BIO/MAR 360 **Optimal diet simulation** **Thomson**

Today's exercise is designed to clarify the nature of simple optimality models that predict the diet that a foraging animal should choose. Although you will recognize that the results are basically artificial, my hope is that the exercise will transform the abstract mathematical expressions in the models into something more tangible and concrete. We attempt this by giving **you** the experience of being a predator who must find and capture prey. We also try to give you some insight into the ways in which morphological specializations of predators might interact with their diet choices.

This game-playing approach is an outgrowth of work by Holling (1959), who had ablindfolded human "predator" search a table for "prey" consisting of sandpaper discs. He was interested in the rate of searching success as a function of density; however, we will be asking different questions. We are concerned with the choices a predator faces in picking its prey, so we have devised artificial environments that include three types of prey that vary in their value to a predator. Which of these types should be taken, and which should be left alone? In nature this is almost certain to be a complex problem, since most predators encounter many different species of potential prey that have different caloric or nutritive values, different catchabilities, and different densities. All these variables affect the way the predator should behave to obtain food most efficiently. Selection should mold a species' behavior, morphology, and physiology so that it is efficient, and different species have evolved different strategies to cope with their environments. One principal dichotomy of such strategies involves the generalist *vs*. the specialist. A good deal of theorizing revolves around this point, most of it based on the intuitively comfortable idea that a jack-of-all-trades is an ace of none. A crossbill, for example, can extract seeds from conifer cones more efficiently than a goldfinch, but the goldfinch can take a number of different foods that would give the crossbill trouble.

Since both crossbills and goldfinches exist in nature, there must be conditions under which both strategies are acceptable. We will try to identify the sorts of conditions that might favor one or the other, using a theoretical approach. We hope the results will provide some new insight into this adaptive problem.

Mathematical models are valuable because they allow precise identification of assumptions and questions, and give hard results based on those assumptions and questions. Major problems are (1) the inevitable sacrifice of realism for simplicity and (2) the mathematics itself, which is often abstruse. The models we will use, which were developed by Schoener (1969, 1971) are very simple mathematically, once the notation is clearly understood. As far as their realism goes, you will have to judge for yourself.

If we consider time and energy to be the important considerations affecting foraging, we can determine the theoretically optimal diet (i.e., the types of prey that should be taken) for a given predator facing a given prey distribution. We need to consider, for each potential prey species, the net energy *gained* per item eaten, and the time *spent* in finding, catching, and eating it. An efficient predator should be able to harvest a lot of energy in a short time; thus the adaptive question becomes how to maximize net energy gain per time, *e/t*.

_E/T_ for consuming a particular food item

Generally,

e/t = (food energy of the item - energy of the search - energy of the pursuit - handling energy) / (search time + handling time)

or, in symbols, $\frac{e}{t} = \frac{E_f - E_s - E_p - E_h}{T_s + T_p + T_h}$.

Since all these terms will be different for each prey type, we need to introduce a second subscript to indicate which prey item we're talking about. For example, for prey type 2,

$$\frac{e_2}{t_2} = \frac{E_{f2} - E_{s2} - E_{p2} - E_{h2}}{T_{s2} + T_{p2} + T_{h2}}.$$

For an unspecified prey type i,

$\frac{e_i}{t_i} = \frac{E_{fi} - E_{si} - E_{pi} - E_{hi}}{T_{si} + T_{pi} + T_{hi}}$, where i can equal 1, 2, 3, etc.

The search, pursuit, and handling energy expenditures can be broken down further: each is the product of the time spent and the energetic cost per unit time. For example,

$E_{si} = (T_{si})$ (cost of searching per unit time) $= (T_{si})(C_{si})$.

So,

$$\frac{e_i}{t_i} = \frac{E_{fi} - T_{si}C_{si} - T_{pi}C_{pi} - T_{hi}C_{hi}}{T_{si} + T_{pi} + T_{hi}}.$$

_E/T_ for a diet (i.e., for a particular set of prey types chosen from those available)

So far, we have written equations for the *e/t* of a single encounter with a single specified prey item. Now we switch gears slightly to write an equation for the *average* *e/t* per encounter when a forager adopts a particular diet. By calculating this average *e/t* for all possible diets, we can decide which diet is the optimal diet—that will be the combination of prey items that gives the highest average *e/t*.

Our exercise simulates a forager who experiences search costs and handling costs, but no pursuit costs. This would be analogous to a seed-eating rodent, for example. For such animals, we can simplify our equations by dropping E_p and T_p terms. Now we will derive an equation for the average *e/t* of such a forager in an environment with three prey types.

First, imagine a forager who searches for prey but never eats any. Therefore, it pays the costs of searching but not any handling costs. It never has any food intake, so of course it will be running a deficit. Its average *e/t* per prey encounter is

$$avg\ e/t = \frac{-E_s}{T_s}, \text{ or } \frac{-C_s T_s}{T_s}.$$

Now, imagine a forager who takes prey of type 1 whenever it encounters one, but does not take prey types 2 or 3. For each encounter, it bears the same search costs as before, but now it also gains food energy and incurs handling costs. However, it does not get these new gains and losses at every encounter, only those encounters that are with prey type 1. If prey type 1 makes up a fraction p_1 of all prey items, the *e/t* of this new diet is

$$avg\ e/t = \frac{-E_s + p_1(E_{f1} - E_{h1})}{T_s + p_1(T_{h1})}.$$

If our forager starts taking items 1 and 2 but not 3, then

$$avg\ e/t = \frac{-E_s + p_1(E_{f1} - E_{h1}) + p_2(E_{f2} - E_{h2})}{T_s + p_1(T_{h1}) + p_2(T_{h2})}.$$

We can write a more general expression using summation notation:

$$avg\ e/t = \frac{-E_s + \sum_i p_i(E_{fi} - E_{hi})}{T_s + \sum_i p_i(T_{hi})}.$$

Again, the E_h terms in the preceding three expressions could be replaced by C_hT_h.

The brute-force way to calclate the optimal diet would be to calculate the average *e/t* for all possible combinations of prey types, but this is inefficient. It is better to first rank the prey types according to their net values as given by

$$\frac{E_{fi} - E_{hi}}{T_{hi}}.$$

If you calculate this quotient for each prey type, then rename the prey so that the prey type with the highest quotient is type 1, the next highest is type 2, *etc.*, you can show algebraically that the optimal diet must be one of these combinations: type 1 only; types 1 and 2; or, types 1, 2, and 3. The other combinations (2 only, 3 only, 2 and 3, 1 and 3) can never constitute the best diet. Note that the abundances of the prey do not enter the formula for ranking. Therefore, a forager should never eliminate a good item from its diet just because that item is rare.