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AN OPTIMIZATION EQUATION FOR PREDATION¹

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Abstract. A general equation is derived for the quantity of different foods a predator consumes in response to food preference and food abundance. It is supposed the predator apportions its efforts among different search modes in order to minimize the discrepancy between actual and desired quantities of each food consumed. Included are the conflict between quantity and composition of the diet and the competition between feeding and nonfeeding activities. The properties of the equation are examined and discussed in light of the literature.

Predation has been the subject of numerous theoretical and experimental investigations in recent years. This paper attempts to incorporate some of the patterns which have emerged into a single, overall equation. The equation states in computable form how the quantities of different foods consumed by a predator (or herbivore) depend upon food abundances and preferences. It is intended primarily as a computational tool of general scope which nonetheless approximates reality.

The equation is based on the teleological assertion that a predator adjusts its efforts in obtaining different foods to control its diet within certain practical limits. It thereby provides, in addition to a computational tool, a working hypothesis for studying predation from the particular point of view which underlies its derivation—optimal control.

The objective is to compute feeding rates as simply as possible, while retaining such common features of predator response to food abundance as (a) saturation of a predator's feeding capacity at high food abundance; (b) shifting proportions of food in the diet at different food abundances; (c) thresholds of food abundance, below which a food is not consumed; (d) maintenance of variety in the diet, even when a food is superabundant.

As a computational tool, the equation can contribute to the quantitative study of ecosystems. Only when we are explicit about the nature of ecosystem transfers like predation can we interpret ecosystem experiments without confounding the effects of those transfers with properties emerging at the ecosystem level.

FORMULATION OF THE PREDATION EQUATION

If a general predation equation is to be valid, there must in fact be some uniformity in nature despite the great variety of means organisms employ to pursue their relatively few kinds of ecological ends. Slobodkin (1965) feared this variety would impede a quantitative ecology, and indeed, even the broad mechanisms which determine the pattern of predator response to food abundance seem different in each new situation studied.

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Holling found predator saturation mediated by a drop in searching effectiveness due to time lost processing food in one instance (Holling 1959) and to a decline in hunting motivation on filling the gut in another (Holling 1966). Tinbergen (1960) postulated a "specific search image" to account for shifting proportions of food in the diet of forest birds, but Royama (1970) felt that a concentration of searching activity in temporarily profitable microhabitats could also account for the same effect. Croze (1970) documented experimentally that both kinds of learning, for food and for habitat, were present in crows.

The foundation of the predation equation to be presented here is adaptation—the ability of organisms to change their operating characteristics in coping with a fluctuating environment—a fundamental feature of life which dominates ecological processes (Slobodkin 1964). It will be assumed that predators shift their feeding behavior with changes in food abundance, optimizing the quantity and composition of their diet. Learning may be involved in some instances, built-in mechanisms in others, but the equation specifies no such details. There is no concern here with what is ultimately being optimized (e.g., survival or reproduction); the standards for an optimal diet of any particular predator are assumed to be given.

Search modes

Let us assume that a predator has m discrete search modes. They might, for example, be different microhabitats, searching techniques, or search images. The average feeding rate (u_{ki}) on food k in search mode i is

$$u_{ki} = v_{ki} N_k \left(1 - \frac{\sum_{k'=1}^n u_{k'i}}{u_{\max}} \right) \quad (1)$$

where v_{ki} = the effectiveness of finding the k th food in the i th search mode

N_k = the abundance of the k th food

n = the number of different foods.

The maximum feeding rate (u_{\max}) is not subscripted

with respect to food, but it could be so subscripted if the situation warranted it.

Rearranging eq. (1) for computational convenience (details in appendix),

$$u_{ki} = \frac{u_{\max} v_{ki} N_k}{u_{\max} + \sum_{k'=1}^n v_{k'i} N_{k'}} \quad (2)$$

Equations (1) and (2) state that the feeding capacity of a predator becomes saturated as increasingly more searching time is lost to processing food at higher rates of food consumption. Equation (2) provides a computational link between the u_{ki} and food abundances N_k . However, it is the u_{ki} , whatever their origin, that are of consequence to the optimization process. If eq. (2) does not apply to a particular situation, the u_{ki} can be obtained by whatever means are appropriate, and the optimization equation derived below still applies.

As a predator can allocate different proportions of its time to different search modes, the total quantity (Y_k) of food k consumed is

$$Y_k = \sum_{i=1}^m u_{ki} x_i \quad (3)$$

where x_i = the proportion of total feeding time spent in the i th search mode.

The emphasis or effort (x_i) placed on different search modes may have dimensions other than time, and search modes may merge into one another; but for the discussion to follow, it will be assumed that search modes are discrete and that the effort placed upon them may be expressed in terms of time. Equation (3) applies to average feeding over a period like a day and asserts no details about fluctuations within that period.

Control view

Let us suppose that the predator "controls" its feeding, to minimize the discrepancy (F) between desired and actual consumptions of various foods:

$$F = (z_T - \sum_{k=1}^n Y_k)^2 + \sum_{k=1}^n w_k (z_k - Y_k)^2 + w_0 (1 - x_{m+1})^2 \quad (4)$$

- where z_k = the desired level of consumption of food k
- z_T = the desired level of total consumption (normally much less than u_{\max})
- w_k = the importance attached to consumption of food k relative to quantity of the diet (i.e., the strength with which consumption (Y_k) is regulated at z_k)
- w_0 = the importance attached to nonfeeding activities relative to quantity of the diet

x_{m+1} = the proportion of time available for feeding which is spent instead on competing, nonfeeding activities.

The first term of eq. (4) represents the discrepancy in total food consumption, the middle terms represent discrepancies in the consumption of each food, and the last term represents the deviation of the actual time spent on nonfeeding activities from a desired proportion of unity.

Although the parameters z and w are assumed to be constant regardless of food abundance, they may change slowly with time as the physiological state of the predator changes due, for example, to age or seasonal change in its environment.

Reward view

An alternative, but exactly equivalent phrasing of eq. (4), may prove more satisfying to those preferring a more mechanistic interpretation of predation. The negative of eq. (4) is a "reward" (G) for the predator to maximize:

$$G = -F = z_T \sum_{k=1}^n Y_k \left(2 - \frac{\sum_{k=1}^n Y_k}{z_T} \right) + \sum_{k=1}^n w_k z_k Y_k \left(2 - \frac{Y_k}{z_k} \right) + w_0 x_{m+1} (2 - x_{m+1}) - K \quad (4a)$$

The positive terms represent rewards, respectively, from total food consumption, from each food in itself, and from nonfeeding activities. For example, the reward from each food is $2w_k z_k$ per unit consumption at low consumption, but with a diminishing reward from additional increments of food, reaching a maximum reward as at z_k ; that is, food is more precious to a hungry predator than to a satiated one.

The term in eq. (4a) which includes x_{m+1} can be paraphrased

$$w_0 x_{m+1} (2 - x_{m+1}) = w_0 \left[1 - \left(\sum_{i=1}^m x_i \right)^2 \right]$$

and considered a cost of feeding effort which is increasingly great as more effort is removed from competing, nonfeeding activities.

K represents terms from eq. (4) which do not contain the decision variable (x_i) and are therefore of no consequence to the optimization:

$$K = z_T^2 + \sum_{k=1}^n w_k z_k^2 + w_0$$

Review of assumptions

Equations (1), (3), and (4) state the assumptions underlying the predation equation. Equation (1) is the "disc equation" of Holling (1959) adapted to a multifeed situation. Equation (3) assumes different search modes exist.

Equation (4) or (4a) includes numerous biological assumptions, some of them implicit.

- a) The predator has the ability to make an optimal decision in distributing its effort among search modes.
- b) There is in reality some desired level of consumption (z_k) for each food.
- c) The discrepancy (F) between actual and desired levels of food consumptions is minimized. (Alternatively, the total reward (G) from consumption of all foods is maximized.)
- d) The relative importances (w_k) attached to discrepancies (or rewards) due to consumption of each food, total consumption, and nonfeeding are constant, regardless of food abundances or levels of consumption.
- e) The perceived discrepancies are quadratic functions of actual discrepancies. (Perceived rewards are quadratic functions of consumption.)
- f) The contributions of each food, total consumption, and nonfeeding activity to the total discrepancy (or reward) are separate and additive.

The existence of search modes is illustrated by birds which feed in a variety of vegetation types and employ a variety of foraging techniques each day (Root 1967). Dawkins (1969) has explored the mechanisms by which chickens maintain a variety of choices in their pecking behavior. That animals are capable of minimization "decisions" is illustrated by lobsters which orient their bodies by minimizing the discharge rate from their statocyst organs (Cohen 1955).

The notion of a desired level of consumption (z_k) for each food may seem artificial; however, the fact that animals are observed to take foods in fixed proportions when the foods are all superabundant suggests the existence of z_k . Brown (1969) observed this in seed selection by pigeons, and Lat (1967) reviewed the consistent food preferences of laboratory rats which lead to a nutritionally balanced diet.

A feature of eq. (4) which indeed is arbitrary is that the "perceived" nutritional error is the square of actual error. It is reasonable to suppose that some exponent is appropriate because perceived differences have been shown generally to be a power function of actual differences (Weber's Law). Examples (Stevens 1966) range from human and animal discrimination of pitch, loudness, and brightness to human attitudes. The exponent is less than one in most cases (often about one-half), but some quantities are perceived with an exponent greater than one (e.g., 3.5 for the exponent of perceived electric current).

The assumption of additivity is also arbitrary. However, studies on body orientation have shown that sensory signals from different organs may be treated as an algebraic sum. Pigeons evaluate head

position in this way from separate sensors in the head and neck (Mittelstaedt 1964), and fish add the cues from dorsal light and from gravity in orienting their bodies (Holst 1950).

To summarize, the mechanisms of feeding behavior are not known well enough to validate completely the above assumptions, but similar abilities and similar relationships have been observed in other kinds of behavior. Further experimental observation must determine how well they apply to predation.

The predation equation may, however, provide an adequate description of predator response to food abundance, even under circumstances where it is not strictly correct as an explanation. For example, a predator may not literally possess desired levels of food consumption, but its response pattern may be as though that were the case.

MATHEMATICAL SOLUTION

Substituting (3) in (4), the formal optimization problem is to minimize:

$$F(x_i) = \left(z_T - \sum_{k=1}^n \sum_{i=1}^m u_{ki} x_i \right)^2 + \sum_{k=1}^n w_k \left(z_k - \sum_{i=1}^m u_{ki} x_i \right)^2 + w_0 (1 - x_{m+1})^2, \quad (5)$$

subject to constraints on the "decision variables" x_i

$$\sum_{i=1}^{m+1} x_i = 1 \quad (6a)$$

$$x_i \geq 0 \quad i = 1, \dots, m+1. \quad (6b)$$

The equality constraint (6a) specifies that the predator has a limited amount of effort available for feeding. The inequalities (6b) specify the physical constraint that effort or time cannot be negative.

Equation (5) and constraints (6) represent a quadratic programming problem, and the quadratic form of eq. (5) is in fact critical to the relatively simple solution outlined below. If eq. (5) should have a more complex form, as may be demanded by reality under some circumstances, it might be necessary to resort to a numerical, "steepest descent" search technique of the sort described by Nelder and Mead (1965). Although search techniques can deal with any arbitrary function to be minimized, they are expensive in computer time and not feasible with more than five or so decision variables. Moreover, a complicated function could have numerous minima, which would not only present computing problems, but could also prove confusing to a real predator.

A quadratic programming problem may be solved by the method of Wolfe (1959), an extension of linear programming, if one already has a computer program for the relatively lengthy and complicated

procedure. Presented below is an ad hoc solution to the problem, which leads to the relatively simple computer program in Fig. 1. The solution proceeds in two stages. First, Lagrange multipliers are used to minimize eq. (5), subject to equality constraint (6a). Second, in the next section, the inequality constraints (6b) are handled by setting some of the x_i to zero.

The problem is treated below in algebraic terms because algebra allows precise computational statements which are general for any number of decision variables (i.e., search modes). Although a geometric treatment of the problem is limited to three dimensions, it can add to an intuitive understanding of the algebra and procedures presented below. A geometric picture is not developed here, but the reader may find a diagram of a quadratic function like eq. (5) and constraints like (6) in Kunzi and Krelle (1966: 87).

Lagrange multiplier solution

Lagrange multipliers are a classical optimization method which cannot deal practically with complicated functions or inequality constraints, but they are fully effective for eq. (5) and (6a). They have the advantage that they lead to a general, algebraic solution which applies for all possible parameter values. Applying Lagrange multipliers (Hillier and Lieberman 1967: 605), the values of x_i which minimize eq. (5), subject to equality constraint (6a), must satisfy the following equations:

$$\frac{\partial F}{\partial x_i} = \frac{\partial F}{\partial x_{m+1}} \quad i = 1, \dots, m. \quad (7)$$

(Note that the $\partial F/\partial x_i$ are also all equal to each other.)

Equations (6a) and (7) form the basis for the predation equation. Equation (7) states that F is minimized when the increment in F induced by a small shift in effort from nonfeeding to a particular search mode is exactly compensated by the decrement in F due to increased food consumption. (Similarly, a change in F due to shifting effort from one search mode is exactly compensated by the effort shifted to another search mode.)

Predators do not have Lagrange multipliers at their disposal, but animals are remarkably able at bringing perceived quantities into balance. This is what eq. (7) says they can do, and it does not seem to require super powers. For example, Mittelstaedt (1964) showed that head orientation in pigeons is achieved by balancing signals from receptor organs. Fraenkel and Gunn (1961) have reviewed numerous instances of tropotaxis (p. 76-89) and dorsal light reaction (p. 120-132) in invertebrates and fish, where the body is oriented by simultaneously balancing light intensity on bilateral light receptors.

Computation

The reader who is not concerned with computational details may wish to skip this section and the following one on nonnegativity constraints. All computational procedures from the two sections are included in the computer program (Fig. 1).

Equation (5) may be rephrased:

$$F(x_i) = \sum_{i=1}^{m+1} \sum_{j=1}^{m+1} q_{ij} x_i x_j - 2 \sum_{i=1}^{m+1} c_i x_i + K \quad (8)$$

$$\left. \begin{aligned} \text{where } q_{ij} &= \left(\sum_{k=1}^n u_{ki} \right) \left(\sum_{k=1}^n u_{kj} \right) \\ &+ \sum_{k=1}^n w_k u_{ki} u_{kj} \\ & \quad \quad \quad i = 1, \dots, m \\ & \quad \quad \quad j = 1, \dots, m \\ c_i &= \sum_{k=1}^n u_{ki} (w_k z_k + z_T) \\ q_{i, m+1} &= q_{m+1, i} = 0 \\ c_{m+1} &= q_{m+1, m+1} = w_0. \end{aligned} \right\} \quad (9)$$

Examination of the matrix \mathbf{Q} over numerous random values for the u_{ki} and w_k has shown \mathbf{Q} is almost always positive definite by the criterion of positive determinants outlined by Kunzi and Krelle (1966: 35). This means (Kunzi and Krelle 1966: 38) that equation (8) has a single minimum which is the minimum for all decision variables x_i , a well-defined optimization problem.

The partial derivatives of (8) are

$$\frac{\partial F}{\partial x_i} = 2 \left(\sum_{j=1}^{m+1} q_{ij} x_j - c_i \right) \quad i = 1, \dots, m+1. \quad (10)$$

Substituting (10) in (7) and dividing by two yields m equations:

$$\sum_{j=1}^{m+1} a_{ij} x_j = b_i \quad i = 1, \dots, m \quad (11)$$

$$\left. \begin{aligned} \text{where } a_{ij} &= q_{ij} - q_{m+1, j} \\ b_i &= c_i - c_{m+1}. \end{aligned} \right\} \quad (12)$$

These m equations are to be solved simultaneously with the equality constraint from eq. (6a):

$$\sum_{j=1}^{m+1} a_{m+1, j} x_j = b_{m+1} \quad (13)$$

$$\text{where } a_{m+1, j} = b_{m+1} = 1. \quad (12a)$$

In matrix notation, eq. (11) and (13) are

$$\mathbf{Ax} = \mathbf{b} \quad (14)$$

where \mathbf{A} is an $(m+1) \times (m+1)$ matrix whose elements are a_{ij}

\mathbf{x} is an $(m + 1) \times 1$ vector whose elements are x_i

\mathbf{b} is an $(m + 1) \times 1$ vector whose elements are b_i .

Solving for \mathbf{x} ,

$$\mathbf{x} = (\mathbf{A})^{-1}\mathbf{b} \quad (15)$$

Substituting (15) in (3) and expressing in matrix form,

$$\mathbf{Y} = \mathbf{u}(\mathbf{A})^{-1}\mathbf{b} \quad (16)$$

where \mathbf{Y} is an $n \times 1$ vector whose elements are Y_k

\mathbf{u} is an $n \times (m + 1)$ matrix whose elements are u_{ki} (with $u_{k,m+1} = 0$).

Equation (16) is the predation equation. The objective is to compute the Y_k , given parameters w_k , w_0 , z_k , z_T , v_{ki} , and u_{max} and the "independent variables" N_k . The computational procedure is to calculate in the following order:

- a) the u_{ki} using eq. (2),
- b) the q_{ij} and c_i from eq. (9),
- c) the a_{ij} and b_i from eq. (12) and (12a),
- d) the x_i and Y_k from eq. (15) and (16).

Computation of eq. (16) is straightforward and simple, no matter how many foods there may be. It is simply a matter of matrix inversion and matrix multiplication, operations routinely available on all computers. Experience has shown matrix \mathbf{A} to be well-conditioned in the sense described by Conte (1965: Sec. 5.4); it is therefore susceptible to inversion with reasonable precision. One circumstance in which \mathbf{A} may be ill-conditioned is when two search modes have u_{ki} so similar that they are not really distinct search modes.

Nonnegativity constraints

There is one complication however—that eq. (15) can generate negative x_i , which violate constraint (6b). This means some of the x_i must be set to zero and treated in eq. (15) as though they do not exist. That is, under some regimes of food abundances the predator may not utilize some search modes at all. The computational problem is to decide which x_i should be set to zero and which should be positive (i.e., included in eq. (15)).

The procedure presented below resembles that of Theil and Van de Panne (1961). It depends upon two conditions of the optimal solution: a) all x_i are nonnegative; b) an x_i equals zero only if its partial derivative, eq. (10), at the solution is larger (less negative) than the partial derivatives of the positive x_i . The first condition deals with the error of including an x_i in eq. (15) when it should be set to zero. The second condition deals with the opposite error of setting an x_i to zero when it should be positive.

The second condition deserves further explanation. The partial derivatives $\partial F/\partial x_i$, eq. (10), of all the nonzero x_i generated from eq. (15) are all equal to each other at a solution. Equation (15) simply implements eq. (7), which specifies that the derivatives are all equal. However, the derivatives of the zero x_i at the solution are not equal to the derivatives of the nonzero x_i , because the zero x_i were not included in eq. (15). If the derivative $\partial F/\partial x_i$ of any zero x_i is more negative than the derivatives of the nonzero x_i , then F will be decreased by shifting some effort to that x_i (making it positive), and it should be included in the solution of eq. (15). Conversely, if the derivative of a zero x_i is less negative than the derivatives of the nonzero x_i , then it is correctly set to zero.

The basic procedure is to start with an initial guess of which x_i should be zero and which should be positive. The zero x_i are removed from eq. (15) by deleting their rows and columns from the matrix \mathbf{A} and deleting their elements from the vector \mathbf{b} . (If x_0 is set to zero, the a_{ij} and b_i , eq. (12), must be redefined with one of the q_{ij} and c_i as negative terms in place of the $q_{m+1,j}$ and c_{m+1} .) Equation (15) is then solved. If the resulting x_i satisfy both conditions of the optimal solution, the problem is solved, and the Y_k may be computed from eq. (16).

If either or both of the conditions are not satisfied, then the status of x_i violating the conditions must be changed. Any nonzero x_i which are negative must be set to zero by deleting their elements from \mathbf{A} and \mathbf{b} before the next solution of eq. (15). Any zero x_i whose derivatives are more negative than those of the nonzero x_i must be returned to eq. (15) by adding their elements to \mathbf{A} and \mathbf{b} before the next solution. This process of solving eq. (15), checking for the two conditions of optimality, and setting x_i to zero or returning them to the solution is repeated until the two conditions are satisfied.

It is conceivable that a particular x_i may be set to zero and then restored to positive status before the optimal solution is reached, or vice versa. However, experience has shown there is never a problem of oscillation without reaching the optimal solution, and in fact the procedure has always converged rapidly to the optimum within a few steps, regardless of the initial guess.

In some situations the initial guess of which x_i should be zero and which should be positive may be a good one. For example, the values of x_i obtained from the previous step in a computer simulation or in the previous step of computing a response curve may provide the information. Computation is shorter if the initial guess is correct because solution of eq. (15) need not be repeated.

In some situations there may be no information for the initial guess. Experience has shown that as-

signing a positive value to all x_i in the initial guess results in rapid convergence to the solution. This is facilitated by the fact that eq. (15) never generates negative x_i which should be positive in the optimal solution, provided the elimination process starts with all x_i included in eq. (15).

PARAMETER ESTIMATION

If eq. (16) is to be verified experimentally, its parameters must be susceptible to measurement. This is easiest when the time (x_i) allocated to a particular search mode or the quantity (Y_k) of a particular food consumed is equal to one of the parameters. It is a matter of devising situations in which all parameters but one are of negligible effect.

For example, u_{\max} is the rate of consumption in a short period when the predator is hungry and food is in superabundance. The v_{ki} may be measured as the discovery rate when there is only food k and the predator is hungry and searching at maximum effectiveness. Alternatively, the u_{ki} may be measured as the quantities of different foods which are consumed under a particular regime of food abundances when the predator is in search mode i . All this supposes that the different search modes can be distinguished observationally and induced experimentally.

There are numerous ways to measure z_k and w_k

```

SUBROUTINE FEED(N,M,XN,V,UMAX,W,W0,Z,ZT,X,Y;
DIMENSION XN(1),V(5,5),W(1),Z(1),X(1),Y(1)
DIMENSION Q(6,6),A(6,6),U(6,6)
DIMENSION C(6),B(6),XX(6),DFDX(6),SUMUK(6)
M1 = M+1
DO 2 I=1,M
C INITIALIZE SUMMATIONS.
SUMUK(I) = 0.
C(I) = 0.
DENOM = 0.
C COMPUTE U FROM EQUATION (2).
DO 1 KP=1,N
1 DENOM = DENOM+V(KP,I)*XN(KP)
DENOM = UMAX+DENOM
DO 2 K=1,N
U(K,M1) = 0.
2 U(K,I) = UMAX*V(K,I)*XN(K)/DENOM
DO 5 I=1,M
C COMPUTE Q AND C FROM EQUATION (9).
Q(M1,I) = 0.
Q(I,M1) = 0.
DO 3 K=1,N
SUMUK(I) = SUMUK(I)+U(K,I)
3 C(I) = C(I)+U(K,I)*(W(K)*Z(K)+ZT)
DO 5 J=1,I
Q(I,J) = SUMUK(I)*SUMUK(J)
DO 4 K=1,N
4 Q(I,J) = Q(I,J)+W(K)*U(K,I)*U(K,J)
5 Q(J,I) = Q(I,J)
Q(M1,M1) = W0
C(M1) = W0
104 NI = 0
C ELIMINATE ZERO X(I) FROM A AND B.
DO 107 I=1,M1
IF(X(I))107,107,105
105 NI = NI+1
B(NI) = C(I)
NJ = 0
DO 107 J=1,M1
IF(X(J))107,107,106
106 NJ = NJ+1
A(NI,NJ) = Q(I,J)
107 CONTINUE
IMAX = NI-1

```

```

C COMPUTE A AND B FROM EQUATION (12) AND (12A).
DO 108 I=1,IMAX
B(I) = B(I)-B(NI)
DO 108 J=1,NI
108 A(I,J) = A(I,J)-A(NI,J)
DO 109 J=1,NI
109 A(NI,J) = 1.
B(NI) = 1.
C COMPUTE X FROM EQUATION (15).
CALL INVRT(A,NI)
CALL MULT(A,B,XX,NI,NI,1)
L = 0
NI = 0
DO 113 I=1,M1
IF(X(I))113,113,110
110 NI = NI+1
X(I) = XX(NI)
113 CONTINUE
C COMPUTE DERIVATIVES FROM EQUATION (11).
CALL MULT(Q,X,DFDX,M1,M1,1)
DO 115 I=1,M1
DFDX(I) = DFDX(I)-C(I)
IF(X(I))115,115,114
114 DER = DFDX(I)
115 CONTINUE
DO 118 I=1,M1
IF(X(I))120,116,118
C CHECK ZERO X(I) FOR DERIVATIVES MORE
C NEGATIVE THAN POSITIVE X(I).
116 IF(DFDX(I)-DER)117,118,118
C RETURN TO COMPUTATIONS ANY X(I) INCORRECTLY
C SET TO ZERO IN THE INITIAL GUESS.
117 X(I) = 1.
L = 1
GO TO 118
C SET NEGATIVE X(I) TO ZERO.
120 X(I) = 0.
L=1
118 CONTINUE
IF(L)119,119,104
C COMPUTE Y FROM EQUATION (16).
119 CALL MULT(U,X,Y,N,M1,1)
RETURN
END

```

Fig. 1. The computer program used for solving eq. (15) and (16) subject to constraints (6a) and (6b). The argument list of the computer program is $(n, m, N_k, v_{ki}, u_{\max}, w_k, w_0, z_k, z_T, x_i, Y_k)$. The first 10 arguments are input to the subroutine and the last two arguments are output. Note that x_i ($i = 1, m + 1$) is both input (each x_i set to either zero or any positive value, as an initial guess) and output. A duplicate of the first dimension statement must appear in the calling program, with dimensions set at n or larger ($m + 1$, in the case of x). The dimensions in the second and third dimension statements must be at least $m + 1$. The user must supply two subroutines for matrix operations. Subroutine INVRT (A, n_A) inverts matrix A of dimension n_A . Subroutine MULT (A, B, P, n_1, n_2, n_3) multiplies matrix A of dimensions $n_1 \times n_2$ by matrix B of dimensions $n_2 \times n_3$ to yield matrix P . The reader may verify for himself that the values of Y_k generated by this program are in fact optimal. If all primary determinants of the matrix Q are positive, then F in eq. (4) has only one minimum (Kunzi and Krelle 1966: 35-38). Whether the solution Y_k is at that minimum can be ascertained by computing the value of F in the neighborhood of the solution in order to see if any and all deviations from the solution cause F to become larger than at the solution. First compute F from eq. (4), based on the solution values of Y_k , and then recompute F from values of Y_k based on x_i adjacent to the solution values of x_i (subject to the constraints that the x_i must be nonnegative and sum to one).

in this fashion. For example, z_k is the quantity of the k th food which is consumed when there is no competition with desired consumption of any other food,

with total consumption, or with nonfeeding activity. This pertains when the k th food is present in superabundance (thereby requiring negligible time for its consumption and removing competition with non-feeding activity) and with an alternate, staple food in superabundance. (A staple food is considered here to have its consumption loosely controlled, i.e., w_k is small, and fills the gap between desired consumption of the test food z_k and total consumption z_T .) The parameter z_T may be measured separately as the quantity of staple food consumed when by itself in superabundance.

The weighting factor w_k is the strength with which the k th food is controlled at its desired consumption, despite competing demands for the predator's effort. Competition with nonfeeding activity is eliminated by having the k th food alone and in superabundance. Solving eq. (15) for this situation (derivation in appendix),

$$w_k = \frac{z_T - Y_k}{Y_k - z_k} \quad (17)$$

The value of w_k is indicated by where food consumption (Y_k) falls in the interval from z_k to z_T . If w_k is small (relative to the unity importance of total food consumption), consumption is near z_T ; if w_k is large, consumption is near z_k . Since all w_k will usually

be much less than unity, it may not be feasible with eq. (17) to measure the w_k with sufficient precision to assign them values relative to each other. It therefore may be appropriate to measure one or two w_k as above to ascertain their approximate magnitude, and then devise a test with foods in competition two at a time to determine the relative magnitudes of the w_k .

The weight w_0 may be measured from the time budget (x_i) when there is only a small quantity of staple food (derivation in appendix):

$$w_0 = \frac{z_T u_{ki}}{x_i} \quad (18)$$

CHARACTERISTICS OF THE PREDATION EQUATION

The properties of the predation equation will now be illustrated with a simplified version which retains the features of the general equation, using as few parameters as possible. The following simplifications have been applied to eq. (16):

- a) There is one search mode for each food; i.e., $m = n$ and all u_{ki} and v_{ki} are zero for k not equal to i .
- b) The total quantity of food desired is the sum of the desired quantities of each food, i.e.,

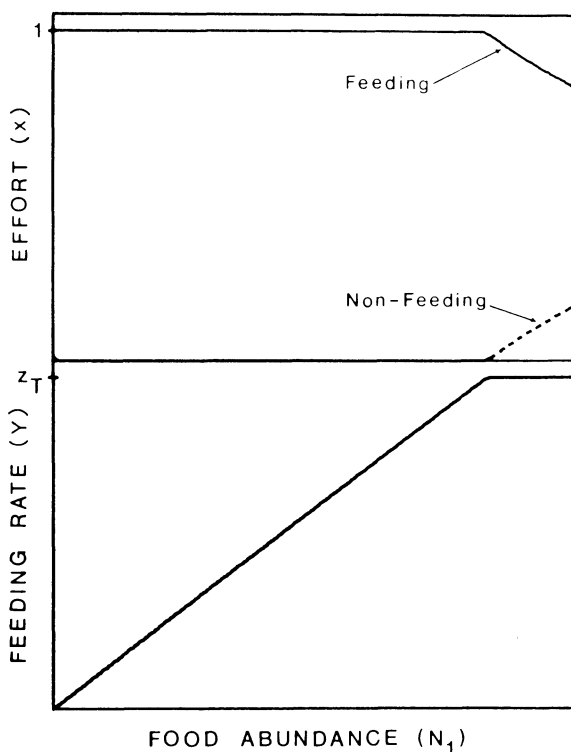


FIG. 2. Feeding rate proportional to food abundance until saturation: $n = 1, v_1 = 1.2, u_{max} = \infty, w_0 = 0, z_1 = 1$. Effort and food abundance in all figures have a full scale of unity.

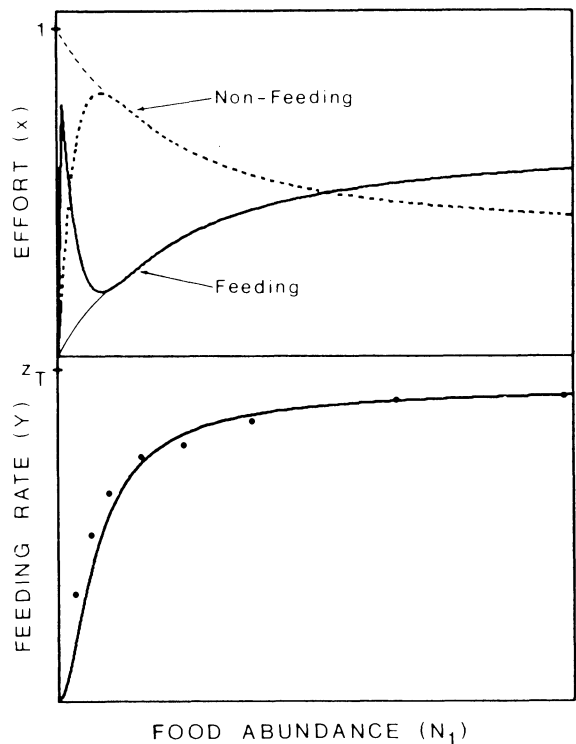


FIG. 3. Hyperbolic feeding response: $n = 1, v_1 = 2, u_{max} = 2.75, w_0 = 500, z_1 = 1$. The data points are for mantises feeding upon flies (Holling 1966). (The fitted curve is slightly sigmoid; the thin lines show the distribution of effort in a pure hyperbolic response.)

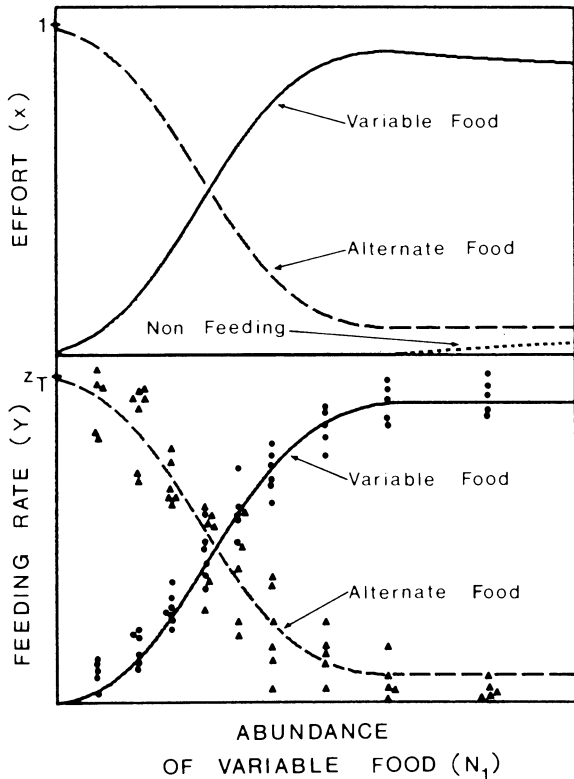


FIG. 4. Sigmoid feeding response: $n = 2$, $v_1 = 12$, $v_2 N_2 = 10$, $u_{max} = 1.1$, $w_1 = .8$, $w_0 = .008$, $z_1 = .92$, $z_2 = .08$. The data points are for deer mice feeding upon sawfly larvae with dog biscuits in superabundance as alternate food (Holling 1965). The alternate food in all figures is constant in abundance.

$$z_T = \sum_{k=1}^n z_k \quad (19)$$

c) The importance coefficients (w_k) have the same value for all foods.

The parameters of this special case are w_1 , w_0 , z_k , v_{kk} ($k = 1, \dots, n$), and u_{max} . The curves discussed below were generated with the computer program given in Fig. 1.

The predation equation can generate predator response curves with all the shapes reported in the literature. For example, a straight line to saturation (Fig. 2) is expected when the maximum processing rate (u_{max}) is much larger than desired feeding rate (z_T) and nonfeeding activities do not compete with feeding (i.e., w_0 is small). This results in a total effort being placed into feeding until the full feeding requirement is met.

Another kind of predator response is the hyperbolic curve (Fig. 3), which is well documented in a variety of circumstances (Morris 1963, Mook and Davis 1966). For example, u_{max} may be only slightly larger than z_T , in which case the hyperbolic character of eq. (1) dominates the feeding response. Alternately,

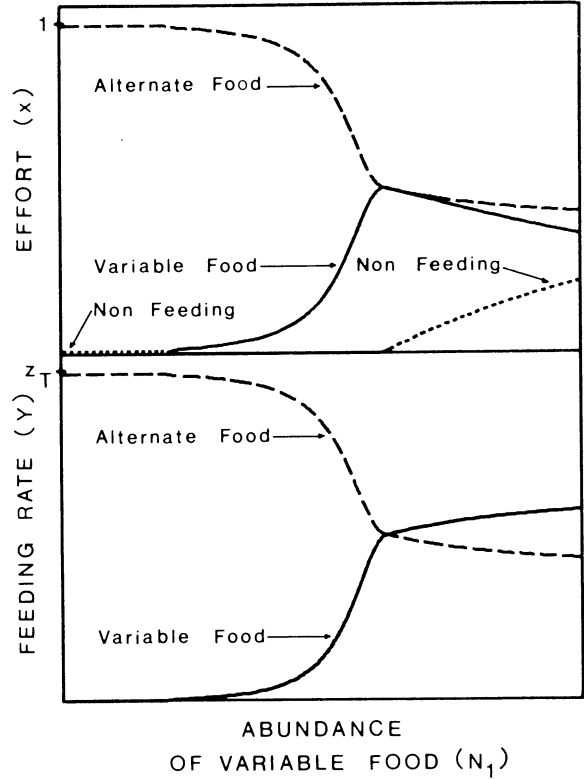


FIG. 5. Sigmoid feeding response with threshold and variety maintained in the diet: $n = 2$, $v_1 = 1.6$, $v_2 N_2 = .5$, $u_{max} = \infty$, $w_1 = .005$, $w_0 = .01$, $z_1 = .5$, $z_2 = .5$.

tively, w_0 may be large enough that less effort is put into feeding as satiation is approached, more effort being placed into competing, nonfeeding activities. (Nonfeeding activity may be passive, as with the mantis (Holling 1966), which does nothing when it is satiated.) Both effects are present in Fig. 3.

A sigmoid response (Fig. 4) is characteristic of predators which, when food abundances change, shift their emphases upon different foods competing for their attention. In the typical response, no effort is put into a particular food when its abundance is below a threshold; i.e., it is not worth the effort. Murdoch (1969) observed thresholds experimentally in predatory snails feeding upon mussels and barnacles. Above the threshold, the effort directed toward a particular food increases with its abundance, as pursuit of that food brings increasing rewards. Effort finally declines at high abundances as less effort suffices to satisfy food requirements. The sigmoid can be very strong, as in Fig. 5, or it can be weaker, as in Fig. 4. Variety may persist in the diet, even when one food is much more abundant than the other (Fig. 5). The sigmoid response in Fig. 4 and 5 is a consequence of competition between two foods for the predator's effort, but a sigmoid can also be generated by competition between feeding and nonfeeding activities.

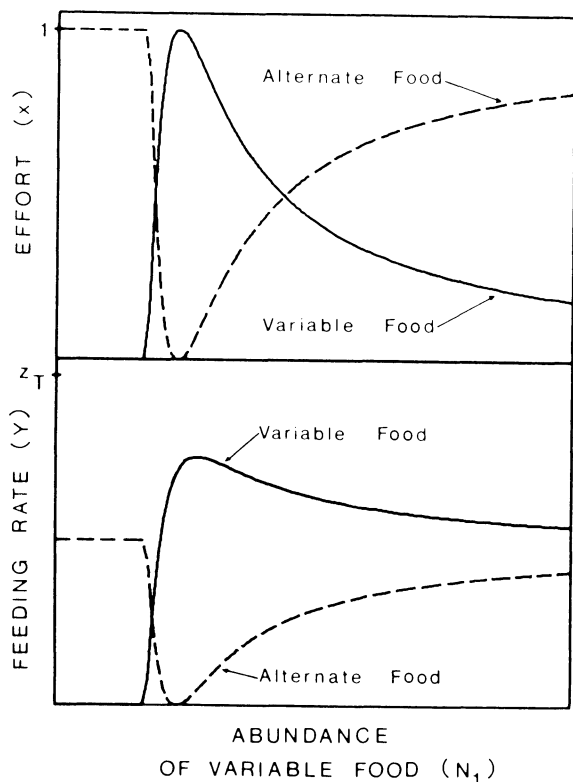


FIG. 6. Feeding response with peak feeding at intermediate abundance: $n = 2$, $v_1 = 4$, $v_2 N_2 = .5$, $u_{\max} = \infty$, $w_1 = .001$, $w_0 = .06$, $z_1 = 0$, $z_2 = 1$. The alternate food is preferred, but it is not available in sufficient abundance to satisfy the predator's total food demand (z_T).

The curves in Fig. 3 and 4 are not the best possible fits of eq. (16) to the data, and different parameter values could generate similar curves. The fit does not prove the validity of the optimization equation because an entirely different equation could conceivably fit the data equally well. What the fit does show is that the optimization equation is at least compatible with patterns of predator response observed in the real world.

Under some circumstances the pattern of first increasing and then decreasing effort as a food's abundance increases is so pronounced that consumption of the food does not increase continuously toward a plateau as it becomes very abundant. Instead, peak consumption of the food is at an intermediate abundance, and consumption declines as the food becomes more abundant. This effect is most pronounced (Fig. 6) when (a) the food is relatively unpalatable (i.e., its z_k is lower than for other foods) and (b) alternative foods are present but not in sufficient abundance to meet the total food demand (z_T). The type of predator response represented in Fig. 6 has not yet been reported in the literature, but it is reasonable to suppose it exists.

In addition to thresholds, there may be discontinuities in the middle of a response curve (Fig. 7),

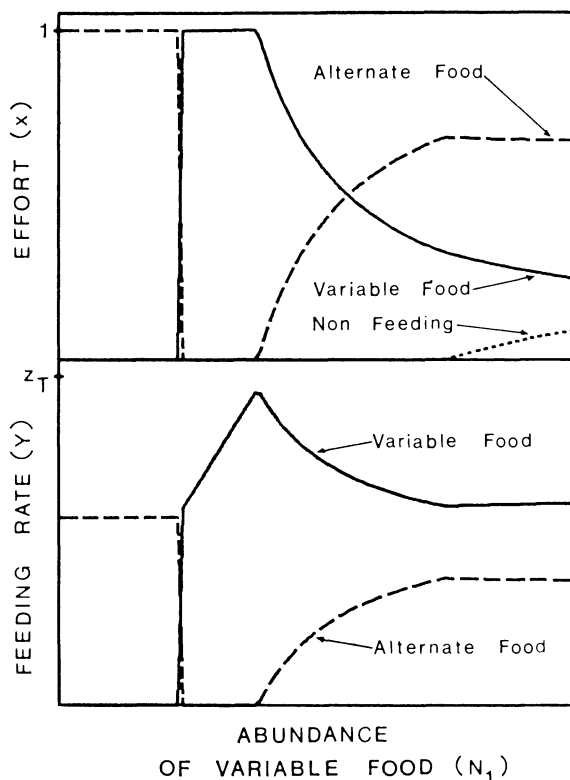


FIG. 7. Predator response similar to Fig. 6, but with discontinuities: $n = 2$, $v_1 = 2.5$, $v_2 N_2 = .5$, $u_{\max} = \infty$, $w_1 = .01$, $w_0 = .01$, $z_1 = 0$, $z_2 = 1$.

as other foods are switched in or out of the diet or as nonfeeding activity is switched in or out. We are not accustomed to thinking of predator responses with discontinuities as in Fig. 7, but such discontinuities may in fact be common.

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APPENDIX

Derivation of equation (2)

It is necessary to derive first the total food consumption ($\sum_k u_{ki}$) in a particular search mode i . From eq. (1),

$$\sum_k u_{ki} = \sum_k \left[v_{ki} N_k \left(1 - \frac{\sum_{k'} u_{k'i}}{u_{\max}} \right) \right].$$

Expanding and multiplying by u_{\max} ,

$$u_{\max} \sum_k u_{ki} = u_{\max} \sum_k v_{ki} N_k - \sum_k v_{ki} N_k \left(\sum_{k'} u_{k'i} \right).$$

$$\text{Noting that } \sum_k v_{ki} N_k \left(\sum_{k'} u_{k'i} \right) = \left(\sum_{k'} u_{k'i} \right) \left(\sum_k v_{ki} N_k \right)$$

and that $\sum_k u_{ki} = \sum_{k'} u_{k'i}$, factoring $\sum_{k'} u_{k'i}$ and $\sum_k u_{ki}$ out of all terms in which they appear, and solving for $\sum_k u_{ki}$

$$\sum_k u_{ki} = \frac{u_{\max} \sum_k v_{ki} N_k}{u_{\max} + \sum_k v_{ki} N_k}. \tag{A-1}$$

Substituting eq. (A-1) in eq. (1),

$$u_{ki} = v_{ki} N_k \left[1 - \left(\frac{u_{\max} \sum_k v_{ki} N_k}{u_{\max} + \sum_k v_{ki} N_k} \right) \right],$$

which yields eq. (2) upon expansion.

Derivation of equations (17) and (18)

Assume only the k th food is present and only one search mode prevails in the experimental situation. From eq. (9),

$$q_{11} = u_{k1}^2 + w_k u_{k1}^2$$

$$q_{12} = q_{21} = 0$$

$$q_{22} = c_2 = w_0$$

$$c_1 = u_{k1} (w_k z_k + z_T).$$

Substituting the above quantities in eq. (16), and solving for x_1 ,

$$x_1 = \frac{u_{k1} (w_k z_k + z_T)}{w_0 + (1 + w_k) u_{k1}^2} \tag{A-2}$$

If $w_k = 0$ (staple food), then

$$x_1 = \frac{u_{k1} z_T}{w_0 + u_{k1}^2}.$$

When u_{k1} is small (food scarce),

$$x_1 = \frac{u_{k1} z_T}{w_0},$$

which yields eq. (18) upon solving for w_0

Assume $w_k \neq 0$ and apply eq. (3) to (A-2):

$$Y_k = \frac{(w_k z_k + z_T) u_{k1}^2}{w_0 + (1 + w_k) u_{k1}^2}.$$

If $u_{k1} = \infty$ (k th food superabundant),

$$Y_k = \frac{w_k z_k + z_T}{1 + w_k},$$

which yields eq. (17) upon solving for w_k .