

Optimal Foraging, the Marginal Value Theorem

ERIC L. CHARNOV*

*Center for Quan. Science in Forestry, Fisheries, and Wildlife,
University of Washington, Seattle, Washington 98195; and
Institute of Animal Resource Ecology UBC, Vancouver 8, Canada*

Received December 26, 1974

There has been much recent work on foraging that derives hypotheses from the assumption that animals are in some way optimizing in their foraging activities. Useful reviews may be found in Krebs (1973) or Schoener (1971). The problems considered usually relate to breadth of diet (Schoener, 1969, 1971; Emlen 1966; MacArthur, 1972; MacArthur and Pianka, 1966; Marten, 1973; Pulliam, 1974; Werner, 1974; Werner and Hall, 1974; Timmins, 1973; Pearson, 1974; Rapport, 1971; Charnov, 1973, 1976; Eggers, 1975), strategies of movement (Cody, 1971; Pyke, 1974; Smith, 1974a, b; Ware, 1975), or use of a patchy environment (Royama, 1970; MacArthur and Pianka, 1966; Pulliam, 1974; Smith and Dawkins, 1971; Tullock, 1970; Emlen, 1973; Krebs, 1973; Krebs, Ryan, and Charnov, 1974; Charnov, Orians, and Hyatt, 1976). The above list of references is provided as a beginning to this fast expanding literature and is far from exhaustive.

This paper will develop a model for the use of a "patchy habitat" by an optimal predator. The general problem may be stated as follows. Food is found in clumps or patches. The predator encounters food items within a patch but spends time in traveling between patches. This is schematically shown in Fig. 1. The predator must make decisions as to which patch types it will visit and when it will leave the patch it is presently in. This paper will focus on the second question. An important assumption of the model is that while the predator is in a patch, its food intake rate for that patch decreases with time spent there. The predator *depresses* (Charnov, Orians, and Hyatt, 1976) the availability of food to itself so that the amount of food gained for T time spent in a patch of type i is $h_i(T)$, where the function rises to an asymptote. A hypothetical example is shown in Fig. 2. While it is not necessary that the first derivative of $h_i(T)$ be decreasing for all T (it might be increasing at first if the predator scares up prey upon arrival in a new patch), I will limit discussion to this case since more

* (Present Address) Department of Biology, University of Utah, Salt Lake City, Utah 84112.

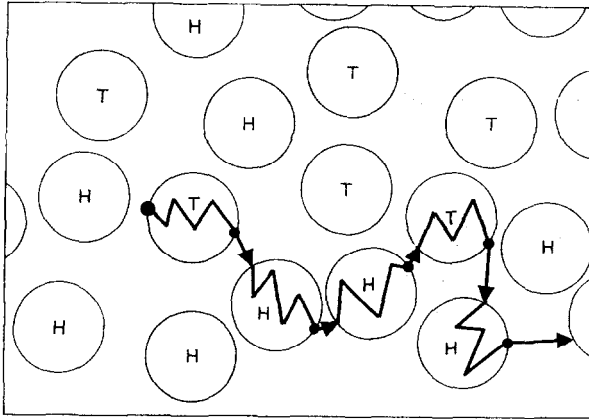


FIG. 1. A hypothetical environment of two patch types. The predator encounters prey only within a patch, but spends time in traveling between patches. Patches were labeled *H* or *T* by the flip of a coin.

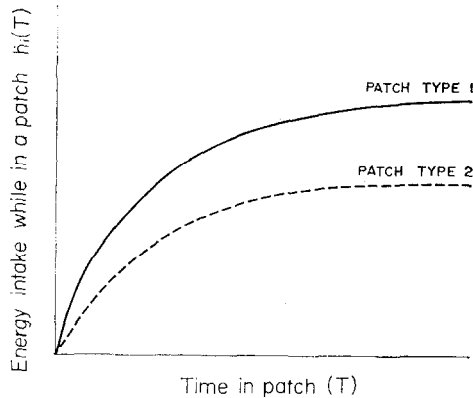


FIG. 2. The energy intake for T time spent in a patch of type i is given by $h_i(T)$. This function is assumed to rise to an asymptote.

complex functions add essentially nothing new to the major conclusions. The model is also completely deterministic, but this is not a major restriction since qualitatively similar results may be shown to follow from a corresponding stochastic model that considers the foraging as a cumulative renewal process (Charnov 1973 and in preparation). What is important is that if the environment is made up of several "patch types," the types be "mixed up" or rather distributed at random relative to one another (Fig. 1), and that many separate patches are visited in a single foraging bout with little or no revisitation. A patch type has associated with it a particular $h_i(T)$ curve. MacArthur (1972) has termed these

assumptions "a repeating environment." One final assumption is necessary. The predator is assumed to make decisions so as to maximize the net rate of energy intake during a foraging bout.

The patch use model

We define as follows:

P_i = proportion of the visited patches that are of type i ($i = 1, 2, \dots, k$).

E_T = energy cost per unit time in traveling between patches.

E_{si} = energy cost per unit time while searching in a patch of type i .

$h_i(T)$ = assimilated energy from hunting for T time units in a patch of type i minus all energy costs except the cost of searching.

$g_i(T) = h_i(T) - E_{si} \cdot T$ = assimilated energy corrected for the cost of searching.

The time for a predator to use a single patch is the interpatch travel time (t) plus the time in the patch. Let T_u be the average time to use one patch.

$$T_u = t + \sum P_i \cdot T_i.$$

T is now written as T_i to indicate that it may be different for each patch type. The average energy from a patch is E_e .

$$E_e = \sum P_i \cdot g_i(T_i).$$

The net energy intake rate (En) is given by:

$$En = \frac{E_e - t \cdot E_T}{T_u}. \quad (1)$$

En may thus be written as

$$En = \frac{\sum P_i \cdot g_i(T_i) - t \cdot E_T}{t + \sum P_i \cdot T_i}. \quad (2)$$

It is easy to show that (2) is an energy balance equation and that En is the net rate of energy intake. With suitable interpretation of $g_i(T_i)$, (2) is identical to Schoener (1971, Eq. (2)).

The predator is assumed to control which patches it will visit and when it will leave a patch. The t is obviously a function of which patches the predator is visiting and in general should increase as more patch types are skipped over. A simple assumption would have t proportional to the distance between patches divided by the predators speed of movement. It should be noted, however, that there is no good reason to believe that t should be at all related to any of the T_i . The length of time between patches should be independent of length of time the predator hunts within any one (although the reverse statement is not true).

This independence is quite important since when it holds, (2) may be written (from the standpoint of a patch type of interest j) as:

$$En = \frac{P_j \cdot g_j(T_j) + A}{P_j \cdot T_j + B}, \quad (3)$$

where A and B are not functions of T_j . A and B are found by equating terms in (2) and (3), naming one patch type as j .

If j is being visited, the predator is assumed to control only T_j . The optimal value of T_j is given by a rather interesting theorem. For some set of patches being visited, write En as En^* when all T_i are at their optimal values. When this is true T_j satisfies the following relation.

$$\frac{\partial g_j(T_j)}{\partial T_j} = En^*, \quad \text{for all } i = j. \quad (4)$$

The predator should leave the patch it is presently in when the *marginal capture rate in the patch* ($\partial g/\partial T$) drops to the *average capture rate for the habitat*.

This rule is found by setting $\partial En/\partial T_i = 0$ for all patch types simultaneously. Since we are assuming here that the $\partial h_i(T_i)/\partial T_i$ are always decreasing, so are the $\partial g_i(T_i)/\partial T_i$ and there is a unique set of T_i that fulfills (4). This set represents a maximum as the associated Hessian matrix is negative-definite (Taha, 1971).

A graphical way of showing this result is in Fig. 3. The $g_i(T_i)$ is plotted as a

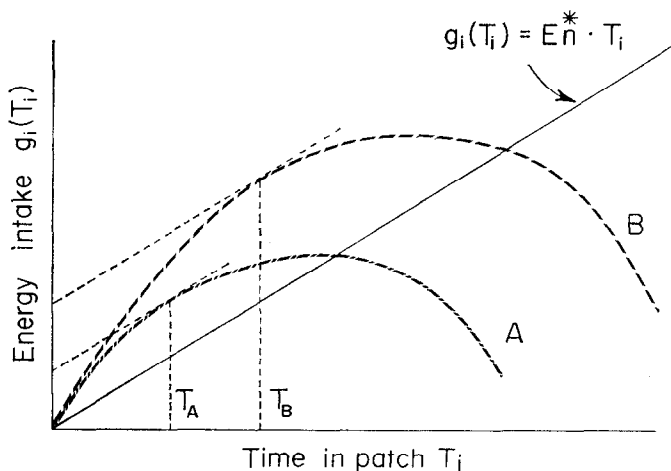


FIG. 3. Optimal use of a patchy habitat. The energy intake functions $g_i(T_i)$, are shown for a habitat with two patch types. If the ray from the origin with slope En^* is plotted, the appropriate time to spend in each patch is found by constructing the *highest* line tangent to a $g_i(T_i)$ curve and parallel to the ray. The lines and the resulting times are shown for the two patch types.

function of T_i for two patch types. If a ray from the origin with slope En^* is then plotted, the optimal T_i are easily found. To find these, simply construct lines with slope En^* and see where they become tangent to the appropriate $g_i(T_i)$ curve. In cases where the $\partial g_i(T_i)/\partial T_i$ are not strictly decreasing with T_i , more than one point of tangency may result. In these cases, the optimal T_i is that associated with the highest line of slope En^* .

DISCUSSION

Two earlier publications (Krebs, Ryan, and Charnov, 1974; Charnov, Orians, and Hyatt, 1976) derived a simplified version of the movement rule given in (4) and discussed some supporting data. Krebs, Ryan, and Charnov 1974 carried out laboratory experiments with chickadees to qualitatively test (4). They defined the time between the last capture and when an individual left a patch (several blocks of wood with mealworms in holes, suspended from an artificial tree) to go to another patch as the "giving up time" (GUT). This was taken to be a measure of the inverse of the capture rate when the bird left the patch (the marginal capture rate). The experimental design consisted of two environments. In the first, the average rate of food intake was high, in the second, it was low. Within each environment there were two or three patch types, each type having a specified number of mealworms. The predictions of the theorem, translated into the GUT measurement, were that (1) GUT should be a constant within an environment across patch types, and (2) GUT should be lower in the rich environment. Both of these predictions were supported by the data. More recent experiments using the Great Tit (*Parus major*) also support the model (R. Cowie, personal communication).

There are little other data that will allow more critical tests of the model although there are many data relating to gross predator behavior relative to clumps of prey. Smith (1974a, b), in some field experiments with thrushes, found that the tendency of a bird to remain in the area where it had already made a capture was greater the lower the overall availability of food in the habitat. The simple tendency for a predator to remain in the area where it was successful has been documented for birds (Tinbergen, Impekovon, and Frank, 1967; Krebs, MacRoberts, and Cullen, 1972); fish (Beukema, 1968); insects (Hafez, 1961; Fleschner, 1950; Laing, 1938; Mitchell, 1963; Dixon, 1959, 1970; Banks, 1957; Richerson and Borden, 1972; Hassell and May, 1973; Murdie and Hassell, 1973). Even unicellular predators exhibit increased frequency of turning following an encounter with food particles, a behavior pattern that results in a more intensive search of the vicinity of the capture (Fraenkel and Gunn, 1940; MacNab and Koshland, 1972).

The rule was used in a slightly different context by Parker and Stuart (1976),

whose derivation is independent of the work here. They showed that male dung flies (*Scatophaga stercoraria*) terminate copulation at a time that maximizes the eggs fertilized/unit time for the male.

CONCLUSIONS

A rule is proposed for the movement of an optimal predator through an environment where food is found in patches, and time is expended in movement between patches. The theorem is rather general and should be useful where predators cause the prey in their immediate vicinity to become less available the longer they remain there. It receives some support from both lab and field studies, but has yet to be tested in a quantitative manner.

ACKNOWLEDGMENTS

The ideas presented here have been drawn from a thesis presented to the University of Washington. The thesis work was generously supported by the Ford Foundation (UW) and by funds supplied by the Institute of Animal Resource Ecology (University of British Columbia). I wish to thank D. G. Chapman, W. H. Hatheway, N. Pearson, C. Fowler, C. S. Holling, J. Krebs, G. Pyke, Thomas Schoener, and G. A. Parker. Gordon Orians provided his usual creative input.

REFERENCES

- BANKS, C. J. 1957. The behavior of individual coccinellid larvae on plants, *J. Anim. Behav.* 5, 12-24.
- BEUKEMA, J. J. 1968. Predation by the three-spined stickleback (*Gasterosteus aculeatus*). The influence of hunger and experience, *Behavior* 31, 1-126.
- CHARNOV, E. L. 1973. Optimal foraging: some theoretical explorations, Ph. D. Thesis, Univ. of Wash.
- CHARNOV, E. L. 1976. Optimal foraging: attack strategy of a mantid, *Amer. Natur.* to appear.
- CHARNOV, E. L., ORIAN, G. H., AND HYATT, K. 1976. Ecological implications of resource depression, *Amer. Natur.* to appear.
- CODY, M. L. 1971. Finch flocks in the Mohave desert, *Theor. Popul. Biol.* 2, 142-158.
- DIXON, A. F. G. 1959. An experimental study of the searching behavior of the predatory coccinellid beetle *Adalia decempunctata*, *J. Anim. Ecol.* 28, 259-281.
- DIXON, A. F. G. 1970. Factors limiting the effectiveness of the coccinellid beetle, *Adalia bipunctata*, as a predator of the sycamore aphid, *Depanosiphum platonoides*, *J. Anim. Ecol.* 39, 739-751.
- EGGERS, D. M. 1975. A synthesis of the feeding behavior and growth of juvenile sockeye salmon in the limnetic environment, Ph. D. Thesis, Univ. of Wash.
- EMLEN, J. M. 1966. The role of time and energy in food preference, *Amer. Natur.* 100, 611-617.

- EMLEN, J. M. 1973. "Ecology; An Evolutionary Approach," p. 493. Addison-Wesley, Reading, Mass.
- FLESCNER, C. A. 1950. Studies on search capacity of the larvae of three predators of the citrus red mite, *Hilgardia* 20, 233-265.
- FRAENKEL, G. S. AND GUNN, D. L. 1940. "The Orientation of Animals," Oxford Book, New York.
- HAFEZ, M. 1961. Seasonal fluctuations of population density of the cabbage aphid *Brevicoryne brassicae* (L.) in the Netherlands and the role of its parasite *Aphidius* (*Diaretiella*) *rapae* (Curtis), *Tijdschr. Plantenziekten.* 67, 445-548.
- HASSELL, M. P. AND MAY, R. M. 1973. Stability in insect host-parasite models, *J. Anim. Ecol.* 42, 693-726.
- KREBS, J. R. 1973. Behavioral aspects of predation, in "Perspectives in Ethology," (Bateson, P. P. G., and Klopfer, P. H., Eds.), pp. 73-111. Plenum, New York.
- KREBS, J. R., MACROBERTS, M. H., AND CULLEN, J. M. 1972. Flocking and feeding in the Great Tit, *Parus major*, an experimental study, *Ibis* 114, 507-530.
- KREBS, J. R., RYAN, J. C., AND CHARNOV, E. L. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees, *J. Anim. Behav.* 22, 953-964.
- LAING, J. 1938. Host finding by insect parasites. II. The chance of *Trichogramma vanescens* finding its hosts, *J. Exp. Biol.* 15, 281-302.
- MACARTHUR, R. H. 1972. "Geographical Ecology," p. 269. Harper and Row, New York.
- MACARTHUR, R. H. AND PIANKA, E. R. 1966. On optimal use of a patchy environment, *Amer. Natur.* 100, 603-609.
- MACNAB, R. M. AND KOSHLAND, D. E. 1972. The gradient-sensing mechanism in bacterial chemotaxis, *PNAS* 69, 2509-2512.
- MARTEN, G. 1973. An optimization equation for predation, *Ecology* 54, 92-101.
- MAYNARD SMITH, J. 1974. "Models in Ecology," p. 146. Cambridge Univ. Press, London/New York.
- MITCHELL, B. 1963. Ecology of two carabid beetles, *Bembidion lampros* and *Trechus quadristriatus*, *J. Anim. Ecol.* 32, 289-299.
- MURDIE, G. AND HASSELL, M. P. 1973. Food distribution, searching success, and predator-prey models, in "The Mathematical Theory of the Dynamics of Biological Populations," (Barlett, M. S. and Hiorns, R. W. (Eds.), Academic Press, New York/London.
- PARKER, G. A. AND STUART, R. A. 1976. Animal behaviour as a strategy optimizer: evolution of resource assessment strategies and optimal emigration thresholds, *Amer. Natur.* to appear.
- PEARSON, N. E. 1974. Optimal foraging theory, Quon. Science Paper No. 39, Center for Quon. Science in Forestry, Fisheries and Wildlife. Univ. of Washington, Seattle, Washington 98195.
- PULLIAM, H. R. 1974. On the theory of optimal diets, *Amer. Natur.* 108, 59-74.
- PYKE, G. H. 1974. Studies in the foraging efficiency of animals, Ph. D. Thesis, Univ of Chicago.
- RAPPORT, D. J. 1971. An optimization model of food selection, *Amer. Natur.* 105, 575-587.
- RICHERSON, J. V. AND BORDEN, J. H. 1972. Host finding of *Coeloides brunneri* (Hymenoptera: Braconidae), *Canad. Entomol.* 104, 1235-1250.
- ROYAMA, T. 1970. Factors governing the hunting behavior and selection of food by the Great Tit, *Parus major*, *J. Anim. Ecol.* 39, 619-668.
- SCHOENER, T. W. 1969. Models of optimal size for a solitary predator, *Amer. Natur.* 103, 277-313.
- SCHOENER, T. W. 1971. Theory of feeding strategies, *Ann. Rev. Ecol. Syst.* 2, 369-404.

- SMITH, J. N. M. 1974. The food searching behavior of two European thrushes. I. Description and analyses of the search paths, *Behavior* **48**, 276-302; II. The adaptiveness of the search patterns, *Behavior* **49**, 1-61.
- SMITH, J. N. M. AND DAWKINS, C. R. 1971. The hunting behaviour of individual Great Tits in relation to spatial variations in their food density, *Anim. Behav.* **19**, 695-706.
- TAHA, H. A. 1971. "Operations Research," p. 703. Macmillan, New York.
- TIMIN, M. E. 1973. A multi-species consumption model, *Math. Biosci.* **16**, 59-66.
- TINBERGEN, N., IMPEKOVEN, M., AND FRANCK, D. 1967. An experiment on spacing-out as a defense against predation, *Behavior* **38**, 307-321.
- TULLOCK, G. 1970. The coal tit as a careful shopper, *Amer. Natur.* **104**, 77-80.
- WARE, D. M. 1975. Growth, metabolism and optimal swimming speed in a pelagic fish, *J. Fish Res. Bd. Canad.* **32**, 33-41.
- WERNER, E. E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. *J. Fish Res. Bd. Canad.* **31**, 153-1536.
- WERNER, E. E. AND HALL, D. J. 1974. Optimal foraging and size selection of prey by the bluegill sunfish (*Lepomis mochochirus*), *Ecology* **55**, 1042-1052.