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OPPORTUNITY-COST FORAGING MODELS FOR STATIONARY AND MOBILE PREDATORS

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Here I develop an extension of optimal foraging theory by relating diet breadth decisions to other fitness-enhancing activities through the concept of opportunity costs.

Optimal foraging theory guides current ecological research on the feeding behaviors of predators (reviews in Orians 1971; Schoener 1971; Charnov and Orians 1973; Pyke et al. 1977; Krebs 1978; Hassell and Southwood 1978; see also Kamil and Sargent 1981). The analytic procedure involves (1) choice of a currency, a measurable parameter which is taken to be a direct proxy for fitness; (2) construction of a model based on cost-benefit functions which reflect constraints appropriate to an adaptive problem; and (3) solution for the optimal behavior (Schoener 1971, p. 369). Time and energy, expressed as an efficiency or net rate parameter, are the currencies most widely used (Smith 1979), although economic or linear programming models which consider nutrients and other food components are being applied to foraging behavior analysis (Altmann and Wagner 1978; Belovsky 1978; Westoby 1978; Rapport 1980; Keene 1981). The cost-benefit functions may consider diet breadth (Emlen 1966; MacArthur and Pianka 1966; Schoener 1969*a*, 1969*b*; Rapport 1971; Pulliam 1975, 1981*a*, 1981*b*; Norberg 1977; Hughes 1979; McNair 1979); use of patches or different habitats (Charnov 1976*b*; Charnov et al. 1976; Parker and Stuart 1976; Oaten 1977; Morrison 1978; Green 1980); foraging group size and use of space (Brown 1964; Horn 1968; Hamilton and Watt 1970; Covich 1976; Verner 1977; Dill 1978; Caraco 1979*a*, 1979*b*; Mitani and Rodman 1979; Orians and Pearson 1979); and foraging time period (Schoener 1974). Each of these functions is treated as one element in a "decision" hierarchy (Charnov and Orians 1973, pp. 9–10).

Hypotheses about adaptive behavior are based on the expectation that organisms will have evolved the ability to optimize their performance of fitness-enhancing activities relative to time and energy costs (Cody 1974; cf. Lewontin 1979; Maynard Smith 1978), and that the outcome of such a process can be investigated with simple models (Levins 1966). Limited confirmation of some predictions has been achieved in the laboratory (Charnov 1976*a*; Krebs and Cowie

1976; Werner and Hall 1979; Rapport 1980; Sih 1980) and in field studies (Belovsky 1981; Cowie 1977; Davies 1977), including some by anthropologists analyzing hunter-gatherer behavior (O'Connell and Hawkes 1981; Smith 1981; Winterhalder 1980, 1981; Hames and Vickers 1982; Hawkes et al. 1982).

Models of diet breadth based on simple time-energy currencies are used extensively in optimal foraging research. One type considers mobile, searching predators in a "fine-grained" (MacArthur and Pianka 1966) environment. The solution to this optimality model, expressed as a set of hypotheses, has been reached independently several times (Pyke et al. 1977, p. 141). The second model applies to stationary foragers, those which search without cost. Schoener (1974, p. 4170) has suggested that an organism of this type may be either a time minimizer or an energy maximizer. Hypotheses deriving from this model are based on the time-minimizer, energy-maximizer distinction. I will call these the searching and stationary models, respectively.

Here I present a graphical interpretation of foraging which can be adapted to each of these two models. It has several advantages: (1) It more explicitly recognizes that the time and energy costs and benefits accruing to foraging are "opportunity" costs and benefits. Thus, they can be assessed or have value to the organism only in relative terms, by their effects on fitness-related activities other than foraging. (2) It expands the concepts of time minimization and energy maximization by showing that these are end points of a more general measure, the fitness value to the organism of marginal trade-offs between time and energy. Given this operational meaning, these concepts apply to both searching and stationary foragers. (3) In some instances it extends predictions deriving from the searching and stationary diet-breadth models.

DEFINITIONS AND MODEL

Two initial concepts are necessary. The *opportunity cost* of an activity (A) is the value of some alternative foregone because resources are invested in (A) rather than the alternative (Mishan 1975). This concept assumes that resources are limited relative to potential uses, and that one among these alternative uses can be identified as the appropriate substitute measure. It also assumes that the potential courses of action are to be evaluated relative to one another. These assumptions are consistent with evolutionary ecology theory. The second concept, marginal value, recognizes that the cost of continuing to produce, or the value of continuing to consume, a good is likely to depend on the amount already produced or consumed. Thus, an economic decision to produce or consume each additional unit will focus on its marginal cost or marginal value, respectively. Similarly, the value or cost of an activity often changes as a function of its duration. Here an economic decision to cease or continue a particular behavior will focus on the value of the next, or marginal unit of that behavior. The marginal value theorem (Charnov 1976b) is an example of the usefulness of this concept; marginal value will be related to fitness isocline analysis below.

The basic model is presented graphically in figures 1–4. It occupies one quadrant of an x – y plane. Foraging activities are represented in the right portion of the

quadrant; all nonforaging activities in the left portion. The vertical axis on the right shows the net acquisition (E_a) of energy during foraging; the vertical axis on the left shows the energy expenditure (E_e) in nonforaging activities, subject to the constraint that $E_a = E_e$ for a given period. The horizontal axis to the right of the line ($P_C - P_C$) shows the time spent foraging (T_f); that to the left of the line ($P_A - P_C$) shows the time spent in nonforaging activities (T_{nf}). Note that foraging time is read from right to left beginning from the right axis; nonforaging time from left to right, beginning from the left axis. The horizontal axis is subject to the constraint that $T_f + T_{nf} = T_t$, where T_t represents an appropriate interval for analysis. This approach shares with others the assumption that foraging optimization can be studied over fairly short time periods (Katz 1974; Pyke et al. 1977, pp. 139–140).

Combinations of time (T_{nf}) and energy (E_e) used in nonforaging activities can be represented in this quadrant by isoclines which connect points of equal fitness. A point on this isocline map represents the weighted average of time-energy expenditures for a particular set of these nonforaging activities. These isoclines are similar to the indifference curves used in micro-economic analysis; isoclines have been used before in foraging studies by Rapport (1971, 1980) and Covich (1972, 1974). Using standard economic assumptions (see Stonier and Hague 1973), the isoclines are drawn convex to the origin, implying that the scarcer of two jointly used resources is likely to be the relatively more valuable. Thus, the marginal value of good or activity (A) increases, or what amounts to the same thing, its relative rate of substitution for (B) decreases, as the quantity of B grows. An organism with abundant nonforaging time, but insufficient energy, will probably value (in terms of fitness) an additional unit of energy more than one of time, and vice versa. Isoclines more distant from the origin have higher value.

Time and energy are both necessary for the performance of nonforaging activities, although not in fixed proportions. Hence, the fitness isoclines cannot cross either axis (E_e or T_{nf}). In Tilman's (1980) detailed terminology for indifference maps, to which the reader is referred, these are "interactive essential" resources. In figures 1–4 a straight line from the origin (0 to α) shows the minimum rate of energy expenditure compatible with survival (the resting or basal metabolic rate) as a function of time. Another (0 to β) shows the maximum physiological rate of energy expenditure possible for nonforaging activities also as a function of time. It will be straight if fatigue does not occur or can be ignored. The actual energy-time fitness combinations available to a predator are constrained by these two boundaries.

A fitness isocline map is a sufficient parameter (see Levins 1966) which can be quite sensitive to an organism's adaptive circumstances. Because time and energy are interactive, essential resources, an organism limited in one may be limited to some degree in the other. Nonetheless, this model offers operational distinctions which pass continuously from the strictly energy-limited to the strictly time-limited cases. If the fitness from a marginal unit of energy gained by foraging is greater than that attached to an additional unit of time freed from foraging, then the organism is energy limited. The isoclines will tend toward the horizontal (fig. 1). If the gain to a marginal unit of nonforaging time is the larger, the organism is time limited and represented by a fitness map which is more nearly vertical (fig. 2).

FIG. 1.—Opportunity-cost model for a stationary forager which is energy limited. Density of high ranking prey is greater in A than in B. The highest ranking resource disappears entirely from the environment of forager C. The following symbols are used in this and subsequent figures: T_f , time spent foraging in an interval T_i ; T_{nf} , time spent in nonforaging activities in T_i ; T_i , total time of interval chosen for analysis; E_a , net energy acquired while foraging; E_e , energy expended in nonforaging activities; $f_1 \dots f_n$, isoclines of increasing fitness; α , line showing minimum survivable rate of energy expenditure in nonforaging activities as a function of time; β , line showing maximum possible rate of energy expenditure in nonforaging activities as a function of time; *, optimal diet breadth as specified by the relevant model; $P_c - P_c$, partition between T_{nf} and T_f , the former read left to right and the latter right to left.

Formally, if the fitness isocline is given by a function f , then the relative rate of substitution at some point x is given by the negative of the slope of the tangent to f at x ; for values < 1 the organism is energy limited, for values > 1 it is time limited. An organism can behave as one or the other depending on its location on the fitness map. The form of the isoclines can be adjusted to reflect seasonality, life cycle, or other adaptive circumstances.

The foraging model represented in figures 1 and 2 is that for a stationary predator. The optimal diet is derived by the following procedure (Schoener 1969a, 1969b, 1971, pp. 369–370): Arrange potential prey types as end-to-end line segments of slope e_i/h_i (net energy gain per unit of pursuit and handling time for item i) from the largest to smallest value, beginning at the origin (for foraging time, that to the right). Set the length of each e_i/h_i segment proportional to the number of that prey type which are encountered in the relevant time period. The projection of a segment e_i/h_i onto the horizontal axis represents the time devoted to type i ; the projection onto the vertical axis shows the net energy gain from i . The optimal forager takes all of the highest ranking prey which pass by, adding prey in order of

FIG. 2—General opportunity-cost model for a stationary forager which is time limited. Resource conditions the same as in fig. 1.

decreasing e_i/h_i until it achieves a diet breadth which satisfies its energy requirements. The vertical axis at this diet breadth represents the total net energy acquisition (E_a); the horizontal axis the total time devoted to foraging (T_f).

One important assumption of this model must be mentioned. Search costs are not charged against the foraging of this predator because other activities are assumed to occur in intervals between pursuit and handling of prey. In the present analysis I have retained this assumption, but consider as well activities (T_{nf}) which of expedience or necessity are incompatible with foraging. Avoiding exposure to predators or to hazardous weather are possible examples. It is unlikely that all fitness-related activities could be performed simultaneously with foraging at all times.

The right and left portions of the model are linked in the following way: Each diet breadth is associated with a certain gain of energy (E_a) and an investment of time (T_f). These can be plotted as a *foraging constraint line* on the fitness map. The optimal diet is the point where this line touches the highest possible fitness isocline. This linkage establishes the opportunity costs (time) and benefits (energy) of foraging by evaluating them relative to alternative uses of time and energy in performing other fitness-enhancing activities. Such an approach is necessary because time and energy or other proxy currencies used in foraging studies need not be related to fitness in a strictly linear fashion. In the context of natural selection, an additional joule (or minute) may not be as valuable (or costly) as the last. The combination of foraging constraints and fitness isoclines is analogous to many analyses of consumer choice in micro-economics (see Covich 1972).

The stationary foraging model itself does not give a unique solution to the question of optimal diet breadth because it does not specify how the organism evaluates time and energy. Schoener's (1971) algorithm specifies assignment of an "energy requirement," but as noted above this is relative to adaptive context and to opportunity cost. To determine diet breadth it is necessary to know if the foraging organism needs to save foraging time more than gain energy, or the reverse. The time-minimizer and energy-maximizer concepts do this. The combination of the stationary model with a fitness map gives explicit meaning to the general case by representing all feasible combinations of marginal time and energy valuation.

Results for Stationary Opportunity-Cost Foragers

Figure 1 depicts the general case for an energy-limited stationary forager. I show three foraging constraint curves which differ in the abundance of the higher ranked prey. Density of the highest ranked type decreases from A to B; in C it disappears entirely.

As the environment becomes richer (with e_i/h_i constant for every item) energy intake grows as does time spent foraging. If no new and highly ranked prey appear in the environment, and no highly ranked prey disappear from it, diet breadth will not change (compare A and B). This result can be explained as follows: The greatest fitness is obtained by including all prey types up to and including the last type which has a slope (reading right to left) steeper than the next highest fitness isocline. Designate this item e_{db}/h_{db} , where db = diet boundary. So long as the fitness curves are straight and roughly parallel, as will be the case for a strong energy maximizer, the diet boundary item (e_{db}/h_{db}) will be the same e_i/h_i for a range of resource abundances and constraint lines. If a high ranking prey type is added to or eliminated from the organism's environment, diet breadth will increase or decrease by one item, respectively (compare B and C). If e_i/h_i increases for one or more highly ranked items, then time spent foraging decreases, energy intake increases, but slightly, and again diet breadth remains the same. Stated as a hypothesis, the optimal stationary forager takes all resource types up to and including the last e_i/h_i with a value greater than the marginal fitness value in nonforaging activities of energy with respect to time. Of course, if the efficiency of pursuing and handling an item outside of the diet should become greater than e_{db}/h_{db} , it will enter the optimal diet breadth. These observations can be combined to generate the following prediction: Whether or not an item is included in the diet of a stationary forager tending strongly to time-minimization or energy-maximization strategies depends only on its e_i/h_i , and is independent of the abundance or pursuit and handling efficiencies of items of higher rank.

Figure 2 depicts a stationary forager which is time limited, hence a time minimizer, facing the same foraging constraint curves as given in figure 1. As the abundance of high ranking resources increases, this predator should increase its foraging time and its energy intake. Its diet breadth and foraging efficiency remain the same (compare curves B and A). The effects of changes in the pursuit efficiency for high ranked items are determined as in the previous case. If high

ranking prey disappear from the environment, foraging time may increase (compare B and C). Higher pursuit efficiencies will decrease foraging time, increase energy intake and foraging efficiency. Diet breadth will remain the same, or possibly increase, if one or more items previously just outside of the diet attains an $e_i/h_i > e_{db}/h_{db}$.

Results for Searching Opportunity-Cost Foragers

The stationary forager model itself does not generate a unique solution to the question of diet breadth without specification of the marginal fitness value of various nonforaging time and energy combinations. In contrast, the model for searching predators specifies a unique optimal diet breadth, based on a maximum net rate of intake. It does not, however, indicate how long the organism should forage at this rate nor how much energy it should harvest. Predictions about the latter are possible using an opportunity cost approach.

The fundamental theorem is based on the MacArthur and Pianka (1966) graphical model for mobile predators in a fine-grained environment (as modified by MacArthur 1972, pp. 61–62; Pianka 1978, pp. 263–266; see Schoener 1971, p. 308). Several algebraic models give essentially the same results (Charnov and Orians 1973; Pyke et al. 1977). In this case active search has two interrelated consequences: (a) searching costs are charged to the predator as part of the optimization problem; and (b) foraging by definition occurs exclusive of other activities. That is, foraging takes the organism away (in time and space) from safety, mates, and offspring. The opportunity cost is more direct here than in the stationary forager case. The optimal diet is determined by a trade-off between a declining search cost, and an increasing pursuit and handling cost, per unit of prey captured, as less and less valuable prey are added to the diet. In MacArthur's (1972, p. 62) phrasing, "an animal should elect to pursue an item if and only if, during the time the pursuit would take, it could not expect both to locate and to catch a better item."

Each diet breadth in this model establishes a rate of intake which will appear as a straight foraging constraint line in the fitness map (figs. 3, 4). Figure 3 depicts an organism that is energy limited. As the abundance of high ranking prey increases, diet breadth decreases and the net acquisition rate while foraging improves. The foraging constraint line will pivot clockwise (compare A and B). For this isocline map, energy intake increases, and foraging time is reduced slightly. In the richer environment and at the narrower diet breadth this organism forages somewhat less but harvests considerably more energy. An increase in pursuit costs would also narrow the diet breadth, but with a decrease in overall foraging efficiency. In this instance the foraging constraint line would pivot counterclockwise. Figure 4 depicts a time minimizer. As the habitat becomes richer, this organism achieves the highest fitness by simultaneously decreasing time devoted to foraging and, for the fitness map depicted, increasing its energy intake slightly. Were the fitness curves more vertical and linear, foraging time and energy intake would shrink until the organism gathers only enough energy to meet its minimal (T_{nf}) expenditure rate, but that amount would still increase as diet breadth shrinks.

The opportunity-cost approach allows one to predict the optimal foraging time and optimal energy intake for a searching predator. Factors affecting the search for and the pursuit and handling of prey, or those affecting the marginal fitness valuations of the organism, can be incorporated in the model and its predictions by examining their effects on the foraging constraint line, or the fitness isocline map, respectively. For those organisms which do not tend strongly toward an energy-maximizer or time-minimizer strategy, however, actual predictions of an increase or decrease in foraging time or energy intake require a fairly detailed understanding of the fitness map. This suggests that reliable foraging behavior predictions depend on a detailed understanding of the organism's nonforaging activities and constraints and their fitness consequences.

DISCUSSION

The advantage of the present model is its attention to the idea of opportunity costs. Foraging costs and benefits are evaluated relative to the time and energy required for other, fitness-enhancing activities such as avoiding hazards, or engaging in reproductive or social activities. While it generally is recognized that all proxy currencies measure opportunity costs (e.g., Pianka 1978, p. 260), this awareness does not commonly find its way explicitly into models. Time and energy are preferred currencies, partly because they can be measured easily in absolute units. But marginal quantities of these units are relative measures as far as natural selection and fitness are concerned. The opportunity cost approach gets around the sometimes incorrect assumption that fitness varies directly with foraging efficiency or net rate of energy intake (see Pyke et al. 1977; Krebs and Cowie 1976, p. 99).

The time-minimizer and energy-maximizer concepts provide a limited opportunity cost evaluation of foraging. They can be generalized by fitness isoclines which show the evolutionary effects of all combinations of time and energy. In this sense, the time-minimizer, energy-maximizer distinction can be applied both to stationary and to mobile foragers. Although graphically simple, the approach allows somewhat more subtle predictions about foraging behavior than can be obtained from existing models. For instance, in an impoverished environment a searching forager may behave as an energy maximizer. As the environment becomes richer the predator's diet breadth contracts and its foraging efficiency increases, shifting its optimal foraging constraint line into a portion of the fitness map wherein a time-minimizer strategy achieves the highest fitness gains. Additionally, the form of the fitness isoclines can be manipulated to reflect seasonal or life-cycle changes. In nonbreeding seasons of inclement weather the fitness space will reflect the survival priorities of a time minimizer avoiding exposure; in a breeding season of favorable weather, when fitness is highly dependent on provisioning of offspring, the fitness set may reflect the reproductive priorities of an energy maximizer feeding young. The predictions stated above are only basic ones; especially they do not explore possibilities at the margins or the interior of the fitness map.

It should be evident that a currency besides fitness can be adapted to this

approach. For instance, anthropologists investigating the foraging behavior of hunter-gatherers can substitute energy-time utility, or preference, for energy-time fitness.

The opportunity-cost approach can sometimes extend or refine predictions of the simpler cost-benefit models. The extensions apply mainly to the stationary forager case. Here one must have information about marginal valuation of time and energy in order to predict diet breadth, or diet breadth changes. The opportunity-cost model indicates that organisms that are strongly energy maximizers or time minimizers will respond to changing abundances or pursuit efficiencies of high ranking prey by altering the time spent foraging and the energy intake, but in general their diet breadth will remain the same. Refinements apply mainly to the searching forager model. Here the simple cost-benefit model provides a unique optimal diet breadth prediction, unaffected by the organism's marginal valuations of time and energy. An opportunity-cost approach will show in addition how long the organism should forage at the optimum rate and how much energy it will attempt to harvest, a major advantage. Because the model specifies an optimal duration of foraging in some interval, relative to other activities, it may provide a basis for examining the relationship between foraging behavior and temporal resource partitioning (see Schoener 1974).

SUMMARY

A simple graphical technique is presented. It relates two existing foraging models to marginal valuations of the time and energy currencies used as proxies for fitness. For anthropologists it is also capable of relating these proxy currencies to utility or preference. The predictions of the models are responsive to important theoretical assumptions of evolutionary ecology research: costs in behavioral trade-offs are opportunity costs, often evaluated at the margin. The approach offers a flexible and potentially subtle method of analyzing foraging behavior of both stationary and mobile foragers. It leads to extension of some existing hypotheses about stationary predators, and it refines existing hypotheses about mobile, searching predators.

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