RATE MAXIMIZING AND STATE VARIABLE THEORIES OF DIET SELECTION

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In behavioral ecology, diet selection is often predicted by using a theory in which it is assumed that behaviors have evolved to maximize the rate of intake of energy. In this theory, it is assumed that fitness is a monotonic function of energy intake. An alternative is to deal directly with fitness, measured in terms of expected reproduction, and thus connect short term behavior with reproduction. Following the usual assumptions of the theory of diet choice, fitness satisfies a partial differential-difference equation. Conditions under which rate maximizing and state variable theories of diet selection yield identical predictions are identified. When predation, as well as starvation, is a source of mortality, the identification is not as complete.

Introduction. Among the achievements of behavioral ecology is the formula from which predictions on diet selection can be based (see Stephens and Krebs, 1986, for further discussion and history):

$$v(\mathscr{P}) = \frac{\sum\limits_{i=1}^{n} \lambda_i E_1 \mathscr{P}_i}{1 + \sum\limits_{i=1}^{n} \lambda_i h_i \mathscr{P}_i}. \tag{1}$$

In this equation, $v(\mathscr{P})$ is the overall *rate* of gain of energy of the forager, λ_i is the rate (either deterministic or the parameter of a Poisson process) at which the ith food item is encountered, E_i and h_i are the energy gain from, and handling time of, the ith type of food item, $\mathscr{P}_i$ is the probability that the ith type food item is incorporated into the diet, and $\mathscr{P}$ is the vector of the $\mathscr{P}_i$. In using this equation, it is assumed that fitness (expected reproduction) is an increasing function of the rate of energy gain, but the relationship between fitness and energy gain is never specified. Equation (1) can be derived in a deterministic setting by simply equating the total foraging time to the sum of searching and handling times. In the stochastic setting, the renewal theorem is applied assuming: (1) that the foraging time interval of interest is long enough that only the first term (i.e. the mean) in the renewal theorem (Karlin and Taylor, 1975) matters; but (2) that

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the foraging time interval is short enough so that behavior does not change over the interval. In either case, the prediction about behavior is determined by a long-term rate.

The theory of optimal diet selection proceeds by choosing the $\mathcal{P}_i$ to maximize $v(\mathcal{P})$. This leads to a number of strong predictions. (i) Items should be ranked by "profitability" E_i/h_i. (ii) Items are either always included in the diet or never included in the diet (i.e. $\mathcal{P}_i = 1$ or 0). (iii) The inclusion of the jth type of item does not depend upon its encounter rate, but only on the encounter rates of more profitable items. In particular, when there are only two prey types, with prey type 1 more profitable than prey type 2, the second prey type is included in the diet if:

$$\lambda_1 < \frac{E_2}{E_1 h_2 - E_2 h_1}.$$

Although the success of this theory is controversial (Gray, 1987; Godin, 1990; Hughes, 1990), it has been instrumental in the development of behavioral ecology. The theory owes its success to three main features. (i) The theory is easy to use. (ii) All of the parameters in (1) can be determined in the laboratory or field. (iii) Strong predictions emerge.

In the development of (1) many features of the biology of the organism such as physiological constraints and many features of the ecology such as predation, are ignored. One would like to know, however, that those things which are ignored can be ignored without any major effect on the predictions. In this paper, I formulate and solve a state dependent (Mangel and Clark, 1988) theory of diet selection which includes physiological constraints and predation. In many cases (cf. Mangel, 1989) the full state dependent theory and the rate maximizing theory give identical predictions of behavior. To understand why, I analyse the model of diet selection based on state variables and show under what conditions the predictions based on this theory will be the same as those based on rate maximization.

State Dependent Diet Selection: Why a State Variable? In natural resource management and in behavioral ecology, one of Colin Clark's main contributions has been to force us to focus on states of the system, rather than rates (or flows). Of course, knowledge of states over time implies knowledge about rates, but the reverse is not true. Field biologists (e.g. Pierotti and Annett, 1990) are beginning to study the relationship between diet and reproductive performance, recognizing that "reproductive performance is likely to be a better indicator of individual fitness than ability to maximize caloric intake" (Pierotti and Annett, 1990, p. 568).

The notation and procedures of Mangel and Clark (1988) are used, except

that the model is formulated in continuous, rather than discrete, time. This facilitates comparisons with theories based on rate maximization. The foraging organism is characterized by a single state variable $X(t)$ representing physiological reserves at time t. If $X(t) \leqslant x_c$, a critical level, the organism is dead. A physiological constraint restricts $X(t) \leqslant x_m$, a maximum possible level of reserves. For ease of exposition, I concentrate on two food types, with type 1 more profitable that type 2, in the usual context that $E_1/h_1 > E_2/h_2$. The dynamics of the state variable are then:

$$X(t+dt) = \quad X(t) - \alpha(X(t))\, dt$$
if no food type is encountered between t and $t + dt$ or if a food type is encountered and rejected

$$X(t+dt+h_i) = X(t) - \alpha(X(t))\,(dt+h_i) + E_i$$
if the ith food type is encountered between t and $t + dt$ and accepted. $\qquad$ (2)

Here $\alpha(x)$ is the metabolic rate (i.e. the rate at which reserves are lost) when the physiological variable $X(t) = x$. When $\alpha(x)$ is a nonlinear function of x, the second equation in (2) should be understood only as a schematic of the dynamics. That is, (2) is schematic for the differential equation $dX/dt = -\alpha(X(t))$, with jumps of size E_i after h_i units of time when a prey item is accepted. It will be seen in the sequel that the schematic form used in (2) is sufficient for our objectives.

Fitness at the end of the foraging interval is measured by future expected reproduction $\Phi(X(T))$ depending upon the terminal value $X(T)$ of the state variable. Fitness for values of $t < T$ is characterized by a *fitness function*:

$$F(x, t, T) = \max E\{\Phi(X(T)) \mid X(t) = x\}. \qquad (3)$$

Here the maximum is taken over behavioral decisions (i.e. to accept or reject an encountered food item) and $E\{\ \}$ denotes the mathematical expectation over the probabilistic events of finding food (avoiding starvation) and avoiding predation.

Is Starvation Important?   We can begin the analysis by assuming that death is caused only by starvation (i.e. no predators are present) and ask if starvation over the interval $[0, T]$ is likely (also see Houston and McNamara, 1988). In this case, we set $\Phi(X(T)) = 1$ if $X(T) > x_c$ and to 0 otherwise (Mangel and Clark, 1988).

To simplify the analysis, assume that there is only one prey type which is always accepted upon encounter so that the probability of encountering a prey item in the next dt is $\lambda dt + o(dt)$ [where $o(dt)$ denotes terms such that $o(dt)/dt \to 0$ as $dt \to 0$], $\alpha(x) = \alpha$ a constant, and let $x_c = 0$. In addition, let:

$$u(x, t, T) = \Pr\{\text{forager does not starve between } t \text{ and } T | X(t) = x\}. \quad (4)$$

Note the conditioning on the initial time; hence $u(x, t, T)$ will satisfy a backward equation (Feller, 1971). Using the law of total probability (Mangel and Clark, 1988) we have:

$$u(x, t, T) = (1 - \lambda \, dt) \, u(x - \alpha \, dt, t + dt, T) + \lambda \, dt \, u(x - \alpha \, dt + E, t + h + dt, T). \quad (5)$$

Taylor expanding and collecting terms in powers of dt, dividing by dt and letting $dt \to 0$ gives (details of this kind of derivation are given in the next section, in a more general setting):

$$0 = \frac{\partial u}{\partial t} - \alpha \frac{\partial u}{\partial x} + \lambda(u(x + E, t + h, T) - u(x, t, T)). \quad (6)$$

Suppose that we consider a long time interval, for which the stationary version of (6) is of interest. Setting $\partial u / \partial t = 0$, we have:

$$0 = -\alpha \frac{\partial u}{\partial x} + \lambda(u(x + E) - u(x)). \quad (7)$$

One interpretation of (7) is that $u(x)$ is the probability that the forager never starves to death (cf. Peters and Mangel, 1990). Assuming that $u(x) = 1 - e^{-kx}$ (Houston and McNamara, 1985) leads to a non-linear equation for k:

$$\alpha k = \lambda(1 - e^{-kE}). \quad (8)$$

This non-linear equation has a solution $k > 0$ if $\lambda E > \alpha$. To see this, introduce a dimensionless parameter $\varepsilon = \lambda E / \alpha$ and set $q = kE$. Then (8) can be rewritten as $q = \varepsilon(1 - e^{-q})$. When $\varepsilon \leqslant 1$, the only solution of this equation is $q = 0$. However, for $\varepsilon > 1$ there is a positive solution $q > 0$ (Fig. 1). When ε is close to 1, q will be small and starvation will be likely for many values of x. When $\varepsilon \gg 1$, q will be large and starvation is important only for values of x near the critical value (0 in this case). That is, $u(x)$ exhibits boundary layer behavior (Lin and Segel, 1974).

Directly Linking Fitness and Diet Choice.   A similar backward approach can be used for determining fitness in the more general case. The equation that the fitness function satisfies is called an equation of stochastic dynamic programming and is determined by applying the law of total expectation.

To being still assume that there is no predation and that finding food is characterized by:

$$Pr\{\text{find food item type } i \text{ in the next } dt\} = \lambda_i \, dt + o(dt). \quad (9)$$
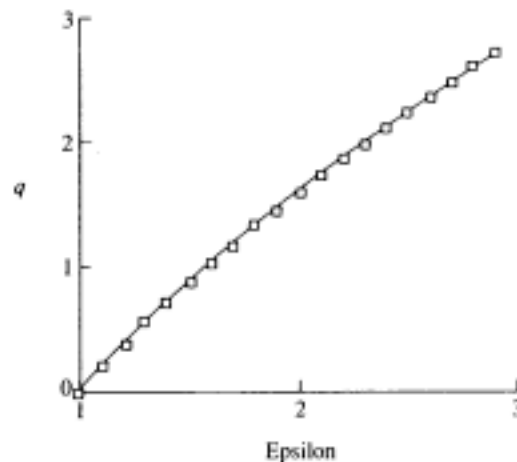
Figure 1. The non-dimensional parameter $q = kE$ as a function of the parameter $\varepsilon = \lambda Y/\alpha$. This is obtained by solving the equation $q = \varepsilon(1 - e^{-q})$ for the positive root when $\varepsilon > 1$.

Applying the law of total expectation (Mangel and Clark, 1988, Ch. 2) to the fitness function $F(x, t, T)$ leads to an equation analogous to (5) for $F(x, t, T)$:

$$F(x, t, T) = (1 - (\lambda_1 + \lambda_2)\, dt + o(dt))F(x - \alpha(x)\, dt, t + dt, T)$$

$$+ \sum_{i=1}^{2} \{\lambda_i\, dt + o(dt)\}\max\{F(x - \alpha(x)\, dt, t + dt, T);$$

$$F(x - \alpha(x)\,(dt + h_i) + E_i, t + h_i + dt, T)\}. \tag{10}$$

The first term on the right hand side of (10) is the expected fitness if no item is encountered between t and $t + dt$. This occurs with probability $1 - (\lambda_1 + \lambda_2)\, dt + o(dt)$. The second term (involving the summation) is the expected fitness if a item of type i is encountered; this is summed over food types. In this case, the forager can either continue searching (first term inside the "max") or eat the encountered prey item (second term inside the "max"). Letting $O(dt)$ denote terms such that $O(dt)/dt \to a$ constant as $dt \to 0$, Taylor expanding in powers of dt gives:

$$F(x, t, T) = (1 - (\lambda_1 + \lambda_2)\, dt)\left\{F(x, t, T) + \left(\frac{\partial F}{\partial t} - \alpha(x)\frac{\partial F}{\partial x}\right)dt + o(dt)\right\}$$

$$+ \sum_{i=1}^{2} \{\lambda_i\, dt + o(dt)\}\max\{F(x, t, T) + O(dt);$$

$$F(x - \alpha(x)h_i + E_i, t + h_i, T) + O(dt)]\}. \tag{11}$$

Since $dtO(dt) = o(dt)$, (11) can be rewritten as:

$$F(x, t, T) = (1 - (\lambda_1 + \lambda_2)\, dt)\left(F(x, t, T) + \left(\frac{\partial F}{\partial t} - \alpha(x)\frac{\partial F}{\partial t}\right)dt\right)$$

$$+ \sum_{i=1}^{2} \{\lambda_i\, dt\, \max\{F(x, t, T);$$

$$F(x - \alpha(x)h_i + E_i, t + h_i, T)\} + o(dt). \tag{12}$$

Subtracting $F(x, t, T)$ from both sides, dividing by dt and letting $dt \to 0$ gives:

$$0 = \frac{\partial F}{\partial t} - \alpha(x)\frac{\partial F}{\partial x} - (\lambda_1 + \lambda_2)F(x, t, T)$$

$$+ \sum_{i=1}^{2} \lambda_i \max\{F(x, t, T); F(x - \alpha(x)h_i + E_i, t + h_i, T)\}. \tag{13}$$

Equation (13) is solved with the "final condition" $F(x, T, T) = \Phi(x)$. This can actually be treated as an initial condition, by introducing the time to go $s = T - t$.

Rate Maximizing Solution of the Dynamic Programming Equation. The forager will always accept food type 1, so that (13) becomes:

$$0 = \frac{\partial F}{\partial t} - \alpha(x)\frac{\partial F}{\partial x} + \lambda_1(F(x - \alpha(x)h_1 + E_1, t + h_1, T) - F(x, t, T))$$

$$+ \lambda_2 \max\{0, F(x - \alpha(x)h_2 + E_2, t + h_2, T) - F(x, t, T)\}. \tag{14}$$

From the definition, we expect that $(F(x, t, T)$ increases as x increases and decreases as t increases. Hence, (14) clearly shows the nature of the trade-off regarding acceptance of food type 2. It can be cast into an explicitly "marginal value" setting by assuming that E_2 and h_2 are small. Then the second food type is accepted whenever:

$$\frac{\partial F}{\partial x}(E_2 - \alpha(x)h_2) + \frac{\partial F}{\partial t}h_2 > 0.$$

Unfortunately, this equation is not very useful because $F(x, t, T)$ is not known. When just one food type is considered, McNamara and Houston (1989, pp. 474 ff) have shown that this marginal value condition leads to the usual criterion for acceptance of the food item.

However, one can seek a rate maximizing solution of (14). The most general form for a rate maximizing solution of (14) is:

$$F(x, t, T) = g(x) + v(x)(T - t) \tag{15}$$

where the function $g(x)$ and the rate $v(x)$ are to be determined. Here $v(x)$ is the rate of energy gain when the state variable is x and fitness increases as the time to go $T - t$ increases.

Since $F(x, T, T) = \Phi(x)$, it must be true from (15) that $g(x) = \Phi(x)$. We then have that $\partial F / \partial t = -v(x)$ and $\partial F / \partial x = \Phi'(x) + v'(x)(T - t)$, where the prime denotes the derivative. Using these in (14) we obtain:

$$
\begin{aligned}
0 = {} & -v(x) - \alpha(x)[\Phi'(x) + v'(x)(T - t)] + \lambda_1[\Phi(x - \alpha(x)h_1 + E_1) \\
& + v(x - \alpha(x)h_1 + E_1)(T - t - h_1) - \Phi(x) - v(x)(T - t)] \\
& + \lambda_2 \max[0, \Phi(x - \alpha(x)h_2 + E_2) + v(x - \alpha(x)h_2 + E_2)(T - t - h_2) \\
& - \Phi(x) - v(x)T - t)].
\end{aligned} \tag{16}
$$

In the usual theories of diet selection the rate v, is independent of state x. Assuming that $v(x) = v_0$ a constant, (16) becomes:

$$
\begin{aligned}
0 = {} & -v_0 - \alpha(x)\Phi'(x) \\
& + \lambda_1[\Phi(x - \alpha(x)h_1 + E_1) - \Phi(x) - v_0 h_1] \\
& + \lambda_2 \max[0, \Phi(x - \alpha(x)h_2 + E_2) - \Phi(x) - v_0 h_2].
\end{aligned} \tag{17}
$$

Equation (17) will have two solutions v_{01} and v_{02}, depending upon which of the terms in the expression following λ_2 is larger. However, for these rates to be independent of state x, it must be true that $\alpha(x) = \alpha$, a constant independent of x and that $\Phi(x) = x$. In that case, neither of the constraints involving x_c nor x_m can apply and metabolic rates are independent of state. With these additional assumptions, (17) becomes:

$$0 = -v_0 - \alpha + \lambda_1[E_1 - \alpha h_1 - v_0 h_1] + \lambda_2 \max[0, E_2 - \alpha h_2 - v_0 h_2]. \tag{18}$$

The two solutions of (18) are:

$$v_{01} = \frac{\lambda_1 E_1}{1 + \lambda_1 h_1} - \alpha \qquad \text{(prey type 2 rejected)}$$

$$v_{02} = \frac{\lambda_1 E_1 + \lambda_2 E_2}{1 + \lambda_1 h_1 + \lambda_2 h_2} - \alpha \qquad \text{(prey type 2 accepted)}.$$

With the exception of α, which could easily be incorporated into (1), one of the two values of v_0 will exactly correspond to the rate maximizing solution for diet selection described by the classical solution.

According to (18), the second prey type should be incorporated into the diet when $E_2 - \alpha h_2 - v_0 h_2 > 0$. Setting $E_2 - \alpha h_2 = v_{02} h_2$ we can find the condition for accepting the second type of item, which turns out to be exactly the same condition obtained from the standard rate maximizing approach (Stephens

and Krebs, 1986). We thus see that the rate maximizing solution is the same as the state variable solution when metabolic rates are constant, physiological constraints and predation are unimportant, and expected future reproduction is equal to the value of the state variable.

Including Predation. Gilliam (1990) recently extended the standard diet model (1) to include predation. He assumed that the probability of death per unit time while searching is μ_s and that the probability of death while handling the ith food type is $\mu_i h_i$. Assuming that optimal behavior maximizes feeding rate divided by mortality rate, Gilliam derives an expression analogous to (1) and asserts that the $\mathcal{P}_i$ should be chosen to maximize:

$$v = \frac{\sum_{i=1}^{n} \lambda_i E_i \mathcal{P}_i}{1 + \sum_{i=1}^{n} \lambda_i h_i \frac{\mu_i}{\mu_s} \mathcal{P}_i}. \tag{19}$$

To derive the dynamic programming equation corresponding to this situation, assume that:

$$\begin{aligned} Pr&\{\text{killed by a predator in the next } dt \text{ while searching}\} \\ &= \mu_s \, dt + o(dt) \end{aligned} \tag{20}$$

$$\begin{aligned} Pr&\{\text{killed while handling a food item of type } i\} \\ &= 1 - \exp\{-\mu_i h_i\}. \end{aligned} \tag{21}$$

The form of (21) is consistent with the assumption that the rate of predation while handling a food item type i is μ_i (see Mangel, 1989, p. 692). The law of total expectation applied to $F(x, t, T)$ is now:

$$\begin{aligned} F(x, t, T) &= (1 - \mu_s \, dt + o(dt)) \, (1 - (\lambda_1 + \lambda_2) \, dt + o(dt))F(x - \alpha(x) \, dt, t + dt, T) \\ &\quad + \sum_{i=1}^{2} \{\lambda_i \, dt + o(dt)\} \max\{(1 - \mu_s \, dt + o(dt)) \\ &\quad F(x - \alpha(x) \, dt, t + dt, T);\, \exp\{-\mu(h_i + dt)\} \\ &\quad F(x - \alpha(x) \, dt + h_i) + E_i, t + h_i + dt, T)\} \end{aligned} \tag{22}$$

and leads to:

$$\begin{aligned} 0 &= \frac{\partial F}{\partial t} - \alpha(x) \frac{\partial F}{\partial x} - (\lambda_1 + \lambda_2 + \mu_s)F(x, t, T) \\ &\quad + \sum_{i=1}^{2} \lambda_i \max\{F(x, t, T);\, \exp\{-\mu_i h_i\}F(x - \alpha(x)h_i + E_i, t + h_i, T)\}. \end{aligned} \tag{23}$$

Setting $F(x, t, T) = e^{\mu_s t} G(x, t, T)$, with $G(x, t, T)$ to be determined, gives:

$$0 = \frac{\partial G}{\partial t} - \alpha(x) \frac{\partial G}{\partial x} + \sum_{i=1}^{2} \lambda_i \max\{0;$$

$$\exp\{h_i(\mu_s - \mu_i)\} G(x - \alpha(x)h_i + E_i, t + h_i, T) - G(x, t, T)\}. \quad (24)$$

The method used to find a rate maximizing solution of (14) does not work for (24). To see this, assume that we set $\alpha(x) = \alpha$, a constant, that prey type 1 is always accepted and that $G(x, t, T) = x + v(T - t)$, with a constant v. Substitution into (24) leads to:

$$0 = -v - \alpha + \lambda_1 [\exp\{h_1(\mu_s - \mu_1)\} \{x - \alpha h_1 + E_1 + v(T - t - h_1)\}$$

$$- \{x + v(T - t)\}] + \lambda_2 \max[0,$$

$$\exp\{h_2(\mu_s - \mu_2)\}\{x - \alpha h_2 + E_2 + v(T - t - h_2)\} - \{x + v(T - t)\}]. \quad (25)$$

The troublesome term in (25) is $\exp\{h_i(\mu_s - \mu_i)\}$; it appears to force a state dependence to v. If we completely ignore state by setting $\alpha = 0$ and by assuming that $G(x, t, T) = v(T - t)$, then we can obtain an analog of Gilliam's criterion (also see Ludwig and Rowe, 1990; McNamara, 1992). However, this is a very special case and the associated assumptions are unsatisfying.

Discussion. The main result of this paper is that rate maximizing provides a solution of the dynamic programming equation for lifetime fitness when: (i) expected reproduction is equated to value of the state variable; (ii) constraints on the state variable are ignored; (iii) metabolic rates do not depend upon state; and (iv) predation can be ignored. These are the assumptions under which the standard diet selection model is usually derived. It appears that when any of these conditions are violated, rate maximizing will not provide a solution of the dynamic programming equation. It might be that *behaviors* predicted by the two methods are still similar (Mangel, 1989), but it remains to be shown how to identify when similar behaviors will be predicted.

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