may make suitable material for a "keynote" address.

For I certainly am concerned about the present condition of ecology and ecologists. I think there is wide agreement that, in practical terms, we are too often wise after the event; to the extent that there are those who say that, since each ecological problem has unique features, ecology is no more a science than the study of human history is. This confusion is reflected in the academic field also, where there is much dispute about how we should train ecologists and how to organise research: I shall return to this aspect later.

Individual variation

In about half a century the emphasis of ecological research has gone through several stages. This is not just a "band wagon" effect. In order to study the complex natural world a scientist must set up hypotheses and to do that he must select aspects of his material. The detection of a profitable set of hypotheses is a rare and important event (Kuhn, 1970) of great value to scientific advance. At the time I first wrote an ecology textbook the concensus among most biologists was that the only way into the complexity of living nature was through the experimental biology of the individual organism. The first breakthrough pioneered, for example, by Lotka (1925) and Elton (1927) was to simplify this field and make it quantitative by measuring single species *population* sizes and their growth and decline. This led on to the study of interactions between populations and also to the concepts of food chain and food web; but always, at that stage, and for the purposes of simplification, treating the individual organisms in the population as in some sense equal and interchangeable.

Since then the ecologist has been obliged to recognise that many other properties which distinguish the individuals within a population must be taken into account. These include the genetical, physiological and behavioural differences between individuals and certain consequences of these which are reflected in life cycle strategies, population regulatory properties, distribution effects, interactions with other species and, always in the background, the long-term effects of selection and evolutionary-

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change. Perhaps it is because different ecologists emphasise the importance of different distinctions between individuals that the applied ecologist often complains that theory is of little value to particular instances.

I should like at this stage to run through just a few examples of such phenomena which will serve to illustrate the limitations of population studies based on pure enumeration. I shall not refer to the problem of accurate enumeration by itself, which is often the weakest link in ecological studies and can make nonsense of some of the more sophisticated approaches.

Environmental temperature

Let us begin with the relatively simple area of physiological attributes and, among these, responses to environmental temperature. Because there are so many species of invertebrates it has been common to accept that the effects of temperature on growth and reproduction are virtually the same in related species and in the same species at different times and places. Classical laboratory studies of competition, e.g. of *Tribolium* by Park and Frank (1948), demonstrated that in fact this one factor could switch the outcome of competitive experiments between two species; many later studies have confirmed the subtle effects which differences in this single abiotic factor have on vital parameters: even more is this true of the synergistic action of several factors.

Even the same species, through local acclimatisation or selective adaptation, may show widely different responses to the same conditions as demonstrated in White's work on grasshoppers at this Conference*. In another example, Block and Young (1978) have shown that antarctic terrestrial mites can have two to four times the metabolic rates of temperate individuals; but the responses were not the same for all life stages (Young, 1979), nor even do individual animals regulate over a short time period to the same extent. The ability of these animals to exhibit super-cooling to temperatures down to - 30°C also involves acclimatisation and depends on starvation and the consequent elimination of oarticles on which crystals can form (Block *et al.* 1978). The differential effects of temperature shown by animals in field conditions are illustrated by McLaren's (1963) studies of zooplankton which migrate daily between warmer rich surface waters where they feed and deeper cooler water in which

their fecundity increases relative to respiratory metabolism. A further twist to this situation is provided by unpublished studies of Coleraine colleagues in Lough Neagh where the entire lake splits up into a series of cylinders of water of some 5 to 10 m diameter rotating under the influence of wind. This exposes the plankton to alternate light and dark conditions at intervals of a few hours.

Life cycle strategies

In the general area of physiological responses to the environment, a great deal of recent interest has focussed on the life cycle strategies, the allocation of resources between growth and reproduction and also the relative advantages of greater size, longer life and their opposites. I trace this topic back to Cole (1954) who introduced the terms *semelparous* and *iteroparous*, later called "big bang" and "repeat" breeding, and to Blower (1969) who provided outstandingly good examples among the millipedes. Among the authors who have recently contributed to this field I have found Southwood (1976), Southwood *et al.* (1974), Calow (1977a, 1977b, 1978a, 1978b) and Calow and Woodhead (1977) particularly stimulating whilst papers by Oosterhof (1977) and by Webb and Elmes (1979) are highly relevant. The last paper for instance shows that the size of all life stages and reproductive capacity in the oribatid mite *Steganacarus magnus* vary greatly, and a principal components analysis was used to relate these variations to soil and plant habitat as well as to Eason. Oosterhoff's (1977) field and laboratory studies of *Cepaea nemoralis*, a banded helioid snail, demonstrated differences in growth rate, maximum size attained, tendency to emigrate, mortality rate and reproductive capacity in relation to population density and to abiotic factors. He found that most of these factors were under hereditary influence and suggested an intraspecific population regulation scheme which he compared with that of Chitty (1960; 1967) for small mammals.

The papers already cited by Southwood and Calow are especially concerned with energy budgets and the partitioning of metabolic activity between growth and reproduction. One example from the latter author (1978a) concerns the life cycles of freshwater gastropods, their "choice" between (a) semelparity (big bang) and iteroparity (repeat breeding), (b) egg size and egg numbers and (c) hermaphroditism versus gonochorism (the single sex or dioecious condition). The wide range in such parameters exhibited by water snails can be linked with patchiness and nutritional status of food, littoral versus benthic and lotic versus lentic habitat and in general with the kinds of conditions which have come to be associated with r and K selection

* "Adaptation, Energy and Conservation - a grass hopper biology." New Zealand Ecological Society slide-tape package.

strategies. In other words the fundamental parameters of population dynamics are all subject to the influence of environmental conditions and selective pressures and it is particularly between closely related sympatric species that the values of these parameters are likely to show the greatest differences.

Southwood (1976) and Southwood *et al.* (1974) stress that absolute size and time, as experienced by organisms, are not the best measures of impact on their life cycle strategies. Of more importance is the ratio between generation time 't' and habitat stability H (which may for instance be a seasonal breeding period). If this ratio is small, permitting many generations in a period, the penalty of excessive reproductive rate is exhaustion of resources; whilst a ratio of unity will allow a population to deploy a high rate of increase with impunity (the "r selection" case). In evolutionary terms they hypothesise that prolonged periods of reproductive restraint and heavy selection for biotic advantage ("K selection") lead to increase in size and to evolutionary inflexibility and ultimate extinction. These are features which are familiar in the geological record.

Behavioural variation

Concerning the effects of variability of behaviour on population parameters, I shall say little. It is of course clear that especially among land vertebrates the great differences between individuals in their responses to the same environmental situation and in their capacity for learning must influence food gathering capacity, reproductive success and survival. The detection of a hereditary basis for some of these characteristics in polymorphic populations of small mammals is a key theme in the work of Chitty (1960; 1967) and Krebs and Meyers (1974). Under this heading we can also include the interactive effects of habitat variation and patchiness which bring about differences in density and in the values of population parameters such as growth and reproductive rates, which depend on feeding rate, as well as mortality. Spectacular examples, of course, include the phase changes of locusts and effects of crowding on many other insects (e.g. Long's (1953) work on *Vanessa urticae*). The stabilising effects of patchiness on predator-prey interactions referred to below are the subject of a paper by Murdoch (1977). At the very least the effects of individual behavioural differences must increase the variance of population parameters and frequently lead to segregation of groups within a population, distinguished by sex, age and hereditary endowment.

Interspecific interactions

Next I should like briefly to consider some effects

of interactions between species which have frequently evolved in such a way as to favour survival of both partners even when one is, in some sense, the exploiter of the other. In doing so population parameters are modified.

It is now widely recognised that at least a certain level of herbivorous attack frequently leads to an increased yield of plant material to the exploiter. Many examples are quoted in van Emden (1972).

A particularly surprising recent report is that of Dyer (1980) who showed that the action of saliva of mice on the cut surfaces of sorghum seedlings produced a 15 % increase in root growth which persists through the life of the plant. The chemical involved apparently stimulates nucleic acid synthesis.

On the predator / prey level there have been a number of demonstrations that grazing of soil fungi by micro-arthropods can promote fungal growth and this in turn the rate of decomposition of organic matter (Lohm and Persson, 1977). Springett (1980) not only detected a 10% increase in decomposition rate in a laboratory trial with the springtail *Foisomia candida* feeding on fungus but also a further 8 % when small numbers of predatory mites were added to the system. The whole question of predator-prey relations has for me been illuminated by the studies of Murdoch (1977; 1979). Murdoch and Oaten (1975) and Murdoch and Sih (1978) to which I shall refer later.

Another interspecific effect which is neither the result of competition nor predation is reported by Arthur (1978) in two species of the polymorphic banded snails *Cepaea*. This is the effect, through a common predator, of improvement of the concealment pattern in one species which then increases selection pressure on a sympatric species; each species thus being the selective agent which acts on morph frequency in the other. This is not of course a case of introgressive hybridisation nor of character displacement. Similar hypotheses have been used to explain the parallel evolution of mimicry in sympatric species of butterflies and of the timing of multi-species periodic cicada cycles (e.g. Lloyd and Dybas, 1966).

Genetic variation

Examples of genetic variation in parameters of importance to population performance are now numerous. I think of the work of Chitty (1960; 1967) followed by Krebs and Myers (1974) on small mammals, of Wellington (1957) on tent caterpillars and Oosterhoff (1977) on practically all relevant biological attributes of the land snail *Cepaea*, which refer to the influence of polymorphic variation of genotypes within the same population at the same time on growth and reproductive rates, mortality

and behaviour. Changes in the genotype ratios concerned appear to vary under different environmental conditions. Obviously if vital ecological parameters can vary over short periods and between members of a population, both at the same time and at different times under changing conditions, we have come a long way from treating members of the population as equivalent.

Any characteristic which currently exhibits hereditary variability will, of necessity, be subject to selective pressures and this in turn means that changing environmental pressures must bring about changes in ecological responses. Few changes are more rapid than those brought about by human activity, whether intentional or not, and those associated with agricultural practices certainly provide outstanding examples. The effects of changes in English farm management on partridge populations both via their insect food and in other ways provide an excellent example (Potts and Vickerman, 1974; Potts, 1980).

Co-evolution of organisms

Variations in the extent to which herbivores and predators manipulate the yield from the organisms which they exploit have led a number of authors to suggest that groups of interacting species of different trophic levels have evolved together, thereby stabilising or conserving the structure or content of an ecosystem to the mutual advantage of the constituent organisms. Such suggestions have taken several forms. For instance, Mattson and Addy (1975), following on from demonstrations of increased yield from plants attacked by insects, stress the regulatory action of herbivorous insects in forests. They claim that most pest outbreaks occur when plants are under stress or deficient in resources and that the resultant regrowth after an attack and the increased nutrient circulation from damaged plants and insect faeces, tend to restore the level of primary production. This line of argument is pursued further by Springett (1978) in the context of Australian eucalypt forests which are particularly heavily grazed by insects in regions of poor soils and erratic climate. He argues that this situation requires a major revision of management practices and in particular much more detailed study of the effects of insects on plants when they are not at peak densities. He is also concerned with the longer term effects of invertebrates in relation to mineralisation of plant nutrients.

The latter theme has been applied to decomposer organisms more generally, especially by Ausmus (1977) and Ausmus, Edwards and Witkamp (1976). They suggest that conservation of plant nutrients in

microbial and invertebrate tissue is related to seasonal likelihood of loss by leaching in such a way as to conserve these ions in the system. Another Australian example comes from Lee and Buckerfield's (1980) preliminary study of nematode attack on wheat. The story is complicated by soil and other factors but, in general, plants which are attacked at a young stage overcompensate and yield no less grain than those not attacked. Yield, if anything, is negatively correlated with the "white cyst count", the conventional criterion of nematode attack.

If such examples, where organisms have evolved together over long periods, seem to have counter-intuitive effects on each other's populations, it follows that some kind of selection process at an ecosystem level has influenced the values of single species population parameters. Models, therefore, which may work in laboratory cultures could be of limited value in field situations.

The "evolutionary individual"

Another way in which simple enumeration of individual organisms can lead one astray has been amusingly illustrated by Janzen (1977) in his discussion of asexually reproducing dandelions and aphids. The former are largely apomictic, have all the characteristics of an "r-selected" pioneer species capable of colonising temporary habitats without immediate competition. Having the same genetic endowment, all the individuals of one provenance in an area can be regarded as members of a single "evolutionary individual" (EI) which can be very long lived and of great effective size. The appearance of areas of suitable soil for germination leads to an increase in the "size" of the EI but not of numbers in the sense of greater genetic diversity. Also the chances of elimination by a herbivore or disease are reduced for such a diffusely spread "organism". When the idea is extended to the asexually reproducing aphids it will be seen that advantages can also be gained from spreading the damage done to food - supplying plants in relation to the "size" of the organism.

Owen (1978) has speculated that production of the biologically unique sugar melezitose by aphids may favour free-living nitrogen-synthesising bacteria which in turn benefit the plant: another possible example of ecosystem evolution with extensive long-term effects on population parameters.

Populations as ecosystem components

You will have noticed that, in my discussion up to now, I have been obliged to use concepts which are customarily regarded as proper to the fields of ecological energetics, population genetics and ecosystem theory. It seems to me that such

excursions into areas of ecology outside strict population dynamics are inevitable if we are to understand how natural populations grow, change and decline.

Different workers have faced this situation in different ways. Beddington and Lawton (1978) for instance, applying stability analysis to small collections of interacting species, affirm that the community-ecologists' argument that an ecosystem can only be studied as an immensely complicated system of mutually interacting species is false and that in practice, only a very few competitive or predatory effects operate on anyone species. In effect there are small "clusters" or "guilds" of interacting species relatively isolated from the rest of the system and in any case the time delays inherent in many ecological interactions dampen the impact of one species or another; only demonstrable density dependent interactions are of real significance. It will be interesting to see whether supporting field data can be produced to settle this argument, but I imagine that, as so often in ecology, examples will be selected and universalised too widely if we are not careful.

Some ecologists, on the other hand, having accepted that ecosystems are complex and, seeking short-cuts, have concentrated their attention on the metabolic effects of species rather than their numbers. This approach was adopted in much of the International Biological Programme and its fruitfulness is a matter of opinion. Perhaps it has worked best in the case of rather simple systems such as those in the polar and desert regions: certainly the attempt to feed rough "guestimates" into systems models which lead to the slogan "garbage in, garbage out" was often an expensive failure. But in many cases less ambitious studies have shown up ways in which attributes of particular species do not conform to expectation and these have caused the ecologist to look harder at the individual biology of organisms in a way which has been fruitful.

Even at the whole ecosystem level we have been made aware of overall constraints within which all the organisms must operate. The surprising consistency of net primary production levels (Macfadyen, 1963; Odum, 1969) often in very dissimilar systems, the way in which production/biomass ratios differ by orders of magnitude when macrophyte systems are compared with those based on single cell plants, and the very widespread tendency for the decomposition "industry" to exceed in importance the herbivore-based food webs (Odum and Smalley, 1959; Macfadyen, 1964; Kajak and Hillbricht-

Ilkowska, 1972), are examples of such unexpected general insights.

There have certainly been many attempts to group together the organisms of one major taxon or life form or habitat and treat them as one. The history of attempts to measure production of freshwater benthic invertebrates, beginning with Hynes (1968) and more recently summarised by Waters (1977) provides good examples of a bold attempt to simplify by avoiding detailed identification, followed by successive requirements to classify according to trophic level, length of life cycle, size class and other features so that not very much effort is ultimately saved without serious loss of information. One particularly useful distinction in the ecosystem energetics field, which is very relevant to population problems but does not seem to have been widely taken up, is that of Wiegert and Owen (1971) who stress the fundamental difference in effect between saprophages and biophages. The latter, feeding on living organisms, are always in danger of "killing the goose which lays the golden egg" if they escape control. Such species, therefore, tend to be held at much lower population levels, at which damage to their food source is minimised, and by mechanisms other than food shortage, as was first suggested by Hairston, Smith and Slobodkin (1960).

Possible directions for research and training in ecology.

There must be a danger that this long list of complexities will have reduced you to a state of despair. If there are so many idiosyncratic features of individual organisms, so many externally imposed constraints and so many ways in which interaction between even two species can operate counter-intuitively, how can the ecologist hope to produce a testable model of a particular situation and hope to predict the outcome of any attempt to modify it? If so many areas of biology and environmental science can be relevant to the ecological situation how can one train the people who are to be the ecologists of the future? Certainly there is no agreement about the answers to these questions, I can only suggest my own approach. On the methods of tackling ecological problems I think it must be recognised that there is no one short-cut. I think that Usher *et al.* (1979) in considering the problem of the great diversity of soil organisms and our failure to understand how they are functionally related, have the right approach: neither the field-based "divisive" (roughly the "synecological") nor the laboratory-based "agglomerative" (accumulation of "autecological" studies) approaches can give us the whole story and it is essential to combine the two in a study of the same system. In addition the

extension of experiments into the field, as advocated twenty years ago by Varley (1957) is essential if we are to relate the two approaches.

As regards the training of ecologists and the organisation of research, some would say that we need bigger and better teams of specialists; whilst others would have all ecologists join the latest bandwagon, be it energetics or computer modelling for instance. If there is one lesson to be drawn from this review it is surely that even simple organisms are unpredictable in important ways under field conditions. This must mean that the day of the observant field naturalist is far from over and, indeed, that all ecologists need a wide understanding of fauna, flora and habitat. There must, of course, be specialist services available to research teams and provided by experts in the physical sciences and mathematics, and ecologists must be able to apply their techniques, but the main direction of an ecological study can only be determined by the ecologist himself.

As regards the training of ecologists, I feel that current academic courses frequently fail in two respects. Firstly, somewhere along the line so many young people lose just the involvement with living things and powers of observation which I think are so essential: instead their attention is directed to a limited range of received wisdom as purveyed by lectures and books. Secondly, when I think of the amount of time and effort wasted in many courses that I have personally been involved in, either as pupil or teacher, I am sure that the biggest time waster of all is the presentation of information to people not at that particular time attuned to receive it. This is coupled, of course, with the ignorance of the student of the kind of information which will potentially satisfy his present needs. I suppose there must always be a major element of luck in bringing the right people together in any educational situation but I am sure that the less rigid the structure the better the chances of fruitful exchange. One way of rectifying this situation is, of course, to hold scientific meetings like this one.

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