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A GENERAL MODEL OF OPTIMAL DIET

STUART A. ALTMANN and STEPHEN S. WAGNER

Department of Biology, University of Chicago
5712 S. Ingleside Avenue, Chicago, Illinois 60637

Recent field studies of primates, such as those reported in this symposium, have greatly extended our knowledge of what primates eat in the wild and have clearly demonstrated that each primate is, in its own way, a selective feeder. If we want to substantiate a claim that this selective feeding is adaptive, we must show that there is a reasonable approximation of what the animals eat to what they ought to eat. This, in turn, means that we must be able to specify an optimal diet. Those individuals in a population whose diets come closest to the optimum should have the highest expected fitness.

THE PROBLEM

The question that we pose is this: given the foods that are available to an animal, how much of each should it consume so as to be above its minimum for every nutrient, below its maximum for every toxin, and concurrently, either to minimize some cost function, such as time expended in foraging or exposure to predators while feeding, or else to maximize some benefit obtained from feeding, such as protein or caloric intake? We now describe how in general such optimal diets can be specified. The technique is currently being applied to an analysis of feeding behavior of baboons in Amboseli National Park, Kenya.

We consider food components not only in the conventional sense of chemical compounds (e.g. riboflavin) or classes of compounds (e.g. lipids, proteins), for each of which the amount ingested is some fraction of the weight of each food type consumed, but also in a more general sense to include properties, such as calories, cost, foraging time, and so forth, that may be expressed in units other than weight but that nonetheless are linear functions of the amount of each food type that is ingested. For every food component there is a minimum required intake rate, which in some cases may be small enough (e.g. zero) to have no coercive significance. A *nutrient* is a chemical component of food with a non-zero minimum, such that sickness or some other form of reduction in expected fitness occurs if an individual falls below this minimum for a sufficiently long period of time. Similarly there is an upper limit for every food component on the amount per unit time that can be consumed with impunity by the animal. Chemical components for which the upper limit is less than gut capacity are called *toxins* in the narrow sense. Many nutrients are known to be toxins at high intake levels. Beyond that, many toxic secondary compounds occur in wild plants, and may serve to protect plants from herbivores and microorganisms (Freeland & Janzen, 1974; Huges & Genast, 1973; Leopold & Ardrey, 1972; Levin, 1976; McKey, 1973;

Watt & Breyer-Brandwijk, 1962; Willamen & Schubert, 1961) and thus may be toxic at low levels of consumption. For nonchemical components, such as foraging time and cost, other factors will establish an upper limit.

For every component except one, intake variations above the minimum but below the maximum are assumed for the purpose of this model to have no significant effects on fitness. We further assume that within these upper and lower bounds, fitness is maximized only if the one exceptional component is maximized (if it is beneficial) or minimized (if it is detrimental). The amount in the diet of that component will be referred to either as a *cost function* or as a *profit function*, as appropriate.

THE MODEL

The following method treats in a single analytic framework the problems of meeting the requirements of food component minima (for nutrients, etc.) and maxima (for toxins, etc.), and satisfying the requirements of a cost or profit function.

Let p_{ij} be the amount per unit weight (e.g. proportion, calories per gram, minutes per gram, etc.) of the i-th component in the j-th available food and let M_i and T_i be respectively the required minimum and maximum for the i-th component. A diet is an ordered n-tuple $x = (x_1,.. x_n)$ of non-negative numbers, where x_j represents the amount of food j that is eaten and n is the number of available foods. Thus, in any diet x the amount of, say, the first component will be $p_{11}x_1+...+p_{1n}x_n$. If there are m components to be considered and the animal has n foods from which to choose, his adequate diets (i.e. those within his upper and lower bounds) are the set of all points satisfying the constraints

$$\begin{aligned} M_1 &\leq p_{11}x_1 +...+ p_{1n}x_n \leq T_1 \\ M_2 &\leq p_{21}x_1 +...+ p_{2n}x_n \leq T_2 \\ &\vdots \\ M_m &\leq p_{m1}x_1 +...+ p_{mn}x_n \leq T_m \end{aligned} \qquad (1)$$

where m is the number of components and

$$x_j \geq 0 \text{ for all } j.$$

If the i-th component is the one to be optimized (maximized or minimized), we define a function $F(x)$ equal to the summation in the i-th row of equations (1):

$$F(x) = p_{i1}x_1 + p_{i2}x_2 +...+ p_{in}x_n \;. \qquad (2)$$

The problem of finding the optimal diet is that of maximizing or minimizing F subject to the above constraints.

GRAPHIC INTERPRETATION

The linear diet model has a simple geometric interpretation. Suppose, for simplicity, that we are dealing with diets made up of just two foods, x_1 and x_2. If each axis of a graph is used to represent the amount of one

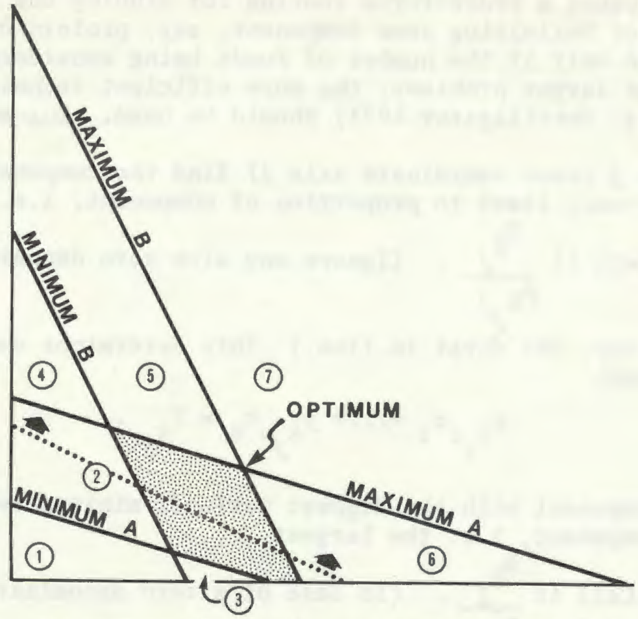

Figure 1. *Optimal diet problem with two foods (I and II), two components (A and B) and a profit function (dotted line). The dotted line is moved upward without changing slope until it cannot be moved higher without leaving the region of adequate diets (shaded area). It then touches the adequate region at the optimum (arrow). Circled areas represent unacceptable diets: 1 = not enough A and B; 2 = not enough B; 3 = not enough A; 4 = not enough B but too much A; 5 = too much A; 6 = too much B; 7 = too much A and B.*

food in the diet (Figure 1), every possible diet (every combination of x_1 and x_2) can be represented by a point. The set of all diets that contain the minimum acceptable amount of any given nutrient can be represented by a straight line, and likewise for the maximum of each toxin. Consequently, nutritionally adequate diets will form a convex polygon consisting of points that lie above all minima and below all maxima (shaded area on Figure). The component to be, say, maximized is represented in the Figure by the dotted line. To find the optimal diet geometrically, move this line upward, without changing its slope, until it cannot be moved higher without going outside the region of adequate diets. (If the component is to be minimized, the line is moved downward in the same manner.) The optimal diet is the adequate diet point (or points) that the dotted line then touches.

FINDING THE OPTIMUM

The constraint equations (1) determine a closed, bounded and convex subset of Euclidean n-space, representing all nutritionally adequate diets. The optimum is a corner point of this convex set or conceivable (but unlikely) an edge or facet defined by several such points. The optimum can be found by brute-force computation, e.g. finding all corner points, then choosing the one(s) for which F is minimal or maximal, as appropriate. We present without proof a brute-force routine for finding the optimal diet, worded in terms of maximizing some component, say, protein or calorie intake. It is practicable only if the number of foods being considered is small, say two to four. For larger problems, the more efficient techniques of linear optimization (e.g. Intriligator 1971) should be used. Our method is as follows.

For each food j (each coordinate axis j) find the component with the lowest ratio of toxic limit to proportion of component, i.e. the smallest of $\frac{T_1}{p_{1j}},\ldots,\frac{T_m}{p_{mj}}$. Call it $\frac{T_{k_j}}{p_{k_j j}}$. (Ignore any with zero denominator; in case of a tie, take, say, the first in line.) This determines one of the equations we shall use:

$$p_{k_j 1}x_1 + \ldots + p_{k_j n}x_n = T_{k_j} .$$

Also find the component with the highest ratio of minimum requirement to proportion of component, i.e. the largest $\frac{M_1}{p_{1j}},\ldots,\frac{M_m}{p_{mj}}$. Call it $\frac{M_{h_j}}{p_{h_j j}}$. (In case of a zero denominator, take that one; in case of a tie, do as before.) Check to see if $\frac{M_{h_j}}{p_{h_j j}}$ is greater than $\frac{T_{k_j}}{p_{k_j j}}$; if so, we use the equation

$$p_{h_j 1}x_1 + \ldots + p_{h_j n}x_n = T_{h_j} .$$

(If not, we shall use the equation $x_i = 0$.) Thus we have a set

$$\begin{array}{c} p_{k_1 1}x_1 + \ldots + p_{k_1 n}x_n = T_{k_1} \\ \vdots \\ p_{k_n 1}x_1 + \ldots + p_{k_n n}x_n = T_{k_n} \\ (p_{h_1 1}x_1 + \ldots + p_{h_1 n}x_n = M_{h_1}) \\ \vdots \\ (p_{h_n 1}x_1 + \ldots + p_{h_n n}x_n = M_{h_n}) \\ x_1 = 0 \\ \vdots \\ x_n = 0 \end{array} \qquad (3)$$

where the parentheses indicate that we omit the equation if $\frac{M_{h_j}}{p_{h_j j}} \le \frac{T_{k_j}}{p_{k_j j}}$.

From among these, we select a set of n equations to solve for $x = (x_1,\ldots,x_n)$. If they have a unique solution, we test the values in the inequalities of Equations (1) to see if it is an adequate diet. If so, it is a 'boundary point'. (If not, we ignore it.) We repeat this procedure for every possible set of n equations from among the set (3), in each case obtaining a boundary point diet if a unique solution exists. The convex hull of the set of all such boundary points is the set of nutritionally acceptable diets. We now examine all the boundary point diets to see which gives the largest F. That is the optimal diet. In case two or more give the maximum value of F, the convex hull of the set of all such is the set of optimal diets.

EXAMPLE

The procedure described above will now be applied to a human example. For simplicity, we assume that only three foods are available (fried breast of chicken, pink grapefruit, and pumpernickel bread) and that only three nutrients are involved (protein, vitamin A and iron). Nutritional requirements are for an adult male human (NRC/NAS 1974) and are given in Table I. Nutritional compositions were obtained from the literature (USDA, 1964). Toxic limits (Table I) were obtained from Davidson *et al.* (1972). Gut capacity was estimated to be 5 kg per day. Costs are those at our local grocery, February 10, 1975. The food budget was taken to be \$3.00 per day. The question is, what amounts of these three foods provide an optimal diet, here taken to be a nutritionally adequate diet at the least possible cost?

TABLE I

Food Components: daily minima, proportions in three foods, and daily maxima. Notation: 7.5*E*-7 *means* 7.5×10^{-7}

Component	Min	Foods: Fried Chicken	Foods: Pumpernickel Bread	Foods: Grapefruit	Max
Protein (g)	44.0	0.27	0.0903	0.0041	5000
Vitamin A (g)	7.5*E*-7	2.23*E*-7	0.0	6.72*E*-7	0.03
Iron (g)	0.01	1.38*E*-5	2.4*E*-5	2.08*E*-6	0.1
Other (g)	0.0	0.716	0.9096	0.9958	5000
Cost (U.S.\$)	0.0	1.607*E*-3	1.046*E*-3	1.55*E*-4	3.00
Weight (g)	0.0	1.0	1.0	1.0	5000

For these data, solution of 56 sets of linear equations yielded exactly nine boundary point diets. The composition of these diets and their costs are given in Table II. The convex hull of the set of boundary point diets is the set of nutritionally adequate diets. These are shown in Figure 2. The unique optimal diet is Diet 2.

DISCUSSION

We assume as a first approximation that the various nutrients and toxins exert their effects independently. Some interaction effects are known, however. For example, gut absorption of sugars, amino acids, and several

TABLE II

Boundary point diets (gm/day), based on data in Table I.

	Foods			Components				
Diet	Fried Chicken	Pump. Bread	Grape-fruit	Protein	Vitamin A	Iron	Other	Cost/Day($)
1	0.0	487.2	1.12	min	min	.012	488.3	0.509
2	3.36	477.2	0.0	min	min	.011	480.6	0.504
3	0.0	272.6	4727.4	min	3.18*E*-3	.016	max	1.02
4	88.38	0.0	4911.6	min	3.32*E*-3	.011	max	0.903
5	0.0	2867.9	1.12	258.9	min	.068	2869	max
6	3.36	2862.9	0.0	258.4	min	.068	2606.5	max
7	0.0	2497.1	2502.8	235.7	1.68*E*-3	.065	max	max
8	1532.4	0.0	3467.6	427.9	2.67*E*-3	.028	max	max
9	1866.8	0.0	0.0	504	4.16*E*-4	.025	1866.8	max

other nonelectrolytes depends on the sodium concentration in the intestinal lumen (Schultz & Curran, 1968; Crane, 1968), and amino acids may compete for absorption (Cori, 1926-27). If these interaction effects are of appreciable magnitude, nonlinear optimization may be required (Intriligator, 1971).

Because the p_{ij}'s in equations (1) and (2) are not required to be less than one but can take on any real value, our model is able to accommodate hierarchically arranged food component requirements. Calories, for example, are obtained from just three food components, proteins, lipids, and carbohydrates, and although each of these has its own dietary minimum and maximum, there is as well a dietary requirement for calories. By using 'Atwater factors,' the number of calories per unit weight of each food can be calculated as a linear function of the amount of protein, lipid, and carbohydrate in that food (Southgate & Durnin, 1970), but all that is required for the model are the results, that is, the number of calories per gram for each food, which are then used to write a constraint equation for calories. A separate constraint equation is also written for the limits on each of the three contributors to calories.

Beyond that, caloric intake may in some cases be the appropriate function to be maximized. Many current theories of foraging behavior are based on energy maximization (Charnov, 1975; Estabrook & Dunham, 1976; Pulliam, 1975; Schoener, 1971; and references therein). As Estabrook and Dunham note, none have dealt with the problem of a balanced diet, yet it is well known that calories alone are not sufficient to run the machinery of the body. In a future publication, we shall demonstrate the applicability of the optimal diet model presented here to analysis of feeding behavior in wild primates.

After developing the above model of optimal diet, we learned about the pioneering work on the optimal diet problem by Stigler (1945) and subsequent related work in linear programming. Stigler searched for least-cost combinations of food that were nutritionally adequate, but had no general solution to the problem of minimizing a linear function with linear constraints. Since that time, the least-cost diet that satisfies requirements for nutrient minima has become one of the favorite textbook illustrations of a linear optimization problem, even (as one of us recently learned from his child) at the ninth-grade level. Pulliam (1975) has used linear optimization to

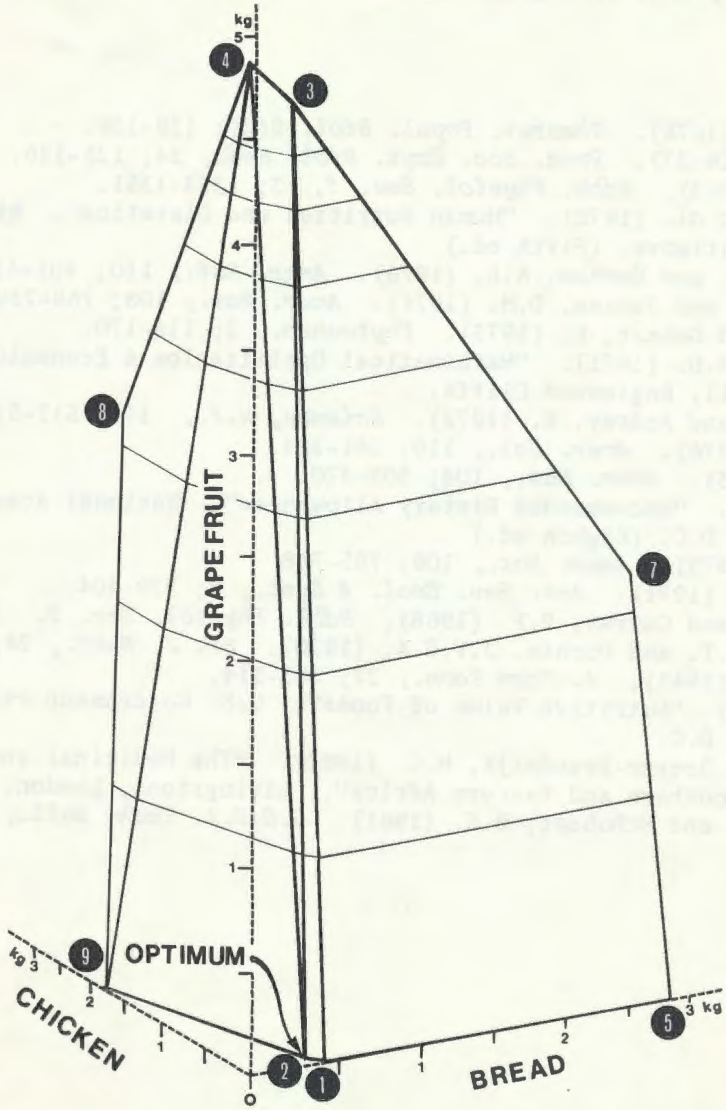

Figure 2. Adequate diets (polyhedron) and optimal diet (point 2). Based on Table II. Points are numbered to correspond to the boundary point diets in Table II.

model a mobile predator maximizing its rate of caloric intake, with lower bounds set by nutrient requirements and upper bounds set by the rate at which the predator encounters its prey.

The significance of our model is that it places into a single analytic framework the problem of finding an optimal diet in the face of nutrient requirements, toxin limits and hierarchically-organized food components, and does so in a way that can be related to the fitness of the organism.

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