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Source: *The American Naturalist*, Vol. 131, No. 6 (Jun., 1988), pp. 837-846

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/2461816>

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OPTIMAL FORAGING ON ARBITRARY FOOD DISTRIBUTIONS AND THE DEFINITION OF HABITAT PATCHES

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Submitted October 14, 1986; Revised May 18, 1987; Accepted August 17, 1987

Since its conception (MacArthur and Pianka 1966), one of the main problems of optimal foraging theory is the way in which an animal allocates its feeding activity in space and time, assuming that it maximizes the food intake. (We do not consider here the problem of diet optimization.) Most theoretical and empirical work has concentrated on behavioral studies of animals facing distributions of food in distinct patches (reviews in Krebs et al. 1983; Pyke 1984). However, as pointed out by Lessells and Stephens (1983), the assumption of patchy distribution is often not acceptable. In the strict sense used in theoretical models, a patch is a well-delimited area within which food is uniformly distributed, with no food in the surrounding area. Consequently, the foraging animal is assumed to exhibit two distinct patterns of behavior: traveling between patches, and feeding within patches. This is true sometimes, but animals often combine traveling and feeding when they move across their habitat, as in the example of an antelope grazing in the African savanna (Krebs and McCleery 1984). In such cases, the delimitation of patches is impossible.

It is therefore necessary to develop a theory for non-patchy habitats. A few studies (e.g., Andersson 1978) have assumed that the food is uniformly distributed. In the present paper, we totally renounce any particular assumption about the nature of the spatial distribution of the food resource. As special cases, distribution can be patchy or uniform, but we can deal with any complex type of heterogeneous distribution.

The classical model for the optimal exploitation of food patches is the "marginal-value theorem" (MVT) of Charnov (1976). It assumes that the forager successively encounters equidistant patches, which it should deplete until the marginal return rate equals the overall average return rate. In this paper, we present two variants of a model that generalizes the MVT to arbitrary habitats. This new model describes the optimal allocation of time to each *point* of the habitat.

In the general two- or three-dimensional situation (fig. 1), the optimal strategy

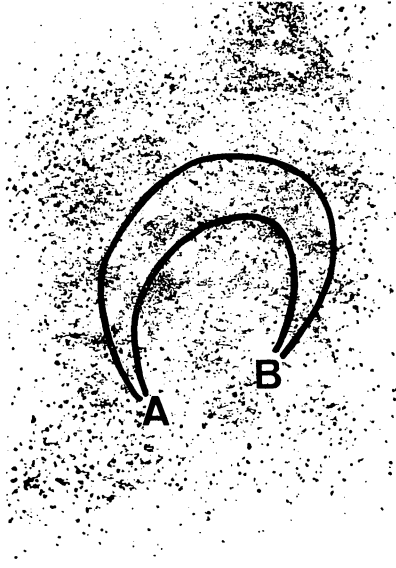


FIG. 1.—The general two-dimensional problem. This figure presents a food resource with an arbitrary spatial distribution, with two possible trajectories of an animal going from A to B in the available foraging time, T . The strategy that maximizes the energy collected must be described (1) by the geometrical path, (2) by the schedule along the path.

must be described in two ways: on the one hand, by the geometry of the path of the animal; and, on the other hand, by the duration of presence at each point along this path. This problem presents serious mathematical difficulties. Considering a one-dimensional habitat, as a first approach, simplifies the problem, since the path becomes identical to the habitat. One-dimensional situations are not uncommon: many species of birds and small mammals live in hedges or along rivers and river banks to which they exhibit a strong fidelity. Shorebirds, also, are often restricted to specific portions of the shores of lakes and seas. In most of these cases, the habitat can be safely modeled as one-dimensional if at any time that animal has simultaneous access to the whole width of it.

The full mathematical details of our model have already been published (Arditi and Dacorogna 1985, 1987). In this paper, we start by summarizing the previous work, in a form that will assist the nonmathematical reader. We also attempt to make our assumptions as explicit and biologically relevant as possible. We then show that this model of the behavior of individuals can be extended to model the distribution of a population. We discuss thereafter the relevance of published field studies to the model's predictions. Finally, the model points to some difficulties that arise when patches need to be defined operationally.

ASSUMPTIONS OF THE MODEL

The distribution of the food density can be represented by any function $\rho(x)$ (fig. 2). In the first variant of the model, we assume that the habitat is bounded, for

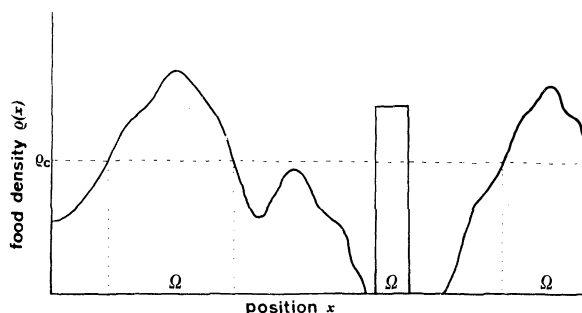


FIG. 2.—The one-dimensional problem. Given an arbitrary function for the food distribution, $\rho(x)$, how should the animal allocate its feeding activity in space? The optimal strategy is that of equalizing the food density to a critical value ρ_c determined by the behavioral parameters and the food distribution. Where the available density is lower than this threshold, the animal must travel as fast as possible, without eating. In this example, the distribution has discontinuities, with one strict “patch” in the middle.

example, by neighboring individuals or by physical obstacles. In the second variant, we assume that the habitat is unbounded and that the extent of the feeding range is also subject to optimization.

In Schoener’s (1983) classification, the animal is assumed to be a “time-constrained energy maximizer”: the currency is taken as the total energy acquired during a fixed foraging time T , and the animal is assumed to know the food distribution beforehand. The animal can be required to return to its starting place, but this assumption has no effect on the qualitative predictions of the model.

It is assumed that the velocity has an upper bound, β , set by physiological limits, and that a “detection section” r is attached to the animal (Andersson 1978). If it moves at point x at maximum velocity, β , this point remains within the section for the duration r/β . This represents, therefore, the time that the animal must spend to pass each point. If the velocity is $v(x)$, slower than β , the animal spends some extra time $\tau(x)$ at point x :

$$\tau(x) = r/v(x) - r/\beta. \quad (1)$$

It is assumed that the animal feeds during this time $\tau(x)$. In this way, the classical distinction between travel time and feeding time is transposed to the infinitesimal scale.

The functional response (rate of food intake as a function of food density) can be any strictly increasing function; it cannot belong to the rare domed type (Holling 1961). For mathematical convenience, the simple linear Lotka-Volterra functional response is used here: at point x , the rate of feeding is $a\rho(x)$, where a is the attack efficiency. During the time that the animal spends at this point, $\tau(x)$, the density decreases exponentially at this same rate, and the energy gained at x is finally

$$g(x) = \rho(x)(1 - e^{-a\tau(x)}). \quad (2)$$

The problem is then to find, out of all possible functions τ , the function $\bar{\tau}$ that maximizes the gain over the whole traversed habitat:

$$\bar{\tau} = \max_{\tau} \int_0^{\bar{x}} g(x) dx, \quad (3)$$

where \bar{x} is the point at which the animal stops foraging. This point is set to the fixed value 1 in the bounded model; in the unbounded model, it is left free and the optimal value must be determined.

The maximization (3) is subject to the constraint that the total time needed to reach \bar{x} is the available foraging time T :

$$\int_0^{\bar{x}} \frac{1}{v(x)} dx = T. \quad (4)$$

Costs of basal metabolism, searching, handling, and locomotion can be subtracted from $g(x)$; but we have shown (Arditi and Dacorogna 1985) that this does not change the formal nature of problem (3) and (4).

RESULTS

The Optimal Strategy

We have solved the problem with the purely analytical methods of the branch of mathematics known as the "calculus of variations." The solution can be computed explicitly, but it is possible to express it only by rather complex equations (Arditi and Dacorogna 1985, 1987). The optimal strategy works as follows. The four behavioral parameters a , r , β , and T , together with the food distribution $\rho(x)$, determine the stopping point \bar{x} (in the unbounded model) and a critical density ρ_c . This critical density separates the habitat into two subsets: a richer subset Ω , where the food density is higher than ρ_c , and a poorer subset Ω^c , where it is lower. In Ω , the feeding time spent at each point is what is necessary for reducing the food density to the value ρ_c . In Ω^c , the animal moves at maximum velocity β without eating (fig. 2). In other terms, the animal's behavior changes from pure travel to mixed travel and feeding when the food density exceeds the threshold, ρ_c . The relative importance of the feeding activity is then proportional to local richness.

Generalization of the Marginal-Value Theorem

This model is, in essence, an extension of the MVT to arbitrary habitats. Although it was represented on a two-dimensional figure (Charnov 1976), the original theorem is, in fact, a one-dimensional model, since the animal is assumed to encounter patches successively with equal travel times and with no revisitation; the path of the animal can therefore be "unwound" on a straight line with no loss of generality. A further generalization lies in the MVT's implicit assumption that the foraging time, as well as the number of patches, is infinite; these can be finite in the present model. Under the MVT prediction, the length of time that an animal

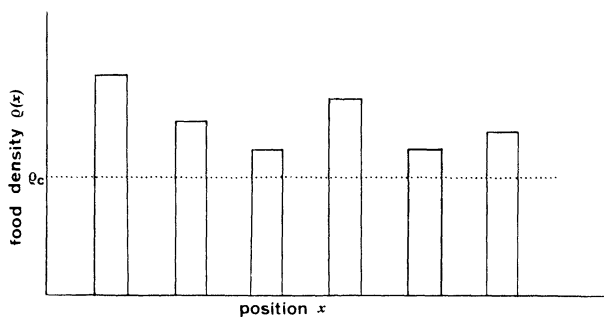


FIG. 3.—The special case of a patchy food distribution. If the habitat is made up of equidistant patches and if the foraging time tends to infinity, the optimal solution becomes identical to the familiar marginal-value theorem (Charnov 1976).

should spend in each patch is such that it renders the marginal return rate equal to the average return rate of the habitat. If the same functional response applies in all patches, as in the present case, the theorem predicts that the patch richness itself will be equalized. For the special case in which the function $\rho(x)$ is taken as an unlimited series of equally spaced patches (fig. 3), it can be proved that the unbounded version of the new model predicts the same strategy as the MVT when the foraging time, T , tends to infinity.

Distribution in Time

Time is also an ecological variable that is, of course, one-dimensional. For cases in which the food density varies in time rather than space, the model can easily be reinterpreted to describe the optimal allocation of foraging effort, if it is assumed that the animal has a fixed total foraging effort to spend.

Population Distribution

The model can also be used to describe the distribution of the population density rather than the distribution of an individual's foraging activity. This can be accomplished in much the same way as the construction of the well-known "ideal free distribution." This model (Fretwell 1972) predicts the distribution of individuals among habitat patches of different "suitabilities." It does not assume that exploitation depletes the habitat in the course of time, but instead that the suitability decreases with increasing consumer density. The patch suitability can therefore be seen as the per capita rate of food supply in the patch. The individuals are assumed to move freely and do not interact directly. If all individuals are assumed to maximize the energy gain, it was shown that they aggregate in the richer patches until the marginal suitability equals the average. This model is, in fact, the strict analogue of the MVT for population distribution rather than foraging distribution. This analogy may make a change of scale necessary, since the grain of the environment of individuals is not necessarily the same as that of populations.

In exactly the same way, and with the same general assumptions, our model can be reinterpreted to describe the distribution of a population in an environment

where the rate of food production per unit of length $\sigma(x)$ is an arbitrary function of space. The model predicts then that individuals will aggregate in the places where this rate is higher than some threshold; in these places, the density of individuals will follow the spatial variations of food production.

DISCUSSION

Testing the Behavioral Model

The present model shares a common assumption with several others, in that the animal has perfect prior knowledge of the abundance and distribution of food. Therefore, it can apply only to animals repeatedly exploiting an environment that is regularly renewed.

To the best of our knowledge, no laboratory tests have yet been performed in non-patchy conditions, although ample experimental evidence for differential use of patchy environments has accumulated since the early papers on foraging (e.g., Smith and Dawkins 1971; Smith and Sweatman 1974). Any experiment devised to test the model should create a food distribution with distinctive non-patchy and nonuniform patterns, with the certainty that they will be perceived as such by the animal. In the absence of such experiments, field studies can be relevant if they provide two pieces of information: the food distribution on the one hand, and the distribution of the foraging effort of consumers on the other hand.

To test the model, it is also essential to assess the food distribution independently of the observation of the consumer's strategy. This estimate must be made in all parts of the animal's home range, including the places where it does not feed. Figure 2 shows that predicted feeding can be zero in places where the food density is not zero, because the optimal strategy is characterized by a threshold effect.

This is an important qualitative feature of the model that can be tested in favorable cases. Threshold effects are often predicted by optimal foraging models but rarely observed directly because many factors can conceal the basic all-or-nothing phenomenon (Krebs and McCleery 1984; Avery 1985; Krebs and Avery 1985). However, in a recent field study on the bat *Pipistrellus pipistrellus*, Racey and Swift (1985) observed that, when food density was monitored throughout an entire night, the foraging effort of lactating females followed the variations of insect density, with an abrupt discontinuance below a critical value. This pattern is very similar to that of figure 2, except that it varies in time rather than space. As mentioned earlier, our model is easily adapted to this situation and therefore gives qualitative agreement. If the feeding rate is plotted as a response to food density, the model predicts a step at ρ_c (fig. 4). The same field study reports for pregnant females a clear illustration of a similar response (type II), with a distinct threshold. The authors were able to determine that bats did not remain in areas where insect densities were lower than the threshold.

The studies of Goss-Custard (1970, 1977) on the redshank, *Tringa totanus*, of Goss-Custard et al. (1982) on the oystercatcher, *Haematopus ostralegus*, and of Zach and Falls (1975, 1979) and Zach and Smith (1981) on the ovenbird, *Seiurus aurocapillus*, also showed that birds in the wild tend to make a differential use of their habitat according to prey distribution, with some indication of a lower

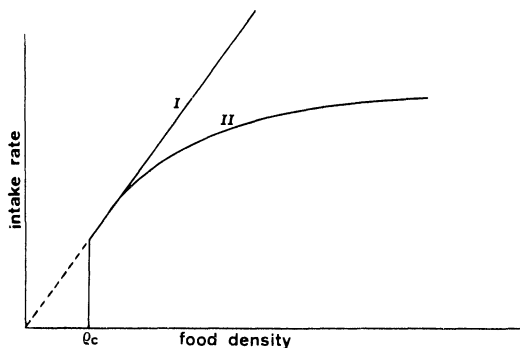


FIG. 4.—The optimal strategy predicts that the response of the intake rate to food density must present a step at ρ_c . *Broken curve*, intrinsic functional response; *solid curve*, optimal response. I, response of type I; II, response of type II.

threshold. However, these studies show that field estimates of food availability can be very delicate and difficult. What is relevant to energy maximization is not the standing density but rather the acquisition rate, which is related to the density by some law of return. Our model uses the density only with the assumption that the same return law applies in all parts of the environment. In field studies, differences in terrain or in prey types must be taken into account to “rescale” the food abundance so that it is measured as a common unit of return. Moreover, this measurement must be made “from the animal’s point of view” (Pyke 1984, p. 554). This is the source of major difficulties because many additional factors must be known. These include the nature of the different potential prey, their nutritional values, their handling times, and their accessibility.

The second piece of information necessary to test the model—the distribution of foraging effort—can be derived from studies of home ranges (Don and Rennolls 1983). Modern studies not only describe sizes and shapes of ranges but also make quantitative estimates of the “utilization distribution” (Van Winkle 1975). Of course, foraging is not the only determinant of space use, and due account must be taken of other factors such as social interaction and predator avoidance. However, foraging behavior can be assumed to be the primary factor for animals under critical energy conditions and low predation risk as, for example, in the aforementioned case of the pipistrelle bat. Mace et al. (1983) suggested that this assumption might hold for many adult female mammals. Home-range use has been quantified for many species of mammals ranging from the black bear, *Ursus americanus* (see Samuel et al. 1985), and the fox *Vulpes vulpes* (see Ables 1969) to the chipmunk *Tamias striatus* (see Getty 1981), the mole *Talpa europea* (see Stone 1986), and soricids (Genoud 1981). Some studies even deal with one-dimensional habitats, such as a hedge for the shrew *Crocidura russula* (see Ricci and Vogel 1984) or a river for the desman *Galemys pyrenaicus* (see Stone and Gorman 1985) and the water shrew *Neomys fodiens* (see Lardet 1987).

On the Definition of Habitat Patches

Covich (1976) noted that many species can impose a high degree of behavioral complexity on relatively homogeneous habitats, such as the arctic tundra or the

benthos of large lakes. Given the assumptions of the present model, figure 2 also shows that the distribution of the feeding activity can appear to be patchy (i.e., discontinuous) although the food abundance varies in a continuous manner. This phenomenon touches the problem of the assessment of habitat patchiness.

In a review of this question, Wiens (1976) insisted that patchiness must be considered in terms of the perceptions of the animal rather than of those of the investigator. Ultimately, patches should be delineated by measuring fitness differentials. Since this task is difficult, if not impossible, Wiens suggested defining patches operationally, "in terms of nonrandom distributions of activity or resource utilization" (p. 84). That is, the patchiness of the habitat would be assessed by the patchiness of the distribution of consumers. This method emphasizes the "animal's point of view," but patches so defined can be very different from the usual acceptance of this concept. As already pointed out, figure 2 shows that a "patchy" distribution of consumption may well be compatible with a continuous distribution of the food resource. This example also shows that, if the foraging time, T , were slightly higher, ρ_c would be lower, and consumption would present one more "patch," although the food distribution would remain unchanged. With this definition, "patches" are therefore the result of the complex interactions among several factors: the food distribution; an internal factor, the animal's morphological and physiological needs and capabilities; and the ecological factors determining the foraging time.

SUMMARY

Most models for the optimal allocation of foraging effort in space and time assume that food is distributed in distinct patches. This assumption is often not justified. The problem, therefore, is in finding the optimal strategy for an animal exploiting a resource with an arbitrary spatial distribution, whether or not it is patchy. In this paper, we deal with the situation of a one-dimensional habitat. The model describes the optimal allocation of time to each point of the habitat. It is a generalization to arbitrary habitats of the classical "marginal-value theorem," which is obtained as the special case of an infinite environment with equally spaced patches. The model can also be extended to describe the optimal distribution of a population, thereby generalizing the "ideal free distribution." The model predicts that foraging should be restricted to places where food availability is higher than some threshold. In these places only, the foraging activity should follow the spatial variations in richness. A field study on insectivorous bats illustrates the model's predictions. Finally, the model points to the difficulty of delimiting food patches when they need to be defined operationally, because a "patchy" distribution of consumers can overlies a continuous food distribution.

ACKNOWLEDGMENTS

We thank B. Botteron, M. Genoud, L. R. Ginzburg, M. Milinski, N. Perrin, D. Slice, L. B. Slobodkin, and especially R. D. Stone for help, discussions, and editorial comments. This work was supported at various stages by the Swiss

National Foundation for Scientific Research (grants 3.263.82, 2.727.85, and 3.152.85). The revision was prepared at the State University of New York at Stony Brook while R.A. was holding the Félix Bonjour fellowship awarded by the Société Académique Vaudoise.

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