HABITAT, THE TEMPLET FOR ECOLOGICAL STRATEGIES?

PRESIDENTIAL ADDRESS TO THE BRITISH ECOLOGICAL SOCIETY,
5 JANUARY 1977

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INTRODUCTION

The very etymology of Ecology, from the Greek 'Oikos', 'the household', implies that ecologists should devote some attention to the 'house' or habitat of the population or community they are studying. However, as Charles Elton (1966) has so forcibly pointed out, 'definition of habitats, or rather lack of it, is one of the chief blind spots in Zoology'. Elton himself has provided us with a qualitative classification of habitats, while another past President, Alex Watt (1947) highlighted the dynamic nature of habitats by his phrase, 'pattern and process'.

Elton referred to the need to quantify habitat characteristics. In this Address I will attempt some quantification; however, you will all be aware that in doing this I will not be able to emulate those former Presidents who have been able to provide a definitive synthesis of a field or of their own studies, my offering can be but a small beginning, an indication of the type of characteristics we should quantify. In considering ecosystem patterns and environment R. M. May (1974) writes 'it is to be emphasized that although patterns may underlie the rich and varied tapestry of the natural world, there is no single simple pattern. Theories must be pluralistic'. Indeed, the complexity of the subject is daunting and in any attempt to formulate some type of general framework, one is continually beset with exceptions. In stressing the need for a framework I am echoing a plea of my predecessor Amyan Macfadyen (1975) who cited K. E. F. Watt’s (1971) vivid image ‘if we do not develop a strong theoretical core that will bring all parts of ecology back together we shall all be washed out to sea in an immense tide of unrelated information’.

In some ways I think we may see ourselves at a similar point to the inorganic chemist before the development of the periodic table; then he could not predict, for example, how soluble a particular sulphate would be, or what was the likelihood of a particular reaction occurring. Each fact had to be discovered for itself and each must be remembered in isolation. It is noteworthy that from Dobereiner’s early efforts in 1816 it took more than fifty years before Mendeleeff formulated his Periodic Law (1869) and even after this there were various attempts at rearrangement. Another parallel may be drawn with astronomy before the development of the Hertzsprung-Russell diagram that relates the evolution and the properties of stars.

Again in our own subject biology, the situation is somewhat analogous to that before the formulation of the Linnean system of classification; but now from this system of classification, we are able to organize our knowledge of, for example, the functional morphology of organisms and we can even make assumptions, with a high probability
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that they will be correct, about the structure and physiology of a particular organism from previous findings about other related species. We will note that there are always exceptions: there are for example, many apterous insects, but this does not invalidate the general utility of the ordinal classification system of insects based largely on wing form and structure.

Over the last decade several ecologists have made notable contributions to areas of our subject indicating a framework within which we could begin to organize our facts. One thinks, for example, of Charles Elton, G. E. Hutchinson, Robert MacArthur and many others who have illuminated our ideas of niche and the assembly of niches into an ecosystem (Vandermeer 1972; Whittaker, Levin & Root 1973). Peters (1976) has recently suggested that many basic theories, including natural selection, are tautologies and as such are not subject to empirical falsification and incapable of prediction. This problem is not a new one for philosophers and it is not one that appeals to me. Peters' definition of a tautology as an argument that 'consists of premises or axioms and the ramifications which follow by logical necessity' seems unduly broad and to embrace all logic. In a field as complex as ecology I believe that progress will require a mixture of both induction and deduction. Theoretical ecology suggests various generalizations, from these we may deduce how particular field populations or ecosystems will behave. These we can test and if all or most of our deductions fail to accord with field data, then the general statement will have been found to be false. We can then examine the field evidence and attempt by inductive inference to suggest a new generalization. The mathematical consistency of this with known ecological constraints (e.g. 'negative populations do not exist') will test its theoretical generality, whilst fieldwork will search for what the logician terms 'contradictory instances'. This may be visualized as an iterative approach to the 'true' theory. So long as we base the theory on one set of premises (and their logical implications) and test it against independent observations this seems an adequate 'scientific test'.

The aim in developing a classification of ecological strategies is not only, as T. H. Huxley wrote 'to facilitate the operation of the mind in clearly conceiving and retaining in the memory the characters of the objects in question', but to allow predictions to be made that can be tested against field observations. As always with classifications of nature, it is easy to find exceptions; the real challenge, the constructive work, is not to find the exception, but to use this to improve, modify or even change the general framework.

THE REPRODUCTIVE SUCCESS AND RELATED MATRICES

In the course of evolution the members of a species will evolve those strategies that maximize the numbers of their descendents in their habitat which must be viewed from the two dimensions emphasized by several ecologists including Burges (1960), Birch (1971) and Taylor & Taylor (1977), namely time and space. Briefly, the choices open to any organism with respect to its breeding may be expressed in a two by two matrix with 'now' and 'later' on the time axis and 'here' and 'elsewhere' on the space axis. Each of these conditions may be considered to offer a level of favourableness for reproduction (Fig. 1); this favourableness is expressed in terms of \( r \), the mean intrinsic rate of increase, that the organism could achieve in these different situations in the time-space matrix. The parallel will be noted with the use of the net reproductive rate (\( R_0 = e^{rt} \)) and its variance by Reddingius & den Boer (1970) in their model on heterogeneity and the spreading of risk. However, this is by no means a complete expression of the probability
of reproductive success in relation to these strategies, for there is an expectancy of 'being there': the chances of surviving dormancy or migration and in the latter finding a new habitat and being able to breed (Fig. 2). Of course, $E_a \approx 1$, whilst $E_b$, $E_c$ and $E_d$ will be less. These two matrices could be combined to provide an average outcome matrix with values $E_a r_a$, $E_b r_b$. . . . There is a unique solution to all the values in this matrix and, in such a deterministic view of habitat, evolution would clearly favour the strategy that provided the largest value. However, this does not take account of the variations in time or in space of favourableness: 'the random environmental fluctuations (measured by a characteristic variance)' (May 1973). These variations may be expressed as $V$-values (Fig. 3). The appropriate $r$-plus or minus the appropriate $V$-value give the upper and lower limits for, say, 99% of the outcomes. One then gets the complete reproductive success matrix by combining the first three matrices (Fig. 4). There will be two values for each strategy, their range is a measure of the uncertainty of that particular strategy.

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**Fig. 1.** The favourableness matrix—the potential rates of increase if different strategies are followed.

<table>
<thead>
<tr>
<th>TIME</th>
<th>Now</th>
<th>Later</th>
</tr>
</thead>
<tbody>
<tr>
<td>SPACE</td>
<td>Here</td>
<td>$r_a$</td>
</tr>
<tr>
<td>Elsewhere</td>
<td>$r_c$</td>
<td>$r_d$</td>
</tr>
</tbody>
</table>

**Fig. 2.** The expectancy of 'being-there' matrix—survival expectancies in time and/or space.

<table>
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<td>SPACE</td>
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**Fig. 3.** The 'uncertainty' (or 'risk') matrix—variance of $r$ (Fig. 1) in time and space.
Clearly it is therefore possible for an overlap between the values of these strategies. When this occurs evolution is likely to lead to polymorphism in regard to the particular strategy; I will elaborate on this later. I hope to show how the values in the boxes will depend on the characteristics of the habitat (as well as those of the organism), the habitat acts as a templet.

**HABITAT CHARACTERISTICS**

Many workers have pointed out that habitats must be considered in terms of their heterogeneity in time and their heterogeneity in space (May 1974), these are the axes of the reproduction matrix (Fig. 4). If we regard organisms as resources for their predators then we can see from Fig. 5 several examples from nature of the variations in levels of resource in time. Such variations must be related to the time scale of the organism, the predator that is being considered, and specifically to its generation time. For organisms other than homeotherms, the influence of temperature (expressed as day degrees) and other environmental variables, must be incorporated to provide an accurate measure (cf. Gilbert et al. 1976). However, I regard this as a refinement, important in inductive analytical models, but not influencing the general concepts.

![Fig. 4. The reproductive success matrix—the number of descendents resulting from each strategy.](image)

A theoretical scheme for the general description of heterogeneity in time is shown in Fig. 6. There are two important parameters that derive from the characteristics of the habitat. $F$, which equals the length of the favourable period (permits breeding) and $L$, the length of the unfavourable period. Another important parameter, and one in which I personally have long been interested, is $H$, which equals the length of time the location remains suitable for breeding. $H$ will therefore be the sum of $F$ and $L$ until such time as the length of a period that is unfavourable is greater than the length of generation time. Each of these parameters will have its own variability; the variance of $r$ with time will contribute to the appropriate $V$-values in the risk matrix (Fig. 3), whilst the variance in $L$ is a measure of the unpredictability of the favourable periods and will contribute to the value of $E_b$ in the expectancy of 'being there' matrix (Fig. 2). As will be seen from Fig. 6 where one has three imaginary species, $A$, $B$ and $C$, each with very different generation times, the individual expressions of $H$ are different because of the relationships between generation time and $L$ and both these combine to give different values of the $H/T$ index for the same habitat. One can think of many real examples that illustrate this. As May (1974, 1976a), Blackith (1974) and others have shown such temporal heterogeneity will increase instability in population size; species with short generation times will track...
variations in the environment more precisely than those with long generation times. This is dramatically illustrated by the work on Tawny Owls (Strix aluco L.) (long generation times) and rodents (short generation times) studied in Wytham Wood and described by Southern (1970) in his Presidential Address.

It must be emphasized that natural habitats will provide a complete spectrum of types with regard to these different characters, but some of the types which may be taken to represent particular conditions in this multi-dimensional spectrum are represented in Fig. 7. A predictable habitat is one which is relatively permanent and has, in this particular case, a relatively low favourability variance. The unpredictable habitat differs in the greater variance of the length of unfavourable periods (L) and the greater variance...
in the level of favourableness at different times. Of a different type is the ephemeral habitat which has a large variance, but with a relatively short $H$ and a small or insignificant $L$. An example of the first might be taken to be the flushes of foliage in temperate vegetation (Fig. 5(a)) and of the second, perhaps the growth of annuals in semi-arid areas with erratic rainfall. Habitats that are relatively early in any natural recolonization succession are of the third type; such habitats may be termed ephemeral or temporary.

![Diagram of habitats](https://example.com/diagram.png)

**Fig. 6.** Heterogeneity of habitats in time. $F$, length of favourable period (permits breeding); $L$, length of unfavourable period (permits existence); $H$, length of time a location remains suitable for breeding—

$$H = F + L.$$

(Note when $L' > \tau$ this marks the end of $H$; var. $\tau$ = variance of $\tau$ with time = $V$; var. $L$ = unpredictability of favourable periods.

(Southwood 1962a, b): examples include carrion (Chapman & Sankey 1955), dung (Mohr 1943), rotting fruit, temporary pools (Evans 1958, 1959; Kitching 1971; Pajunen 1971) and ruderal plants. The longevity of plants or plant colonies is the determinant of $H$ for phytophagous insects. The work on Tamm, reviewed by Harper (1967) showed the different ‘half-lives’ for colonies of herbaceous plants. Assuming colonies of only moderate size there will be few, if any plants left after four half-lives and so for univoltine insects on the species illustrated by Harper, $H$-values will range from about 8 for Centaurea jacea (L.), to over 200 for Sanicula europaea (L.). These may be compared with the
half-life expectancy of a mature redwood (over 200 years old) of 300 years (Namkoong & Roberds 1974), which gives \( H = 1400 \).

Generations of long-lived species, like the tawny owl, will experience less variation in the average \( r \)-value, than those of short-lived species. They will average out the fluctuations and will approach a stable age structure. Exceptionally high \( V \)-values, and especially catastrophes, may lead to uniform-aged populations even in long-lived species, e.g. balsam fir in eastern North America (Greenbank 1963; Hett & Loucks 1976).

A parallel classification can be adopted to describe the heterogeneity of habitats in space. In this context, however, there are two scales that derive from the organism. First, the trivial range \( R_t \), the range over which the organism gathers its food. For a tree this will simply be its canopy area, but for an animal it has certain behavioural characteristics (Kennedy 1961, 1975; Southwood 1962a, b, 1977c; Taylor 1965, 1974; Johnson 1969). The other spatial scale provided by the organism is the migratory range. The area over which it can move when it is not reproducing. For plants this is the distance that may be moved as propagules, and is influenced by their structure, but for animals once again it has a precise behavioural definition (Kennedy 1961 etc., see above).

Habitats may be characterized with regard to the favourable areas expressed as the

![Diagram](image-url)
patch size, $S$, and the unfavourable, inter-patch areas expressed as $U$. The level of favourability within each patch will be variable and this spatial variance will contribute to the $V$ values in the 'risk matrix'. The variance in the distances between the patches, in $U$, will be a measure of the unpredictability of finding a new habitat and will contribute to $E_c$ in the expectancy of 'being there' matrix (Fig. 2).

As with temporal heterogeneity, so with spatial heterogeneity there is a multi-dimensional continuum in respect of these various characters. Three types are shown in Fig. 9: for appropriate phytophagous insects the large patch may be likened to bracken (*Pteridium aquilinum* L.), whilst the small patch might be likened to a particular climbing plant in a tropical rainforest (Grubb *et al.* 1963). However, one of the key characters of spatial heterogeneity is the balance between the favourability of different habitats, the ratio $r_a + r_b : r_c + r_d$, as I will elaborate later, in the basically stable biosphere, this is proportional to $H/\tau$ measured on the time axis.

There are, for obvious reasons, fewer organisms, that inhabit isolated habitats that are separated by distances in excess of the organisms normal migratory range. Small islands and mountain tops provide examples of this and it is noteworthy to the extent that organisms in such situations have become adapted so as to reduce their migratory potential (Allee & Schmidt 1951; Mani 1962; Richards 1965; Carlquist 1966). Levins (1968) divided habitats into ‘coarse grained’ and ‘fine grained’ and these correspond with large and small patch size, when $U$ is less than the range of the animal.

**PARAMETERS IN THE REPRODUCTIVE SUCCESS MATRIX AND HABITAT CHARACTERISTICS**

The favourableness of the habitat, which is expressed as a mean rate of increase ($r$), will depend on the level of resources (the carrying capacity, $K$) the number of natural enemies
and as, Taylor & Taylor (1977) show in their model, the density of the organism. Where $H/\tau$ is large, that is the habitats are relatively stable, then

$$r_a + r_b \sim r_c + r_d$$

because the frequency with which new habitats arise is low, so that there is a high probability that the organisms present habitat, where it has developed, will be similar to other habitats. That is, where it is 'now' is unlikely to be significantly more or less favourable, either now or in the future, than other habitats elsewhere.

In contrast when $H/\tau$ is small:

$$r_a + r_b < r_c + r_d$$

because new habitats will be arising frequently and those where the organism has developed are bound to be older than average. New habitats will offer unexploited resources and an initial freedom from at least specific natural enemies. Wide seasonal climate cycles will often increase $r_b$ and $r_d$, relative to $r_a$ and $r_c$. The various expectancies of 'being there' ($E_a$, $E_b$, $E_c$, $E_d$) each have different components. As already indicated, $E_a$ closely approximates to unity; all the others are normally smaller. The expectancy ($E_b$) of hiding (diapause or dormancy) and breeding successfully later depends on characters measured on a time scale that is the length of the favourable ($F$) and unfavourable ($L$) periods, the

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**FIG. 9.** Some examples of space characters of habitats.
unpredictability of the latter (variance $L$) and the generation time of the organism. The expectancy ($E_d$) of finding a new habitat to breed depends largely on the characters measured on the spatial scale, i.e. the degree of isolation, the distance between the habitats ($U$) and its variance, the size of the habitat patches ($S$) and the migratory range of the organism. The expectancy $E_a$ combines both the components from $E_b$ and $E_c$. Clearly therefore $E_b$ is relatively large in seasonal habitats with a high predictability related to phenomena such as photoperiod, which the organism can use as a clock (Lees 1970) to ensure that it starts and ends hiding at the right time. Of course there are always very abnormal conditions that lead to catastrophes against which natural selection cannot buffer (Ives & Nairn 1966; Shapiro 1975). The more scattered and isolated the habitats the smaller $E_a$ will be for the same habitat finding abilities of the organism (Fig. 9).

The reproductive risks or $V$-values express the variability (as standard deviation) in the levels of favourableness of the different habitats in space and time (these are the shaded areas in Figs 6–9). The $V$-values will frequently reflect climatic variations, soil conditions and similar physical features of environment. For plankton the level of nutrients may be the dominant factor (Petersen 1975).

THE SELECTION OF ECOLOGICAL STRATEGIES

Types of selection

The reproductive success matrix (Fig. 4) is developed on the basis of classical natural selection, the individual maximizing the number of its own descendants. However, when we start to consider the selection of the diverse ecological strategies there are often suggestions that selection acting at the level of the population—group selection as postulated by Wynne-Edwards (1962)—may be effective. The circumstances and degree to which group selection can override individual selection is still a matter of controversy, but some models support its effectiveness in at least some situations (Levins 1970; Eshel 1972; Gilpin 1975; Wilson 1975). To word the discussion so as to explicitly exclude unrestricted group selection makes it excessively ponderous, but neither here, nor in an earlier paper (Southwood et al. 1974), are there any major conclusions that depend on unrestricted group selection. Group selection could be effective against individual interests in populations which would normally be considered to have genetical kinship among their members; these are the situations in which I suppose it to operate and so the characters in question can be interpreted as advantageous to inclusive fitness (Hamilton 1963, 1964a, 1964b, 1970, 1975; Eberhard 1975; Dawkins 1976). Hamilton has shown how evolution may favour the retention of altruistic characters, in which an individual loses some of its own fitness provided that the individuals that gain are related to it. The closer the relationship, the more altruistic the donor may be. As reformulated by Eberhard the necessary condition for gain ratio and relationship can be expressed:

\[ \text{Gain to beneficiary}/\text{Loss to altruist} > 1/2r_{AB} \]

where $r_{AB}$ is the genetical relatedness of the altruist and the young of the beneficiary. Thus, as emphasised particularly by Eberhard, high gain ratio acts are favoured even when relatedness is low. When acts distribute a general benefit to a whole group, for example sparing the resource, non-fouling of the habitat, then the inclusion of the self-giving beneficiaries gives a mean relatedness of $1/n$, where $n =$ size of group, and this can account for the low-grade selection in models where groups are set at random, as for example in the brief and cryptically explained model of Gilbert et al. (1976). As these
authors point out the group selection effect becomes much more powerful if group members are genetically correlated. Unless this correlation is due to pure assortment (Wilson 1975) the effect can equally correctly be attributed to kin selection. Thus a sacrifice of classical individual fitness may occur in a population if the other members of the population show a measure of relatedness. This will occur in populations of species that are characterized by a low level of migration (Table 1).

Table 1. The contrasting suites of characteristics of the extremes of the r–K selection spectrum

<table>
<thead>
<tr>
<th>r-species</th>
<th>K-species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short generation time</td>
<td>Long generation time</td>
</tr>
<tr>
<td>Small size</td>
<td>Large size</td>
</tr>
<tr>
<td>High level of dispersal</td>
<td>Low level of dispersal</td>
</tr>
<tr>
<td>Much density independent mortality</td>
<td>High survival rate, especially of reproductive stages</td>
</tr>
<tr>
<td>High fecundity</td>
<td>Low fecundity with high parental investment or iteroparity, often with synchronous breeding ('masting')</td>
</tr>
<tr>
<td>Panmictic</td>
<td>Clonal</td>
</tr>
<tr>
<td>Intraspecific competition — often 'scramble type'</td>
<td>Intraspecific competition—often 'contest type'</td>
</tr>
<tr>
<td>Low investment in 'defence' and other interspecific competition mechanisms</td>
<td>High investment in 'defence' and other interspecific competitive mechanisms</td>
</tr>
<tr>
<td>Time efficient</td>
<td>Food and space resource efficient</td>
</tr>
<tr>
<td>Populations often 'overshoot'</td>
<td>Populations seldom 'overshoot'</td>
</tr>
<tr>
<td>Population density very variable—'boom and bust'</td>
<td>Population density relatively constant from generation to generation ( \approx K )</td>
</tr>
<tr>
<td>( H/\tau ) small</td>
<td>( H/\tau ) large</td>
</tr>
</tbody>
</table>

Fig. 10. Behavioural–physiological tactics appropriate to the reproductive success matrix.

The evolution of the basic strategies

Let us consider how selection against the habitat templet will work. If it is assumed that the range of values in one box in the reproductive success matrix (Fig. 4), does not overlap with a range of values in any other box, i.e. that there is a single optimal strategy. Basically such strategies are immediate breeding or dormancy or dispersal or a combination of these as shown in Fig. 10 (Southwood 1977c). However, the characters of the organism will interact with the habitat through the strategy that is adopted to continually
maximize the various parameters in the appropriate box of the reproductive success matrix. I will illustrate this by two hypothetical examples:

Case 1. The largest number of descendents is given in this case by \( E_a r_a \), that is by breeding here and now. Further adaptations will be favoured to increase the value of this expression. The variations in favourableness in time and space (\( V_a \)) will be reduced (i.e. the risks reduced) by an increase in size because this will increase longevity (and potentially generation time) and the spatial range over which resources can be gathered. Size is related to other bionomic characters (Bonner 1965; Heron 1972; Hutchinson 1975; Taylor 1975; Southwood 1976a) such that there develops a positive feedback (Fig. 11). This species will, from the arguments developed above, have a stable habitat (one with a high \( H/I \)). The longer the colony can remain in the same area the longer it can avoid substituting the smaller \( E_c \) for \( E_a \) (\( \sim \)). Mechanisms for defence against predators may be favoured (Southwood et al. 1974) even though they lower fecundity and carry other costs (Levins 1975). Habitats may become unfavourable simply through the accumulation of natural enemies (predators and disease) (e.g. Nielsen & Nielsen 1950), they may also become unfavourable because of overcrowding (Taylor & Taylor 1977). But individual colonies that overshoot and destroy the resource (that is lower \( r_a \) at time plus one) will also pay an evolutionary penalty, compared with the others that do not lower \( r_a \) for the future. If they overshoot completely and destroy the habitat then the minimum cost is the substitution of \( E_c \) for \( E_a \) for the whole population and the maximum cost, the extinction of the whole population. It is hardly surprising that colonies of organisms of this type often seem to have mechanisms that militate against their invasion by individuals of the same species from outside (Mykytowycz 1968; Andrewartha 1971; Mech 1972). In its simplest form the greater survival of the residents may simply derive from their knowledge of the geography of the habitat with the corresponding advantages for feeding and predator avoidance, noticed in animals ranging from Heliconius butterflies (Gilbert 1975; Cook, Thomason & Young 1976) to primates (MacKinnon 1974). Eventually, of course, a balance is struck because all these adaptations have their own costs; the physiological costs of maintenance mount with size. Every strategy involves a trade-off in the allocation of resources to reproduction and survival (Cole 1954; Murdoch

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**Fig. 11.** The 'feed back loop' of K-selection.
1966; Schaffer 1974; Smith & Fretwell 1974; Pianka & Parker 1975) as illustrated, by the hypothetical block-fish (Southwood 1976a). Furthermore, every organism must retain the ability for it or its descendents to change location eventually or face extinction. This tendency towards large size in stable habitats is probably the ecological basis of Cope’s Law (Southwood et al. 1974).

Case 2. The largest value in this case is given by \( E_c r_c \), that is by migrating and then breeding. One will note that there is an approximation in including this under the ‘now’ column of the matrix, because transit time will always be finite and the organisms own resources must initially be switched from reproduction to dispersal. Johnson (1969) pointed out how in insects this gave rise to an oogenesis-flight syndrome and in most insects those that fly have lower levels of fecundity than those that are non-migrants; all this will tend to reduce \( r_c \) relative to \( r_a \) and as \( E_c \) cannot be larger than \( E_a \) (it will usually be much less). The implication of this is that the habitats elsewhere must have a much higher mean favourableness than the habitat already occupied. This will be true of the ephemeral type of habitats, new habitats are continually arising and old ones becoming hostile. Evolution will therefore favour all traits that serve to maximize the expectancy of arriving and surviving to breed \( (E_c) \); i.e. the ability to migrate, the ability to survive the dangers of migration or dispersal and the ability to find (or arrive in) the new habitats. In addition selection will favour those attributes that maximize \( r_c \); an ability to find mates at a low density or to reproduce asexually, an ability to reproduce quickly and exploit the new habitat while it lasts (that is a high fecundity and a short generation time). These are the situations where, in plants, the annual habitat will be favoured over the perennial, because here the probability of a perennial surviving is less than that of a seed germinating (Gadgil 1971; Schaffer & Gadgil 1975). In many plants and animals these abilities are associated with small size (Southwood et al. 1974). The ephemeral nature of the habitats of these organisms, very low \( H/T \) values, mean that the resource in short supply is often time; models that deny that a maximal \( r \) will be evolved in the extreme cases are unrealistic, because they do not allow for the fact that the next generation will have to breed elsewhere; the favourableness of the habitat that they are in, has become very low, not because of their ‘overshooting’, but because of successional change.

If we now relax the condition that the ranges of values shown in each box of the reproduction matrix (Fig. 4) shall not overlap, we can then see that often in a real stochastic situation the maximum number of descendents will sometimes be arrived at by individuals following one strategy and sometimes by following another. That is the species will show polymorphism, either behavioural or structural, where the species has become well adapted to its environment (and this does not always apply in situations where man has drastically altered the habitat). The partitioning of individuals between migrants and non-migrants, or between dormant and non-dormant individuals, will be a reflection of the relative frequencies of levels of reproductive success. Instances of polymorphism in respect of both dispersal ability and dormancy are numerous (Southwood 1962a; Young 1961; 1965a, b; Johnson 1969; Villiers 1975; Lees 1955; Tauber & Tauber 1976), they must be regarded as indicating the optimal strategy for the species habitat.

**Optimal strategy models**

It is therefore possible to construct multi-dimensional models with axes corresponding to the various habitat characteristics that influence the terms of the reproductive success matrix. One corner of the model will represent the condition when one box of the matrix is completely dominant, e.g. when all individuals migrate or become dormant. The
opposite corner will represent the reverse position. In between there will be a substantial region where the population will be polymorphic in respect of the character, the proportions being 'geared to the habitat' (Southwood 1962a, b); the greater the variance the greater the polymorphism. These models will therefore represent three-dimensional continua, but for illustrative purposes (Fig. 12) two surfaces have been inserted to give an indication of the upper and lower faces of the region of polymorphism. The quantitative scales cannot be ascertained without more sophisticated mathematical treatment (e.g. Levins 1962; Templeton & Rothman 1974; Gillespie 1974; Slatkin & Lande 1976).

The general form of the model is identical for migration and for dormancy (including diapause). For migration the axes are:

(i) Durational stability \( (H/\tau) \), which is closely related to the ratio \( r_a : r_c \);
(ii) The spatial variability in favourableness \( (V_a + V_c) \);
(iii) The isolation of suitable habitats, which is \( 1 - E_s \), that is the expectancy of not finding the new habitat.

For dormancy the corresponding axes are:

(i) The constancy in favourableness, \( r_a : r_b \);
(ii) The temporal variability in favourableness \( (V_a + V_b) \);
(iii) The unpredictability of the change in favourableness, which is \( 1 - E_b \).

As already noted the spring flush of foliage in an English woodland has a low 'unpredictability value', but the advent of rain in some desert regions will have a high value.

Polymorphism for dormancy will include not only variations in the proportion entering a dormant period, but variations in its length. An interesting example is provided by the cricket, *Nemobius sylvestris* (Bosc.), which in the northern part of its range (extending into southern Britain) has a two-year life-cycle with an intense egg diapause and a quiescent period in the larval stage (during the second winter). In the southern part of its range, extending into Iberia, it is univoltine with a less intense egg diapause. This change in voltinism represents the evolved modification of the organisms time-scale \( (\tau) \), the bivoltinism in the north increases the resources (proportional to the shaded areas in Figs 6 and 7) available to one generation. However, in central France the species is polymorphic both as regards voltinism and the intensity of egg diapause (Brown 1977). In some years climatic conditions in central France will permit breeding in the first year, but in others the 'later' (i.e. bivoltine) option will be more successful. In terms of this model there is overlap between the values in the reproduction success matrix: neither generation time will always be the 'best' strategy, so the cricket is polymorphic and the weak egg diapause of some individuals makes them particularly sensitive to the climatic characters of particular seasons.

These models, of course, consider only the two left-hand boxes of the reproduction matrix (for migration) or the two top ones (for dormancy). Some corners may represent non-real situations. But they do show how the evolution of two particular ecological strategies may be related to habitat-characteristics in three dimensions. Unfortunately the visual combination of all six dimensions is beyond us!

**THE CONTINUUM OF HABITAT HETEROGENEITY AND SPECIFIC ECOLOGICAL STRATEGIES**

As populations march through their habitats in space and time, their position and magnitude will wax and wane. Taylor & Taylor (1977) in an enlightening analogy liken
Fig. 12. The optimal strategy model; roman type, axes for migration; italic type, axes for dormancy.
this to a reticulate stele of a fern. The form, the extent of branching and fusing, the thickness and constancy of the strands, will be a reflection of the features of the habitat: the templet that, through the reproduction matrix (Fig. 4), has fashioned the evolved ecological strategy of the species.

Coming back to my original challenge, a sort of ecological periodic table, we ought to be able to arrange the various patterns of branching and strand constancy to form continua. However, I trust it is now apparent that habitats cannot be quantitatively characterized by less than a minimum of five parameters and their variances and these must be scaled against three characters of the organism. A sort of periodic table in so many dimensions is clearly not going to be simple to visualize! We must return to the two basic dimensions space and time.

Changes in space (branching in the ‘fern stele’) are in fact most strongly related to a time scale feature of a habitat: its durational stability ($H$), expressed as $H/\tau$, the number of generations that can occur in a single locality and its converse, the frequency with which new habitats arise. The dominance of this character may be recognized from the reproductive success matrix, for as $E_a$ will normally be greater than $E_c$ or $E_d$, movement is evolutionarily advantageous only when $r_e$ (and/or $r_a$) is much larger than $r_a$, a situation that will be most likely to occur when new or vacant habitats are widespread.

Changes in time (changes in the thickness of strands in the fern stele) are expressions of the differences between $r_a \pm V_a$ and $r_b \pm V_b$, the temporal constancy (or variability) (Southwood 1976a, 1977c). Whittaker (1975) termed this ‘adversity selection’.

The durational stability axis

Many biologists have recognized the spectrum associated with the durational stability of the habitat and in my discussion of the evolution of basic strategies I have outlined the pressures that lead to the extremes. The most widely used description is the $r$–$K$ continuum of MacArthur & Wilson (1967), $r$-species being associated with ephemeral habitats (‘case 2’ above) and $K$-species with those with a long durational stability (‘case 1’ above) (Pianka 1970, 1972; Gadgil & Solbrig 1972; Southwood et al. 1974; Allan 1976; Southwood 1976a). These are the terms I will use as convenient labels for the ends of, I stress, a continuum (so most organisms will not be at the extremes). These labels are ‘shorthand’ descriptions of associated suites of characters (Table 1); just as Diptera is a convenient label for two-winged flies, although some Diptera are apterous and some two-winged insects are not Diptera (e.g. male coccoids)! Continuing the taxonomic approach, which betrays my entry-route to biology, I will list a few synonyms (Table 2). Some of these authors have claimed that their divisions differ from the ‘simple’ $r$ or $K$ selection; however I believe the important step is to recognize the main categories of criteria. Disputes about their exact definition or the appropriateness of the names are of secondary importance. When the concept is clearly understood, then a more appropriate name may be suggested: in the meantime one must join Wilbur, Tinkle & Collins (1974) in cautioning against a simplistic approach.

The combination of characters at each extreme (Table 1) will lead to different forms of population dynamics. The role of predators at both extremes will be small, at the $r$-end because of the organisms high mobility, at the $K$-end because of defence mechanisms. Examples of extreme $K$-species are whales, albatrosses, redwoods and oaks ($Quercus robor$ L. and $Q. petrae$ L.); prior to the advent of technological man, mature, but not senescent, examples seldom died from ‘predator’ attacks. However, for species that are intermediate in the continuum, predators are important and, taken with other forms of interspecific
competition, frequently maintain a population equilibrium below the carrying capacity as determined by food and space resources (Paine 1966, 1971; Beddington, Free & Lawton 1975; Connell 1975). Successful biological control and the outbreaks of 'upset pests' following the destruction of predators provide many field examples to support these theoretical conclusions.

This spectrum of population dynamics may be expressed in a three-dimensional model; the characteristic growth rates at different densities (as a proportion of the carrying capacity) are arranged along a third dimension corresponding to the durational stability of the habitat and the r–K continuum (Southwood 1975, 1976a; Southwood & Comins 1976).

Table 2. Some synonyms (partial or complete) of MacArthur & Wilson's (1967) r–K spectrum

<table>
<thead>
<tr>
<th></th>
<th>r-strategists</th>
<th>K-strategists</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hutchinson (1951)</td>
<td>Fugitive species</td>
<td>Sensorimotor</td>
</tr>
<tr>
<td>Kennedy (1956)</td>
<td>Vegetative</td>
<td>Equilibrium species</td>
</tr>
<tr>
<td>MacArthur (1960)</td>
<td>Opportunists</td>
<td>Denizens of permanent habitats</td>
</tr>
<tr>
<td>Southwood (1962a, b)</td>
<td>Denizens of temporary habitats</td>
<td></td>
</tr>
<tr>
<td>Wynne-Edwards (1962)</td>
<td>Pioneering species</td>
<td>Interference competitors</td>
</tr>
<tr>
<td>Miller (1969)</td>
<td>Exploitation competitors</td>
<td></td>
</tr>
<tr>
<td>Mitchell (1974)</td>
<td>l-parasites</td>
<td>m-parasites (partim.)</td>
</tr>
<tr>
<td>Smith (1975)</td>
<td>Fast species</td>
<td>Slow species</td>
</tr>
<tr>
<td>Diamond (1975)</td>
<td>Super tramps</td>
<td>High S-species (partim.)</td>
</tr>
<tr>
<td>Connell (1975)</td>
<td>Small species</td>
<td>Large species</td>
</tr>
<tr>
<td>Gilbert et al. (1976)</td>
<td>Ephemeral species</td>
<td>Sessile species</td>
</tr>
<tr>
<td>Raunkiaer (1937)</td>
<td>Therophytes (partim.)</td>
<td>Phanerophytes</td>
</tr>
</tbody>
</table>

The resulting synoptic model encourages prediction about the behaviour of r-, K- and intermediate-species when they are pests: the type of damage they will cause, the frequency of outbreaks and the appropriate control strategies (Conway 1976; May 1976b; Southwood 1977a, b). These predictions seem to accord with existing data. Likewise the patterns of dynamical behaviour in the populations of various species have been analysed by Hassell, Lawton & May (1976); they find that the majority of species show a monotonic return to a stable equilibrium point; the few exceptions would, on other characters be placed towards the r end of the synoptic model. Thus from a knowledge of the habitat and bionomic characteristics of an organism predictions can be made about its population dynamics that appear to be valid.

The constancy of favourableness (or adversity) axis

Whittaker (1975) pointed out that this 'third type of selection' occurred, in addition to r and K selection. It is really a different axis to the others, ranging from 'harsh' to 'rich' habitats. The adaptation of organisms to environmental adversity was one of the main themes of the ecology in the early part of this century (Chapman 1931). Raunkiaer's (1937) life-forms of plants show the spectrum from phanerophyte to the cryptophyte (except in extreme desert situations). As Schaffer & Gadgil (1975) point out at the extreme of the adversity selection spectrum there are some annual plants (therophytes) whose seeds lay dormant in the location occupied by their parent; these must be distinguished from other therophytes whose propagules have mechanisms for dispersal and are r-strategists. Diapause is a common adaptation in invertebrates (Andrewartha &
Birch 1954; Tauber & Tauber 1976). Relatively few warm blooded vertebrates have a dormancy period, their high resting energy costs pose special problems normally solved by adaptations involving a much lowered body temperature.

McNeill & Lawton (1970) examined life-history strategies in relation to the respiration/productivity ratios of many species of animal. Poikilotherms in the lower part of their figure have 'low respiratory cost resting stages'. Indeed the $y$-(log respiration/unit area/year)-axis of their graph may be approximately equated with the axis of increasing favourableness and the $x$-(productivity/unit area/year)-axis with the $K-r$ (durational instability) axis of Figs 12 and 13.

The special selective forces along the adversity axis would be expected to act for low energy cost resting stages and physiological mechanisms to ensure the synchrony of resumed activity with the return of environmental favourableness (i.e., increasing $E_b$). In environments that are continuously harsh owing to physical (e.g. hot springs or fast rivers) or chemical (e.g. petroleum pools) factors, those species that do adapt will be relatively free of interspecific competition (Hynes 1970). Greenslade (1972) has termed these 'beyond $K$', but I think they are really at the extreme of this axis.

For in the characterization of the habitat

Do I intend to imply that, after allowing for the scale characters of the organisms, the ecological strategies and population dynamics of every species in the same habitat will always be the same? The answer is a categorical 'No'; there are three further aspects that must be evaluated before a species can be placed on the $r-K$-axis of the synoptic model.

What is the resource?

This can be qualitatively illustrated by reference to two pests of the olive in Greece: the olive fly (Dacus oleae (Gmel.)) and the scale insect (Saissetia oleae (Bernard)). The scale insect lives on the leaves and the twigs, feeding on the sap. The numbers of these remain fairly constant from year to year, which is the generation time of the insect. The combination of the small size of the organism with the relatively long durational stability and constancy of resources would suggest an intermediate position; that is the population would normally be kept at a low, natural-enemy-controlled endemic level (i.e. like Cardiaspina albitextura Taylor (Clark 1964; Southwood & Comins 1976). This is supported by field observations, outbreaks are generally related to the application of pesticides that eliminate the natural enemies (S. Pappas, personal communication).

In contrast the olive fly lives as a larva in the pulp of the olive fruit. In Greece, olive fruits become susceptible in late July or early August and remain suitable until harvest or fruit drop. At the beginning of the olive season (August) some larvae are killed if the fruit becomes too hot from the sun (E. C. Young, personal communication), whilst fruits seem less favourable when the oil content builds up prior to harvest. The time of the harvest varies greatly according to variety and region: on the Greek mainland around Athens this will normally be in November, whilst the massive trees of the 'Lianolia' variety in Corfu may retain much of the crop until April. Breeding in the winter months is slowed by low temperatures; generation time therefore varies with season, but there are four or five generations a year. The resource level available at different seasons will vary greatly: the value of $r_a + V_a$ has a wide range; furthermore there tends to be a considerable year to year fluctuation in the number of olive fruits (Fig. 5(b)). Individual trees vary greatly in their cropping and the number of fruits retained after harvest. Late
Fig. 13. Ecological strategies and the habitat template.
in the season, after harvest, wild olives ('Oleasters') provide an important refuge; that is \( r_c \) is greater than \( r_a \) and \( H \) may be small. Thus in contrast to \textit{Saissetia} (in the absence of pesticides), \textit{Dacus oleae} fluctuates greatly from generation to generation and it has no natural enemy equilibrium. It is towards the \( r \)-end of the spectrum; in Andrewartha & Birch's (1954) terms it is limited by its resources and 'a shortage of time when \( r \) is positive'.

Thus the same host plant can have \( r \) and intermediate pests, because of the difference in the favourable period (\( F \)) and its variance of the different resources and the time scale (\( T \)) of the insects.

**Evolutionary history**

I have endeavoured to show how the ecological strategies of a species are evolved in response to the habitat templet, as expressed through the reproductive success matrix (Fig. 4). Clearly if the association is new, evolutionary adjustment will be incomplete. Pimentel (1961) has shown how these adjustments occur through the process of genetic feedback (see also Pimentel & Soans 1971; Levin 1972; Pimentel, Levin & Olson 1977). They may be relatively quick, but as man is currently making so many changes in the environment it is important to emphasize that 'the interlocking features of bionomics, ecology and habitat as we see them today are, as it were, but a single frame in the film of the evolution of the biosphere' (Southwood 1976a).

**Individual population features**

Local events may make a habitat very adverse and the population dynamics atypical, especially near the edge of a species' range. A twelve year study of the viburnum whitefly (\textit{Aleurotrachelus jelinekii} (Fraunf.)) on three bushes, showed that population growth was strongly influenced by climatic and other disturbances (Southwood & Reader 1976). On one bush there was no population growth, but when the resource (the number of leaves) was examined this was found to have fluctuated (because of damage by grey squirrels (\textit{Sciurus carolinensis} Gmelin)). Furthermore, the composition of the sap in the bushes differed, so that the value of \( r_a - V_a \) for this bush was much lower than that of the others. The characters of the habitat must therefore be quantified with care: its \( r \)-value may be less than it appears.

**HABITAT AND ECOSYSTEM CHARACTERS**

Ecosystems, like species, may be arranged in a pattern against the templet. Expressed in the apposite words of Cody & Diamond (1975) 'if the observed patterns in a community structure are products of natural selection, then similar selection by similar environments should provide similar optimal solutions to community structure'. One must note the variation in the population strategies of individual species within the same habitat as exemplified by the olive pests described above: therefore ecosystem characters are an expression of the mix of population strategies and their interaction.

Succession is the community or ecosystem process that is an expression of durational stability, i.e. the space axis of the templet. The time axis is again best expressed as adversity, a measure of the level of favourableness and its constancy. Various features of ecosystems can be arranged against these two axes (Fig. 13).
Succession

It is unnecessary to dwell on the refinements of the simple Clementsian concept of short-lived series evolving to permanent climaxes. The nature and species composition of the climax varies greatly; as Connell (1972, 1975), Horn (1974, 1976) and others have stressed the process is a reflection of the adaptations of the successive species. These adaptations are broadly those of the r-K continuum; the early stages of succession in relatively favourable habitats (represented on land by, for example, ruderal plants) are passed through rapidly and, in general, the time interval for one species to replace another in a Markovian process (Horn 1976) lengthens as the climax is approached, i.e. $H$ becomes larger. However, as Horn (1976) stresses where early successional have to modify the habitat (e.g. mosses on rock) then the time intervals of even early seral stages will be very long. Climaxes themselves are not static, they are a patchwork of pattern and process (Watt 1947), well exemplified by Barclay-Estrup & Gimingham's (1969) studies on the Calluna cycle. All the populations in the community, both animal as well as plant, will interact to form the ecosystem pattern (Janzen 1970).

The spatial complexity of a location increases through successional stages and the variety of niches (niche complexity) follows. This has been elegantly demonstrated with birds, where species number may be related to the foliage height diversity and cover (MacArthur 1964; Karr & Roth 1971; Cody 1975; Roth 1976).

Niche breadth, as represented by generalist feeding strategies is greatest in early seral stages: these are the habitats of high productivity and low use where, for example, Hespenheide (1975) showed that birds tended to have broad niches, or the immature habitats where plankton generalists occur (Goulden 1969). As trophic complexity increases predation will become a more important population factor between trophic levels, whilst between species at higher trophic levels interspecific competition may be significant (Menge & Sutherland 1976).

Standing crop (biomass) increases throughout successional stages, indeed this is the basis for the increase in spatial complexity; elephants and oak trees provide more niches for other organisms than mites and mosses. Productivity frequently, but not invariably, falls in both aquatic and terrestrial environments as the climax is reached (Margalef 1969), so that the turn-over rate (productivity/biomass) invariably falls (Watt 1971).

Resource level and constancy

This axis has long been recognized by biogeographers, but the simple classification into 'temperate' and 'tropical' with general statements as to their characters and stability is misleading (Leigh 1975; Bigger 1976; Southwood 1976b). A better measure, based on an analogy with the reproductive success matrix, is the level of favourableness and the constancy of this within the normal climatic cycle. This may be expressed as

$$r - \frac{r + v}{r - v}$$

where $r$ is a measure of the general physical and chemical favourableness of the environment for life. I will not attempt its precise quantification now, but the availability of water, sunlight and nutrients, the absence of toxic substances and temperatures within the normal ranges are clearly major components. Livingston's (1916) hydrothermal index was an early measure; Levitt (1963) and Watts (1971) discuss others. (Terborgh (1973) rejects the concept of 'favourableness' and considers that the observed differences in plant diversity should be viewed as the product of speciation-extinction type processes,
however, I suggest that these processes themselves largely depend on the characteristics of the habitat.) Organisms living in the same location may experience different levels of favourableness and constancy; for example in a marine environment food resources for suspension feeders may fluctuate more than those for sediment feeders (Levinton 1972).

It is easy to visualize that the smaller the value of

\[
\frac{r - v}{r + v}
\]

the greater the adversity (sensu Whittaker 1975) of the habitat. The greater the adversity, the lower is the biomass and productivity (Reichle, O'Neill & Harris 1975). Difficulties often arise when considering niche breadth because assumptions are made that productivity or diversity remain constant (e.g. Roughgarden 1974) which, of course, does not happen over any significant length of the adversity gradient. Another potential source of confusion is that whereas the breadth of the fundamental niche (sensu Hutchinson 1957) narrows with adversity, the proportionate breadth of the realized niche widens, owing to the reduction in the numbers of competing species (Dobzhansky 1950). Of course when individual communities are experimentally manipulated towards more adverse conditions competitive interactions will initially increase: but soon some species will be driven to extinction. An example of this is provided by Jackson's (1974) study of bivalves which shows that the greater the species diversity in the more favourable tropical regions and the greater geographical range in those species with the 'harsher' and most fluctuating habitats, i.e. those in shallow water.

Trophic complexity will decrease with increased adversity, this decrease is more associated with an increase in niche width than a decrease in spatial complexity, although the latter does occur. (On the durational stability axis the relative importance of these two casual mechanisms for trophic complexity is reversed.) An aspect of this is the reduced intensity of predator attack with increasing adversity (Paine 1966; Janzen 1970; Connell 1975). Kercher & Shugart (1975) have made an interesting attempt to express mathematically the level of trophic complexity.

These ecological processes, that Ricklefs (1973) terms 'decreased specialization and decreased resource diversity in harsh climates', combine to provide the long-recognized inverse relationship between diversity and adversity (Slobodkin & Sanders 1959). Specific examples are provided by Pianka's (1967) studies on lizards and Stout & Vandermeer's (1975) work on rheophilic insects in tropical and mid-latitude streams. The generality of the inverse relationship between environmental fluctuations and species diversity was shown by J. W. MacArthur (1975) who found that for many different climates and groups of organisms the total number of species in a small region is given by:

\[
S = A \ln (1 + B/\eta)
\]

where \(\eta\) is a measure of environmental fluctuation (e.g. temperature range) whilst \(A\) and \(B\) are constants for the area in question (found by a least-squares fit). Their exact biological meaning is unclear, but \(B\) seems to be a measure of the range of resources available and \(A\) expressed various biogeographical conditions—rates of introduction, speciation and establishment and the 'equilibrium number'. In the terms in which I have defined this axis, \(B\) is clearly related to \(r\), whilst \(\eta\) is a measure of \(V\).

The interaction of processes on the two axes

These general relationships between various community characters and succession or adversity are well known and have been widely reviewed in the last decade (e.g. Pianka
The points I wish to emphasize are that any particular habitat will have two positions, one in respect of each axis, and that the relationships are not necessarily linear. Thus all the properties of a series of successional stages in a location will not proceed in a uniform manner because of the different positions at which the characters on the resource level and constancy axes are crossed.

An interesting example of this is provided by the diversity of flowering plants in terrestrial successions at various levels of resource constancy and favourableness. The climaxes of wet tropical regions are in the top left-hand corner of the diagram, here on both axes niche breadth is minimal, and the fauna and flora are very diverse. In contrast habitats like arctic rock or sand lie in the bottom right-hand corner and are often dominated by single species, the moss *Racomitrium lanuginosum* (Brid.) or, where there is more alluvial material, the dandelion, *Taraxacum officinale* (L.). These early seres may be relatively long-lived in these harsh environments, but they are eventually invaded by other species.

Temperate regions are intermediate and the crossing of the niche breadth trend (on the two axes) with increased spatial complexity, through the various seral stages, leads to non-linearity. Vegetation of a particular height and form usually shows greatest diversity in mid-successional stages. This feature is of interest to entomologists, because it means that the probability of a plant being the same as its neighbour falls and then rises as a locality passes through the different successional stages from ploughed field to deciduous woodland. That is host plant patch size falls and then rises: the increased patch size and high durational stability of most climax dominants of temperate regions gives them a high 'apparency' (Feeny 1975, 1976). This influences the type of plant defence mechanism and through this the host plant range and ecological strategies of the insect herbivores (Southwood 1977c).

### WHY THE QUESTION MARK?

The title of this address ends with a question mark. Why? This is because I believe it is important that we do not visualize habitat as a rigid causal templet (or template in the engineering sense). First, an organism may evolve so that it is exposed to a different templet, secondly it may directly influence its own habitat. Habitat and organism are thus parts of a system linked with 'feed back'.

The importance of the time (generation) and space (foraging and migratory ranges) dimensions of an organism in determining how the features of its habitat impinge on its evolution, through the reproductive success matrix, has already been stressed (Figs 6 and 8). The changing diapause strategies and voltinism of the cricket *Nemobius* (Brown 1977) provide an illustration on the time scale. The great variation in size in mammals, and its consequences, demonstrate an evolved response to spatial heterogeneity. The wildebeest, because of its large size, can include much of East Africa in its range: seasonal unfavourability is coped with by movement, in terms of the symbols used earlier (Figs 4, 8 and 9), $E_s$ is relatively high because $R_m$ greatly exceeds $U$. This is not true of a small rodent where $R_m$ will, on purely mechanical grounds, be much less. The wildebeest's distant ancestors, in the late Cretaceous, were of a similar size to the rodent and would have been similarly restricted.

The impact of organisms on their habitats has been widely demonstrated. Herbivores can have both general and specific effects (e.g. Tansley & Adamson 1925; Janzen 1967, 1970; Harper 1969; van der Meijden 1971; Southwood 1973). There are the direct effects
of organisms, especially plants, on the physical features of their habitat; these underlie A. Watt's (1947) pattern and process concept for vegetation. In marine and aquatic environments by exhausting nutrients plankton may have spectacular effects on habitat characteristics. If the plankton themselves release toxic materials on death their influence may, for a time, be all pervasive. In many other situations organisms use chemicals to defend their habitat against other species (Went 1970) or otherwise modify it to their advantage (Walker 1975).

These are some of the mechanisms that underlie Levin's (1974) important point that organisms may themselves introduce heterogeneity into an initially homogeneous environment.

CONCLUSION

The multitude of ecological strategies that we observe in nature arise from the evolutionary 'trade-offs' of costs versus benefits in the process of adaptation to habitats. Natural habitats have at least eight quantitative characters (Figs 6–9) and these must be assessed against the organisms own dimensions in space and time. I suggest that these characters can be condensed into two axes: durational stability, which assesses spatial heterogeneity against time, and resource level and constancy, which expresses the temporal heterogeneity of the same space. Such a two dimensional treatment cannot encapsulate without exception all the complexity of nature, but it will surely be more realistic than attempts to organize ecological strategies along a single dimension.

The parallel with the Periodic Table of Chemistry or the Hertzsprung-Russell diagram of astronomy has already been drawn. The value of the Fig. 13 will have to be tested from both the theoretical and the observational viewpoints and it will surely need much modification. I suggest that it demonstrates the necessity of combining all these approaches: theoretical, experimental and observational. As Professor John Harper (1967) pointed out, ten years ago in his Presidential Address, these developments bring the qualitative observations of the field naturalist into a new and growing quantitative framework. And so I conclude by echoing the pleas of two other past Presidents, Southern (1970) for the continued place of field observation in modern ecology and Evans (1976) for 'really knowing' the organism you study. I must detain you no longer, there is much to be done.

ACKNOWLEDGMENTS

In the formulation of these ideas I have benefited greatly from discussions with many colleagues. M. Birley, V. K. Brown, W. D. Hamilton, M. P. Hassell, R. M. May, S. McNeill, P. M. Reader, J. E. Satchell and L. R. Taylor have been especially helpful whilst preparing this Address; to them and to all those ecologists whose work has influenced my thinking (and particularly those whose citations I have been unable to recall for my text!) I am most grateful.

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