ON OPTIMAL USE OF A PATCHY ENVIRONMENT

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There is a close parallel between the development of theories in economics and population biology. In biology, however, the geometry of the organisms and their environment plays a greater role. Different phenotypes have different abilities at harvesting resources, and the resources are distributed in a patchwork in three dimensions of the environment. In this paper we undertake to determine in which patches a species would feed and which items would form its diet if the species acted in the most economical fashion. Hopefully, natural selection will often have achieved such optimal allocation of time and energy expenditures, but such "optimum theories" are hypotheses for testing rather than anything certain. Some aspects of dietary and patch utilization have been treated in rather different ways by Hutchinson and MacArthur (1959) and by MacArthur and Levins (1964). The best empirical support for the model to be presented is that given by McNab (1963).

The basic procedure for determining optimal utilization of time or energy budgets is very simple: an activity should be enlarged as long as the resulting gain in time spent per unit food exceeds the loss. When any further enlargement would entail a greater loss than gain no such enlargement should take place. The problem is to find which components of a time or energy budget increase and which decrease as certain activities are enlarged.

Consider, first, the optimal number of kinds of items (such as prey species) in the diet. We assume here that the environment is "fine-grained," that is, that during search for food the prey species are located in the proportion in which they occur. In a later paragraph we deal with patchy environments where this is not true. We divide the time spent, per item eaten, into two components: time for search, and time for pursuit capture and eating. (The difference is that the animal searches a fine grained environment for all kinds of items simultaneously but pursues captures and eats them one at a time.) Suppose that the predator already includes N kinds of prey in its diet. Then we may subdivide its time, T_N, per item eaten, into a search time T_N^S and a pursuit (plus capture and eating) time, T_N^P. We can do the same for the predator if he were to enlarge his diet to include $N + 1$ kinds of prey. Writing both down in symbols

$$
\left.
\begin{aligned}
T_{N+1} &= T_{N+1}^S + T_{N+1}^P \\
T_N &= T_N^S + T_N^P \\
\overline{\Delta T_N} &= \overline{\Delta T_N^S} + \overline{\Delta T_N^P}
\end{aligned}
\right\}
\quad \text{(all times are per item of food).}
$$

603

We can subtract and find the change, ΔT_N, in total time which accompanies enlarging the diet from N to $N + 1$ items. If, in some way, the items can be ranked from most profitable to least profitable, then the optimal diet can be calculated by proceeding through the ranked list of items until ΔT_N first becomes negative. At this point no further enlargement should be contemplated. This gives the clue to the method of ranking: it should proceed from items of highest harvest per unit time to those of lowest. More specifically, we notice that ΔT^S is always negative, for the larger the variety of acceptable items, the less the search time, per unit of food. The pursuit time may increase, however, as new, hard-to-catch items are added to the diet. Hence ΔT^P may be positive. In Fig. 1a, 1b, we plot samples of $\Delta T_N{}^P$ and $-\Delta T_N{}^S$. For comparison purposes we actually plot the *reduction* in search time $\Delta S = -\Delta T_N{}^S$ against the increase in pursuit time $\Delta P = \Delta T_N{}^P$, since where these intersect there will be no further benefit from enlarging the diet. Notice that in both Fig. 1a and 1b, the items are ranked so that the reduction in pursuit time exceeds the gain in pursuit time by the greatest amount, i.e., the vertical distance between ΔS and ΔP curves is decreasing. In summary the optimal diet is the first value of N such that ΔT_N is negative, which is the first value of N to the right of the intersection point in the Fig. 1a, 1b.

The ΔS of Fig. 1 is calculated from assuming enlarging a diet from N to $N + 1$ equally abundant species reduces mean search time from $\dfrac{1}{N}$ to $\dfrac{1}{N + 1}$, and so $\Delta S = \dfrac{1}{N} - \dfrac{1}{N + 1}$. The ΔP curve measures the adaptations of the species for the items and must be empirically determined. The arrow indicates the optimal diet; when the species eats four kinds of resources an enlargement of the diet would, for the first time, cause a greater increase (in pursuit time) than decrease (in search time). The $\Delta S'$ curve is double the height of the ΔS curve indicating the effect of halving the density of each resource species. The optimal diet should be expanded to five species of prey. It would also be possible to indicate a more specialized predator by a steeper ΔP curve. This specialized predator should be less sensitive to changes in food density.

The exact shape of the curves is usually unknown and certainly varies from situation to situation. Hence no general prediction of the exact diet is worth attempting. However some interesting comparative predictions can be made. When the search time is multiplied by a constant factor, its decrease is also multiplied by that factor; if T^S in eq. 1 is multiplied by k, so is ΔT^S. Hence, in a productive environment where search time is uniformly reduced, its decrease is reduced; although the pursuit time, which is a function of the abilities of predator and prey, is unaltered and, according to the figure, the optimal diet becomes more restricted. Thus organisms which have low search/pursuit ratios should be more restricted in diet, whether the reason be high food density or high mobility of the prey. Recher has some evidence for this from herons (personal communication).
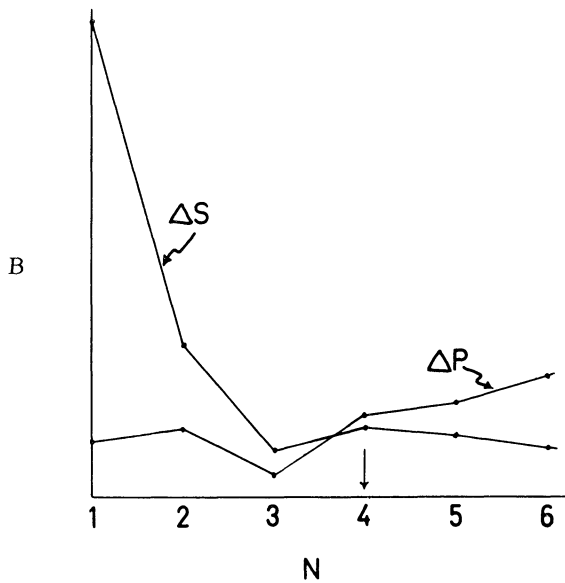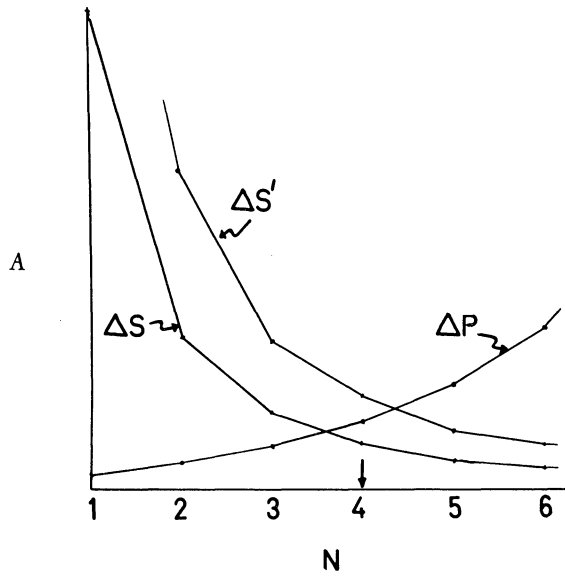
FIG. 1A. Equinumerous resource species. The decrease, ΔS, in mean search time and the increase, ΔP, in mean pursuit time which would accompany enlarging the diet from N to $N + 1$ species of prey are plotted for a hypothetical situation.

FIG. 1B. Resource species not equally numerous. The symbols are the same as in Fig. 1A, but the curves are no longer monotonic. The same qualitative conclusions hold.

The optimal use of patches of habitat is in many ways parallel to that of items in the diet within a patch. Now the time, per item caught, spent within suitable patches is an increasing function of the number of kinds of

patches on the species' itinerary (for as the itinerary is enlarged to include less suitable patches the hunting time clearly increases). We call this hunting time H, and denote by ΔH the *increase* in hunting time per item which accompanies enlarging the itinerary to include the next most satisfactory patch type. The time spent travelling between suitable patches (or to and from the nest if no hunting is done on the trips), is divided by the harvest to give the travelling time, T, per item caught. This is clearly a decreasing function of the number of patch types in the itinerary, and we denote by ΔT the *decrease* which accompanies enlarging the itinerary by one more patch type. The patch types are ranked from most productive (i.e., most prey calories caught per unit time) to least; as before, this is equivalent to a ranking which orders $\Delta H - \Delta T$ from largest to smallest. When the patches are about equally common we get something like Fig. 2; if they are unequally common, Fig. 2 will be modified in the way Fig. 1b was obtained from 1a, with no change in the qualitative predictions.
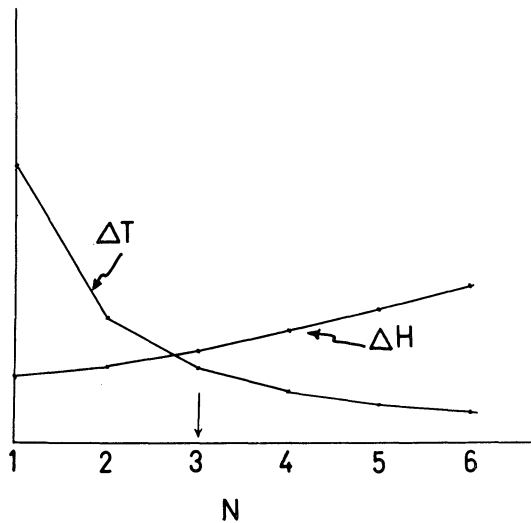

FIG. 2. The decrease, ΔT, associated with adding the next patch type, in the mean travelling time T (per prey item) across unsuitable patches and the increase, ΔH, in mean hunting time within suitable patches (per prey item) due to adding the next patch type, are plotted against the number of types of environmental patches in the species' itinerary. ΔT and ΔH measure the changes which accompany enlarging from N to $N + 1$. As before, the arrow indicates the optimal utilization.

The qualitative predictions from Fig. 2 are not quite parallel to those from Fig. 1. The effect of increased productivity (or more precisely increased food density) is no longer unambiguous, for both ΔH and ΔT are lowered. However, species with large pursuit/search ratios will have their ΔH curves lowered by a reduced amount, for only the search time decreases with increased food density. Hence pursuers more than searchers, should show restricted patch utilization where food is dense.

A second interesting prediction involves the use of different sized patches. Two environments which differ not in the proportion or quality of

their patches but only in the sizes of the patches (e.g., a checkerboard with one acre squares in one, and 1/4 acres squares in the other) will not have different H or ΔH, curves, for these are calculated per item caught and we postulated that the quality of the patches is unchanged. The ΔT curves will differ, though, for travelling distance between patches varies linearly with the linear dimension of the patch, while hunting area within a patch varies as its square. Hence, larger patches offer smaller travel time per unit hunting time, and thus have lower ΔT curves. Hence, by drawing an imaginary ΔT curve lower on Fig. 2, we see that larger patches are used in a more specialized way than are smaller ones, everything else being equal. This patch size effect should be greatly reduced in territorial species, since the travel time to and from the nest is independent of patch size; and only the travelling time from patch to patch across unsuitable ones drops in importance as patches are made larger. Hence, while feeding young in the nest, parents should exhibit nearly the same choice of patches whether they be large or small, but after the nesting, individuals in a large-patch environment should restrict their patch utilization. [Hutchinson (1959, 1965) has commented on other aspects of the relationship between an animal's size and the "grain-size" or texture of the environment.]

The effect of competitors is to reduce the density of some kinds of prey species in some patches. Curiously enough, an optimal predator faced with competition, should respond by shrinking its patch utilization but not (conspicuously) its diet! To see this, we consider the diet first. If a dietary item becomes rare, due to a competitor, its inclusion in the diet will have only a very slight effect on mean search and mean pursuit times. Hence ΔS and ΔP will be reduced toward zero for the item preceding the rare one and then will rise again (i.e., enlargement to include the rare one will cause little change). However, the reduction in the ΔS and ΔP will be roughly proportional to the reduction in abundance of the prey, so that if ΔS exceeded ΔP before the competitor entered, it will afterwards, also. In other words, any dietary item worth eating in the absence of competition is still worth eating afterwards. Patches, on the other hand, are a different story. For if food within one kind of patch becomes scarce, due to competition or any other cause, then to increase the itinerary to include these patches of scarce food means to increase the mean hunting time sharply. ΔH will then show a sharp peak of increase corresponding to the impoverished patch type. ΔT will be independent of the quality of the new patch and thus will not change with competition. Hence the ΔH curve may jump above the ΔT curve at an earlier point, causing a reduction in the optimal patch itinerary.

Next we ask whether the patch structure of the environment imposes any limit on the similarity of coexisting competitors. The answer is yes. Briefly, when the gain to a jack-of-all-trades in reduced travelling time makes up for his lower hunting efficiency compared to the patch specialists, then the jack-of-all-trades will outcompete both specialists. To be more precise, the specialists' harvest of food, per day, is kDH where k is the

hunting rate, D the food density, and H the hunting time, per day. The jack-of-all-trades harvests $k'DH'$ where $k' < k$ (a jack-of-all-trades is a master of none) and $H' > H$ (the jack-of-all-trades, by feeding in a wider variety of patches, travels less between suitable ones and has more time left for hunting). Thus, if $k'H' > kH$ $\left(\text{i.e., } \dfrac{k'}{k} > \dfrac{H}{H'}\right)$ then the jack-of-all-trades can reduce the food density to a lower value of D and still harvest enough to maintain itself. At this value of D the specialists cannot harvest fast enough and so they are eliminated. Or looked at in another way, the specialists can only be expected to coexist and resist invasion by the more generalized foragers if $\dfrac{H}{H'} > \dfrac{k'}{k}$; and, if the specialists become too similar to each other, their hunting rates (k) become closer to the hunting rate of the jack-of-all-trades (k'), with the result that they become more susceptible to invasion and competitive replacement.

One further justification of the whole scheme is worth adding here: the proof that the optimal use by a species is essentially independent of the subtlety of the recognized differences between patches or diet items. In other words, the results are not artifacts of the classification of patch or diet types. Suppose, for instance, that Fig. 2 is calculated from an environment which one biologist considers to be a checkerboard of one acre squares of types A, B, C, D, ... in decreasing order of preference. A second biologist classifies the same environment into quarter acre squares, those formerly labelled B now being of types b_1, b_2, b_3, b_4 and so on. Assuming all a's are still preferable to all b's and these to all c's, then Fig. 2 remains unchanged except that the abscissa should be four times as finely subdivided. Point b_4 will coincide with B, c_4 with C and so on, and the optimal strategy will be essentially independent of the fineness of the subdivision. If there were inverted rankings (say $b_1 < b_2 < c_1 < b_3$....) then there will be changes in the optimal strategy, but these will reflect real differences in food concentration and are not simply artifacts of the naming of patches.

Our conclusions may be summarized by Table 1.

SUMMARY

A graphical method is discussed which allows a specification of the optimal diet of a predator in terms of the net amount of energy gained from a capture of prey as compared to the energy expended in searching for the prey.

The method allows several predictions about changes in the degree of specialization of the diet as the numbers of different prey organisms change. For example, a more productive environment should lead to more restricted diet in numbers of different species eaten. In a patchy environment, however, this will not apply to predators that spend most of their time searching. Moreover, larger patches are used in a more specialized way than smaller patches.

TABLE 1

Factors favoring increased specilization

Of diet	Of patches
Leave ΔP constant, but lower ΔS curve	Leave ΔH constant, but lower ΔT curve
1. Greater food density	1. Greater food density (pursuing species only*)
2. Increased mobility of animal, or decreased environmental resistance to movement, etc.	2. Increased mobility of animal, or decreased environmental resistance to movement, more contiguous patch structure, etc.
	3. Increased patch size relative to organism's size (less pronounced in territorial forms)
Leave ΔS constant, but raise ΔP curve	Leave ΔT constant, but raise ΔH curve
1. Increased differences between prey types, or increased specialization of pursuing behavior	1. Increased differences between patch types (or sizes), or more restricted hunting technique
2. Increased mobility of prey, or greater difficulty in pursuit	2. Increased mobility of prey, or greater difficulty of capturing it
	3. Reduction of food density in some patches by competition

*The hunting time is only independent of food density if it is all pursuit time and none search. The extent to which this is approximated determines our confidence in this effect.

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