

Foraging in Complex Environments: When Prey Availability Varies over Time and Space

GARY E. BELOVSKY

*Department of Biology and School of Natural Resources,
University of Michigan,
Ann Arbor, Michigan 48109*

MARK E. RITCHIE

School of Natural Resources, University of Michigan, Ann Arbor, Michigan 48109

AND

JEFF MOOREHEAD

*Department of Biology, University of Michigan,
Ann Arbor, Michigan 48109*

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An optimal foraging model is presented which combines simultaneous and non-simultaneous modes of search for food. This model is more complex than those in the literature which are constructed using one search mode exclusively. Solutions to this foraging model lead to diets which are seldom composed of a single food or of foods in proportion to their abundance in the environment. Therefore, the most commonly cited qualitative conclusions of optimal foraging theory are not adequate to explain foraging choices under the range of probable search modes. © 1989 Academic Press, Inc.

Optimal foraging theory has been used successfully to predict the diets selected by various animals (Krebs *et al.*, 1983; Stephens and Krebs, 1986; Pyke, 1984), but it has been criticized by some scientists as being too simplistic to deal with complex environments (Pyke, 1984; Schluter, 1981). Tests of the theory have often dealt with very simple laboratory environments (Krebs *et al.*, 1977; Werner and Hall, 1974; Charnov, 1975). Even field tests of the theory have employed environments that have special food distributions: i.e., foods are randomly distributed or highly clumped (e.g., Werner and Mittelbach, 1982; Belovsky, 1978, 1984a, b, c, 1986a, b). The feeding models developed for these environments are not necessarily applicable to more complex environments; this has been argued empirically by Schluter (1981) and theoretically by McNair (1979).

While most of the models developed in foraging theory and their tests are correct, they do not provide a "blanket" formula for understanding foraging in all or possibly many environments. Rather, foraging models should be developed for specific environmental characteristics. In this paper, we develop an optimal foraging model for environments that apply to many organisms: an environment in which prey are available for consumption at different times and places. We will demonstrate how the standard predictions of classical foraging theory change in these more complex environments. These environments, however, are still rather simple compared to many real foraging environments.

SCENARIO

Imagine a predator whose prey are distributed in different patches and vary in the time of day when they are active. The predator's ability to encounter each prey species or type will depend upon whether the predator is active at the same time and place that the prey are active. An example would be ectothermic prey and either an ecto- or endothermic predator. Prey availability to the predator in this case may depend on thermal conditions varying with time of day and microhabitat. This is a common occurrence that has been observed for bats preying on insects (Anthony and Kunz, 1977; Fenton *et al.*, 1977; Kunz, 1974), lizards foraging on ants (Porter *et al.*, 1973) and snakes foraging on frogs (Porter *et al.*, 1975). These examples demonstrate that the potential for encounter between the predator and the prey may be determined by the thermal environment and each species' thermal physiology.

A forager may attempt to optimize its behavior over a certain time period, e.g., a day, and will have some proportion of this time to spend looking for food (Fig. 1). The time available for feeding might be set by

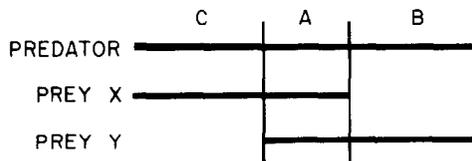


FIG. 1. Given some time out of a day that a predator can feed (predator bar), it might overlap its preys' activity (prey X's and Y's bars) in several ways. Times when the prey are not active at the same time as the predator are not shown as they do not count in the model. Both prey are active at the same time as the predator (region A) or each prey is active at different times (regions B and C). This provides a range of ways that a predator may encounter its prey over a day.

thermal physiology, avoidance of predators, desiccation, etc. Superimposed upon the forager's available feeding time is the time spent active by one or more prey types (Fig. 1). Prey activity time might be set by the same types of limits suggested for the predator. Although the diagram (Fig. 1) and the analysis of the optimal foraging models which follow are restricted to two prey species or types, an N -prey system can also be developed with greater difficulty (see below).

THE OPTIMIZATION MODEL

(A) *Simultaneous Search*

Two forms of time overlap between the predator and the two prey are apparent (Fig. 1). First, the predator can be active at the same time as both prey (region A). Second, the predator can be active at the same time as only one of the prey (regions B and C). If the predator is only active when both prey are active (region A) and both prey occur in the same habitat and are uniformly or randomly distributed in space, then the appropriate foraging model is the classical or "contingency" model (Schoener, 1971; Pulliam, 1974; Charnov, 1976; Werner and Hall, 1974; Krebs *et al.*, 1977). This is the most frequently cited optimal foraging model and is based upon the assumption that the predator can search for its prey at the same time and place, i.e., simultaneously. With simultaneous search, prey are encountered in proportion to their relative densities or encounter rates in the environment (Schoener, 1971; Pulliam, 1974, 1975).

A graphical model can be constructed to portray the contingency model using linear programming (Belovsky, 1978, 1984a) (Fig. 2a). A linear programming model consists of linear segments (Fig. 2a) that describe how different foraging constraints affect the intake of two or more food types. If a forager is limited in its available feeding time, then feeding time will act as a constraint on the consumption of each food type. For the contingency model, this time constraint (T : time) for the amounts (x and y) of two food types (X and Y , respectively) consumed is written as

$$T = (a + b)y + cx \quad \text{if } x \leq (b/d)y \quad (1a)$$

and

$$T = ay + (c + d)x \quad \text{if } x \geq (b/d)y, \quad (1b)$$

where a is the handling time for an item of food Y , b is the search time for an item of food Y , c is the handling time for an item of food X , and d is the search time for an item of food X .

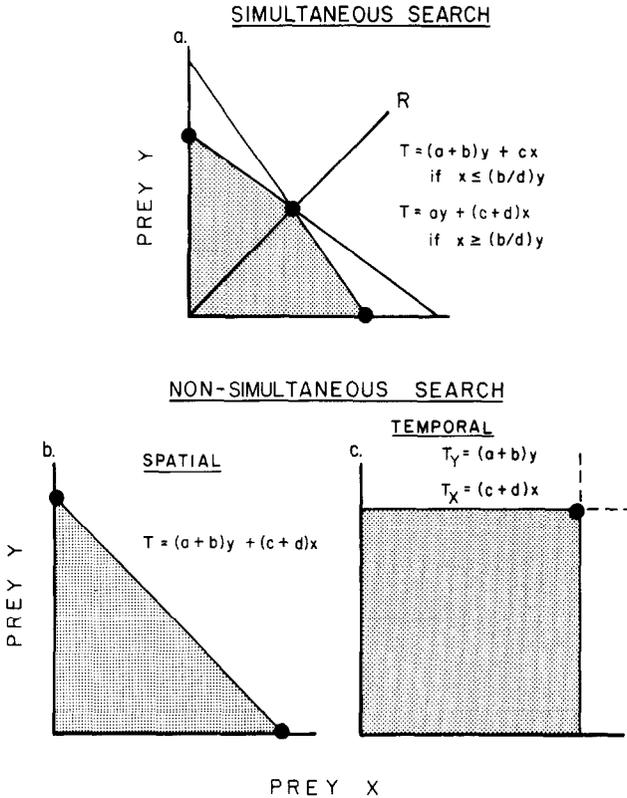


FIG. 2. Graphical foraging models based upon different feeding time constraints (solid line segments) for "pure" types of prey distributions in time and space are presented as functions of the amounts (e.g., mass) of two foods consumed. Shaded regions contain diet combinations which do not exceed the time constraint. (2a) shows simultaneous search, (2b) shows spatial non-simultaneous search, and (2c) shows temporal non-simultaneous search. Each form of search is discussed in the text. The solid dots represent the possible optimal diets for energy or nutrient maximization; also, these points can represent the possible feeding time-minimizing diets, but the absolute amounts of prey consumed will usually be less. *R* is the ratio of the two preys' abundances or encounter rates in the environment.

Together, these segments form a concave surface (relative to the origin) which sets a limit to possible diets selected by the predator. These line segments emerge because the predator's consumption of one prey requires time for ingestion (*handling* time) that reduces the time available for consuming the other prey. However, *searching* for either prey does not reduce consumption of the other, because the predator can look for both at the same time. Obviously, the two line segments intersect at a point reflecting the relative search times (b/d), i.e., encounter rates, of the two food types.

This ratio will often reflect the relative densities of the two food types in the environment, but may also reflect differences in recognition time or other factors that affect search time. In this case (Fig. 2a), the predator's predicted diet can include either prey alone or both prey in proportion to their encounter rates in the environment.

(B) *Non-simultaneous Search*

If the prey are available to the predator at different times of the day (Fig. 1, regions B and C) or the prey occur in different habitats, then foraging models can also be constructed using linear programming (Belovsky 1984a, 1986a). However, under these conditions, the model must incorporate the assumption that the predator cannot look for all prey at the same time. Prey distributions of this type lead to non-simultaneous search, and predators do not necessarily encounter the prey in proportion to their relative densities.

One type of non-simultaneous search emerges because the prey are available at the same time but not in the same habitat. In this case, the time constraint is represented by a single negatively sloped line (Fig. 2b),

$$T = (a + b)y + (c + d)x. \quad (2)$$

This upper limit occurs because feeding on one prey type (e.g., X) precludes feeding on the other (e.g., Y). Consequently, consuming one food type reduces the time available for consuming the other (Fig. 2b). In this case (Fig. 2b) the predicted optimal diets will include only one food type (e.g., either X or Y).

Another type of non-simultaneous search can emerge because the prey are active at different times. The time constraint for this case is represented by two perpendicular lines that are parallel to an axis (Fig. 2c),

$$T_Y = (a + b)y \quad (3a)$$

and

$$T_X = (c + d)x, \quad (3b)$$

where T_Y is the predator's exclusive activity time for feeding on prey Y and T_X is the predator's exclusive activity time for feeding on prey X . This upper limit occurs because each of the prey can be encountered and harvested during different times, so that consumption of one prey type does not reduce the predator's feeding time for consumption of the second type. In this case (Fig. 2c), the predicted optimal diet will always include both prey in a proportion that depends on the predator's available feeding time and rates of ingestion for each prey type. This diet proportion will usually be different from the prey's relative density in the environment.

Both simultaneous and non-simultaneous search models are well developed (Belovsky, 1978, 1984a, b, c, 1986a, b; Schoener, 1971; Charnov, 1975); but we wish to investigate the consequences if both types of search (simultaneous and non-simultaneous) occur during the predator's day. Combinations of the two search modes lead to diet choices very different from the models for either of the component search modes. Each combination of non-simultaneous search and simultaneous search will be addressed below.

COMBINED MODEL SOLUTIONS

The manner in which these search modes combine to determine the predator's optimal diet will depend upon the foraging goal that it "seeks." Two goals are commonly thought to be potentially important to foragers: energy or nutrient maximization, and feeding time minimization (*sensu* Schoener, 1971; Hixon, 1982). An energy or nutrient maximizer presumably has greater survival and reproduction when its energy or nutrient intake increases. A feeding time minimizer, on the other hand, has greater survival and reproduction if it uses less time to satisfy some minimal energy or nutrient requirement. This goal is usually associated with the benefits of spending time hiding from predators, remaining under cover in inclement weather, and/or greater care of young.

The models presented below are simplified. We assume that (1) search times for each prey are the same at different times of predator activity and in different habitats, and (2) the value of non-foraging time does not depend on its position in the time period over which the diet is optimized (e.g., the beginning or end of the day). The models can be constructed with these assumptions relaxed, but this results in many potential solutions that are tedious to explain, and obscures the general pattern we wish to present.

(A) *Solution to an Energy- or Nutrient-Maximizing Goal*

The solution to an energy- or nutrient-maximizing goal is found where a line, called the objective function, becomes tangent to the line segments of the feeding time constraint. The energy or nutrient objective function has a slope which is the negative value of the ratio of the energy or nutrient value of prey X to prey Y . The point at which the objective function is tangent to the time constraint provides the combination of food types X and Y yielding the greatest energy or nutrient intake.

To combine search modes for an energy or nutrient maximizer, the time constraints for each type of search mode (Fig. 2) can be added together to form the time constraint for the combined model (Fig. 3). The combination of line segments forming the time constraint for the combined model is

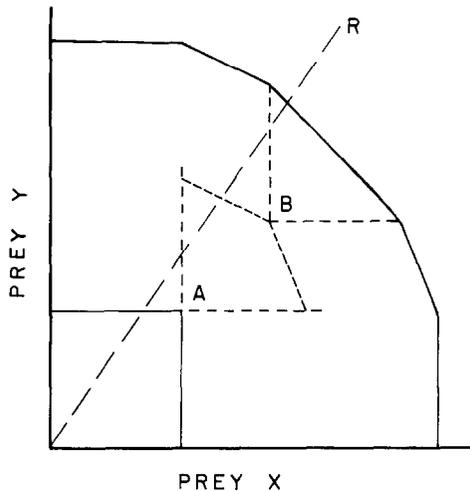


FIG. 3. The manner in which the simple search modes in Fig. 2 can be combined into more complex cases, as discussed in the text, is presented here. This is accomplished by adding search modes in a sequence based upon predator decision-making (Fig. 2c, 2a, 2b; see text) by defining new axes (dashed lines). The new axes' origins are defined at points *A* and *B*. Line *R* has a slope equal to the ratio of prey *Y*'s to prey *X*'s abundances or encounter rates in the environment.

determined by defining a new set of imaginary axes whose origin is at the point on the previous search mode's constraint that is farthest from the origin of its axes (e.g., *A* in Fig. 3).

The individual time constraints can be added only in a particular sequence and fashion. The sequence must produce a concave time constraint (relative to the origin); this is necessary to satisfy Bellman's Principle of Optimality (Bellman and Dreyfus, 1962; Intriligator 1971). This principle states that the solution for each time interval within a longer period must itself be an optimal solution, given initial conditions, if the overall solution is to be optimal. In this case, search modes should be added in the following order based upon how restrictive each search mode is on ingestion of both foods:

- (1) temporal non-simultaneous search—no need for the forager to choose between the foods since ingestion of one does not reduce the time for ingestion of the other;
- (2) simultaneous search—the forager only has to decide how much of each food to handle, since handling time only reduces the time for ingestion of the other food; and
- (3) spatial non-simultaneous search—the forager has to decide how

much of each food to search for and handle, since both factors reduce the ingestion of the other food (Fig. 3).

Mathematical expressions for the different combined search modes appear in the Appendix.

Simultaneous and spatial non-simultaneous search are mutually exclusive, because simultaneous search requires prey to be in the same habitat but spatial non-simultaneous search requires them to be in different habitats. Therefore, for these two search modes to operate within a forager's feeding time, the prey must be randomly or uniformly distributed in the same habitat during part of the day and in different habitats during the rest of the day. Figure 4a presents a graphical model combining these two search modes (Fig. 2a and b). The model provides three line segments: two segments arising from simultaneous search (b and c) and one segment from non-simultaneous search (a). There are four possible solutions, either Y only, X only, or two combinations of X and Y .

Temporal non-simultaneous search and simultaneous search are combined when the two prey occupy the same habitat but have both exclusive and overlapping activity times. Figure 4b presents a graphical model combining these two search modes (Fig. 2a and c). The combined models provide four line segments (Fig. 4b); two segments arising from simultaneous search (b and c) and two segments arising from non-simultaneous search (a and d). There are three possible solutions, which are always combinations of X and Y .

Temporal and spatial non-simultaneous search are combined when the two prey occupy different habitats but have both exclusive and overlapping activity times. Figure 4c presents a graphical model combining these two search modes (Fig. 2a and c). The combined models provide three line segments (Fig. 4c): two segments arising from temporal non-simultaneous search (a and c) and one segment from spatial non-simultaneous search (b). There are two possible solutions, which are always combinations of X and Y .

Temporal and spatial non-simultaneous search and simultaneous search are combined when the prey vary completely in their activity times and habitat use. Figure 4d presents a graphical model combining these three search modes (Fig. 2a, b, and c). The combined models provide five line segments (Fig. 4d): two from the simultaneous search mode (b and d), two from the temporal non-simultaneous mode (a and e), and one from the habitat non-simultaneous mode (c). There are four possible solutions, which are always combinations of X and Y .

There are two patterns to note. (1) The optimal diet will only fortuitously contain prey in proportion to their relative density or encounter

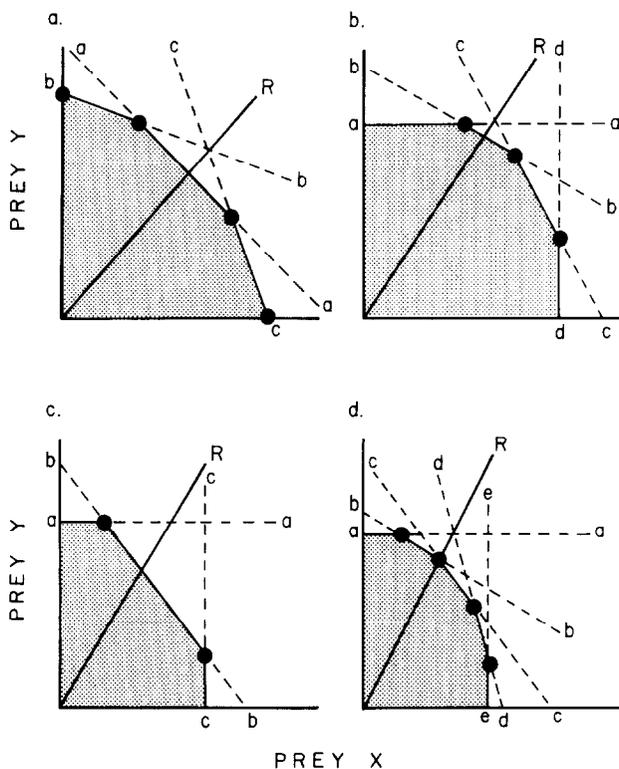


FIG. 4. Graphical models based on different combinations of operative feeding time constraints (solid line segments) are presented for simultaneous search combined with spatial non-simultaneous search (4a), simultaneous search combined with temporal non-simultaneous search (4b), temporal and spatial non-simultaneous search combined (4c) and all three search modes combined (4d). The axes represent the amounts of two foods consumed (e.g., mass). The rationale and means for these combinations are presented in the text. Shaded regions contain diet combinations that do not exceed the time constraint. Solid dots represent the potential energy- or nutrient-maximizing diets; the feeding time-minimizing diets cannot be as easily depicted. *R* represents the relative abundances or encounter rates of the two species in the environment.

rate in the environment. (2) The optimal diet will contain, in most cases, a combination of the two food types which depends on the amount of time spent in each search mode and the consumption rate of each food type.

(B) Solution to a Time-Minimizing Goal

In contrast to the models for energy or nutrient maximization, the solution for time minimization is found by using an algorithm which progressively calculates energy or nutrient intake as feeding time is increased, until the predator's nutritional requirements are just satisfied. In

this case, feeding time is the objective function. However, the nutritional return per unit of feeding time is not a single average value, but changes with the search mode that the predator is using. Therefore, the predator must not only choose its diet within a given search mode, but also choose which search modes it will use. This makes the potential time-minimizing solutions to the combined foraging models more complicated than those for energy or nutrient maximization.

To minimize feeding time the forager must rank its search modes from best to worst in terms of the nutritional value obtained per unit of time spent feeding (net nutrient intake). Consequently, the search modes for a time-minimizer do not necessarily combine in the same order as discussed above for energy or nutrient maximizers. Within each search mode the predator will choose the diet with the greatest net nutrient intake. This can be demonstrated with the following algorithm, which uses a two-step procedure to answer the question: are the predator's energy or nutrient needs just satisfied? If the above question is answered affirmatively in any of the steps, the procedure is terminated.

The two steps are:

(Step 1) Does the predator have a period of simultaneous search? If so, can its energy or nutrient requirements be satisfied in the time allowed and with the optimal diet in this search mode? The optimal solution to this step is defined by the well-established classical or "contingency" model (Schoener, 1971; Werner and Hall, 1974; Charnov, 1975; Pulliam, 1974; Krebs *et al.*, 1977). If the time-minimized diet is achieved in this step, then the optimal diet can be composed of either prey alone or both prey in proportion to their abundances or encounter rates in the environment. This mode has the highest priority since simultaneous search will provide the greatest net rate of nutrient intake. This arises because the predator always has a lower search time per prey item encountered since both prey can be searched for at the same time.

(Step 2) If the predator has a period of non-simultaneous search, can its energy or nutrient requirements be satisfied by the intake in Step 1 plus the intake in this search mode? The foraging time-minimized diet in the period of non-simultaneous search can be of two forms:

(a) The predator consumes only the prey type with the greatest net rate of nutrient intake. This occurs when nutritional requirements are satisfied by consuming the higher-ranked prey type during non-simultaneous search (both temporal and spatial). Note that, for the higher-ranked prey, the predator will not distinguish between temporal and spatial non-simultaneous search modes.

Two possible diets result from adding this diet with that in Step 1. First, if the diet predicted in Step 1 contains only one prey, then this diet will be

composed of only one prey, since the prey providing the highest net rate of nutrient intake would be the same for both search modes. Otherwise, if both prey were consumed in Step 1, then this diet will be composed of both prey, but not in proportion to their relative abundances or encounter rates in the environment.

(b) The predator consumes both prey during non-simultaneous search. This will occur if the predator has not satisfied its nutrient requirements with the prey highest in net rate of nutrient intake in Step 2a. The predator, therefore, will include the lower-ranked prey during that prey's exclusive activity time. The lower-ranked prey, however, will never be eaten by a time minimizer during spatial non-simultaneous search because consuming it would reduce the consumption of higher-ranked prey. In this case, the predator's overall time-minimized diet will always be composed of both prey, and the diet composition will seldom be the same as the preys' relative abundances or encounter rates in the environment.

This procedure for finding the time-minimized diet follows a sequence where each step adds foods with progressively lower energy or nutrient contents per unit of search plus handling time. Finally, the diet which minimizes feeding time is composed of the sum of intakes predicted in previous step(s) and just sufficient intake in the present step to satisfy the remaining energy or nutrient requirements. This analysis suggests that time minimizers will seldom consume diets composed of a single prey or of the prey types in proportion to their abundances or encounter rates in the environment. This is similar to the results for energy or nutrient maximization.

N PREY SYSTEM

A comparable development of the time constraint with *N* prey and three modes of search is possible, but the construction of the vectors composing the combined feeding time constraint is very difficult. The number of intersections of surfaces making up the time constraint in *N* dimensions increases very rapidly as *N* increases. For two prey, at any one instant (e.g., hours) in the larger time period for foraging (e.g., day), only one search mode is possible. With *N* prey, several search modes might be possible (e.g., some prey occur together in one habitat while others do not), adding more complexity. Therefore, the *N*-dimensional hypervolume for the combined time constraint will approach a smooth continuous surface. This means that the number of *potential* optimal solutions approaches infinity, requiring the techniques of non-linear programming to find a single optimum, if one exists (Hadley, 1964; Intriligator, 1971).

DISCUSSION

The results of both the energy- or nutrient-maximized and the feeding time-minimized solutions when different search modes are combined indicate a number of complexities that do not emerge from the "pure" (simultaneous and non-simultaneous search) models. First, the potential range of diet composition is increased dramatically; i.e., simple predictions of diet proportions disappear. Second, it is possible that the predator will avoid consuming one prey in favor of another in periods of simultaneous search, but may consume both prey during periods of temporal non-simultaneous search. Also, it might consume both prey under simultaneous search but only one under spatial non-simultaneous search. This can occur either with energy- or nutrient-maximization or time-minimization. These observations are counter to the results from simultaneous search models (Pyke, 1984; Krebs *et al.*, 1983; Stephens and Krebs, 1986) which are sometimes considered to be the general predictions of "optimal foraging theory."

By adding additional foraging constraints (e.g., digestive capacity) to this model (Fig. 5), the diet predictions can either be simplified (Fig. 5a) or made even more complex (Fig. 5b). This means that the range of possible diets and foraging behaviors is far more diverse than commonly considered in many theoretical discussions.

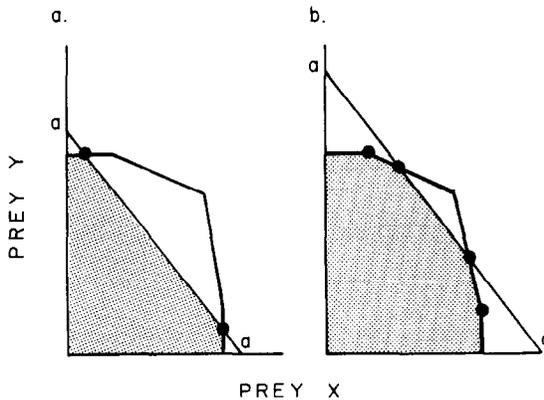


FIG. 5. Using the combination of simultaneous and temporal non-simultaneous search modes as an example, an additional feeding constraint which cannot be exceeded (e.g., digestive capacity) is imposed (line *a-a*). The axes represent the amounts of the two foods consumed (e.g., mass). Solid dots represent the energy- or nutrient-maximizing diets and the shaded region contains all diets that do not exceed the constraints. Additional constraints can either decrease (5a) or increase (5b) the number of potential optimal diets.

The often very simple views of foraging ecology are not incorrect, but are based upon particular food distributions in the environment. General criticisms of optimal foraging theory are unwarranted when based upon observations from environments where prey distributions violate the assumed foraging models' assumptions. Rather, data must be compared with predictions from appropriate models based upon the particular distribution of food in time and space. The main point of this analysis is that appropriate foraging models may be more complex than the classical models commonly cited in the literature and more similar to those presented here. Most importantly, foraging ecology must not seek a single model (or several) and its solution(s) as a general "optimal foraging theory." Rather, foraging ecology must employ appropriate models based on given food distributions observed in the field, and ask whether foragers choose an optimal diet under these conditions.

APPENDIX: MATHEMATICAL EXPRESSIONS FOR THE COMBINED TIME CONSTRAINTS WITH TWO PREY

A number of parameters must be defined:

x = quantity of prey X consumed

y = quantity of prey Y consumed

T_1 = time available to feed only on prey X

T_2 = time available to feed only on prey Y

T_0 = time available to feed on both prey X and Y in the same habitat

T'_0 = time available to feed on both prey X and Y in different habitats

T_{S1} = time to search for an item of prey X

T_{H1} = time to pursue, subdue and ingest an item of prey X

T_{S2} = time to search for an item of prey Y

T_{H2} = time to pursue, subdue and ingest an item of prey Y .

Spatial/Non-simultaneous Search and Simultaneous Search

The three segments of Fig. 4a are

$$(a) \quad y = \frac{T'_0 + T_0 - xT_{H1}}{T_{S2} + T_{H2}} \quad \text{for } x = 0 \text{ to } \frac{T_0 T_{S2}}{T_{H2} T_{S1} + T_{H1} T_{S2} + T_{S1} T_{S2}}$$

$$(b) \quad y = \frac{T'_0 - x(T_{H1} + T_{S1}) + \frac{T_0 T_{S2}(T_{H1} + T_{S1})}{T_{S2} T_{H1} + T_{H2} T_{S1} + T_{S2} T_{S1}}}{T_{H2} + T_{S2}}$$

$$+ \frac{T_0 T_{S1}}{T_{S2} T_{H1} + T_{H2} T_{S1} + T_{S2} T_{S1}}$$

$$\text{for } x = \frac{T_0 T_{S2}}{T_{H2} T_{S1} + T_{H1} T_{S2} + T_{S1} T_{S2}}$$

$$\text{to } \frac{T_0 T_{S2}}{T_{H2} T_{S1} + T_{H1} T_{S2} + T_{S1} T_{S2}} + \frac{T'_0}{T_{S1} + T_{H2}}$$

$$(c) \quad y = \frac{T_0 + T'_0 - x(T_{H1} + T_{S1})}{T_{H2}}$$

$$\text{for } x = \frac{T'_0}{T_{S1} + T_{H2}} + \frac{T_0 T_{S2}}{T_{H2} T_{S1} + T_{H1} T_{S2} + T_{S1} T_{S2}} \text{ to } \frac{T_0 + T'_0}{T_{S1} + T_{H1}}$$

Temporal Non-simultaneous Search and Simultaneous Search

The four segments of the time constraint in Fig. 4b are

$$(a) \quad y = \frac{T_2 + T_0}{T_{S2} + T_{H2}} \quad \text{for } x = 0 \text{ to } \frac{T_1}{T_{S1} + T_{H1}}$$

$$(b) \quad y = \frac{T_0 + T_2 - T_{H1}(x - T_1/(T_{H1} + T_{S1}))}{T_{S2} + T_{H2}}$$

$$\text{for } x = \frac{T_1}{T_{S1} + T_{H1}} \text{ to } \frac{T_1}{T_{S1} + T_{H1}} + \frac{T_0 T_{S2}}{T_{H1} T_{S2} + T_{S1} T_{H2} + T_{S1} T_{S2}}$$

$$(c) \quad y = \frac{T_2}{T_{H2} + T_{S2}} + \frac{T_0 - x(T_{H1} + T_{S1}) + T_1}{T_{H2}}$$

$$\text{for } x = \frac{T_1}{T_{S1} + T_{H1}} + \frac{T_0 T_{S2}}{T_{H1} T_{S2} + T_{S1} T_{H2} + T_{S1} T_{S2}} \text{ to } \frac{T_1 + T_0}{T_{H1} + T_{S1}}$$

$$(d) \quad X = \frac{T_1 + T_0}{T_{H1} + T_{S1}} \quad \text{for } y = 0 \text{ to } \frac{T_2}{T_{S2} + T_{H2}}$$

Temporal and Spatial Non-simultaneous Search

The three segments in Fig. 4c are

$$(a) \quad y = \frac{T_2 + T'_0}{T_{S2} + T_{H2}} \quad \text{for } x = 0 \text{ to } \frac{T_1}{T_{S1} + T_{H1}}$$

$$(b) \quad y = \frac{T'_0 + T_2 - x(T_{H1} + T_{S1}) + T_1}{T_{S2} + T_{H2}}$$

$$\text{for } x = \frac{T_1}{T_{S1} + T_{H1}} \text{ to } \frac{T_1 + T'_0}{T_{S2} + T_{H2}}$$

$$(c) \quad y = \frac{T_1 + T'_0}{T_{H1} + T_{S1}} \quad \text{for } y = 0 \text{ to } \frac{T_1}{T_{S2} + T_{H2}}.$$

Temporal and Spatial Non-simultaneous Search and Simultaneous Search:

The five segments in Fig. 4d are

$$(a) \quad y = \frac{T_2 + T_0 + T'_0}{T_{S2} + T_{H2}} \quad \text{for } x = 0 \text{ to } \frac{T_1}{T_{S1} + T_{H1}}$$

$$(b) \quad y = \frac{T'_0 + T_0 + T_2 - T_{H1}(x - T_1/(T_{H1} + T_{S1}))}{T_{S2} + T_{H2}}$$

$$\text{for } x = \frac{T_1}{T_{S1} + T_{H1}} \text{ to } \frac{T_1}{T_{S1} + T_{H1}} + \frac{T_0 T_{S2}}{T_{H1} T_{S2} + T_{S1} T_{H2} + T_{S1} T_{S2}}$$

(c)

$$y = \frac{T'_0 + T_0 + T_2 + T_1 - (T_{H1} + T_{S1})(x) + \frac{T_0 T_{S1} T_{S2}}{T_{H1} T_{S2} + T_{S1} T_{H2} + T_{S1} T_{S2}}}{T_{S2} + T_{H2}}$$

$$\text{for } x = \frac{T_1}{T_{S1} + T_{H1}} + \frac{T_0 T_{S2}}{T_{H1} T_{S2} + T_{S1} T_{H2} + T_{S1} T_{S2}} \text{ to } \frac{T_1 + T_0}{T_{S1} + T_{H1}} \\ + \frac{T_0 T_{S2}}{T_{H1} T_{S2} + T_{S1} T_{H2} + T_{S1} T_{S2}} + \frac{T'_0}{T_{S1} + T_{H1}}$$

$$(d) \quad x = \frac{T_0 + T_2 - [(T_{H1} T_0 T_{S2}) / (T_{H1} T_{S2} + T_{S1} T_{H2} + T_{S1} T_{S2})]}{T_{S2} + T_{H2}}$$

$$- \frac{[(T_{H1} + T_{S1})(x - T_0 T_{S2}) / (T_{H1} + T_{S1} T_{H2} + T_{S1} T_{S2}) - T_1 - T'_0]}{T_{H2}}$$

$$\text{for } x = \frac{T_1}{T_{S1} + T_{H1}} + \frac{T_0 T_{S2}}{T_{H1} T_{S2} + T_{S1} T_{H2} + T_{S1} T_{S2}} + \frac{T'_0}{T_{S1} + T_{H1}} \\ \text{to } \frac{(T_1 + T'_0 + T_0)}{(T_{S1} + T_{H1})}$$

$$(e) \quad x = \frac{T_1 + T'_0 + T_0}{T_{S1} + T_{H1}} \quad \text{for } y = 0 \text{ to } \frac{T_2}{T_{S2} + T_{H2}}.$$

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