BEYOND SELECTION: OPTIMAL INGESTION RATE AS A FUNCTION OF FOOD VALUE

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Submitted April 29, 1980; Accepted January 12, 1981

Food preference can be expressed in two ways: selection among the food items available to be eaten, and the subsequent setting of the ingestion rate on the item selected (Nicotri 1980). Many factors influence food preferences of animals. Optimal foraging theory has been used increasingly to explain or predict the components of an animal's diet (Schoener 1971; Pyke et al. 1977), most often from the viewpoint of maximizing energy intake per unit time (e.g., Davies 1977; DeBenedictis et al. 1978; Belovsky 1978; but see Goss-Custard [1977] for an exception). Factors other than energy content can affect an animal's choice of food items. Thus, organic nitrogen content (Tenore 1977), essential amino acids (Greenstone 1979), indigestible or toxic components (Milton 1979; Geiselman 1980), ease of absorption (Vadas 1977), and degree of crypsis (Erichsen et al. 1980) of food are important during choice of diet.

An explicit assumption of most optimal foraging models (reviewed by Pyke et al. 1977) is that the forager is indeed capable of choosing among individual food items, placing explicit emphasis on the selection process rather than on feeding rate. While the existence of such behavior-mediated selective ability is a realistic assumption for macrophages, it is probably unrealistic for microphages. Macrophage and microphage are terms originally introduced by Jordan and Hirsch (1927; cited in Yonge 1928). I use these terms here in the sense of Fauchald and Jumars (1979); at the risk of overgeneralization, a macrophage typically treats food items singly, while a microphage handles food items in bulk without manipulating them individually (e.g., most aquatic suspension and deposit feeders are microphages). Hence, contrary to the most basic predictions of classical optimal foraging models for macrophagous predators (Schoener 1971), "unsuitable" items (e.g., items of low food quality) regularly are included in the diets of microphages (e.g., Foster-Smith 1975; Widdows et al. 1979). While deposit and suspension feeders do feed selectively (e.g., Hylleberg 1975; Wilson 1973), their selectivity is most accurately modeled as a stochastic process (e.g., Jumars et al. 1981). Much of the selectivity of tentaculate deposit feeders, for example, appears to be a direct consequence of the mechanics of operation of the feeding appendages (Self and Jumars 1978).
Mobile microphages can select among patches of food for those of highest quality (Robertson et al. 1980), but for sessile and discretely motile (Jumars and Fauchald 1977) microphages patch selection cannot usually occur after initial larval or juvenile settlement. The optimal foraging abilities of these latter types of microphages would at first seem to be limited severely. An earlier deposit feeding model (Taghon et al. 1978) and efforts to test it (Taghon, in prep.) have led, however, to close attention to alteration of ingestion rate as a mechanism for optimizing net rate of energy gain under the constraints imposed upon sessile microphages.

Once an animal has chosen or been exposed to a particular food type, its ingestion rate constitutes another point where control over rate of energy intake is possible. Several factors are known to be capable of influencing ingestion rate: food abundance (in suspension-feeding rotifers [Starkweather et al. 1979]; in suspension-feeding insects [Dadd 1971]; in herbivorous zooplankton [Mullin et al. 1975; Reeve and Walter 1977; Frost 1972]; in suspension-feeding bivalves [Winter 1978]; in anuran larvae [Wassersug 1975; Seale and Wassersug 1979]); food palatability, expressed as either ease of absorption (Calow 1975a; Schindler 1971; Hargrave 1970; Streit 1978; Vadas 1977) or food texture (Kaushik and Hynes 1971; Anderson and Grafius 1975; Grafius and Anderson 1979); food processing capacity and feeding time available (Belovsky 1978); and some measure of nutritional content (e.g., Himmelman and Carefoot 1975; Calow 1975a; Gordon 1966; Hylleberg 1975; Monakov 1972; Frankenberg and Smith 1967; Gelperin 1971; Vadas 1977; Cammen 1980). Given that an animal has both limited selective abilities among food items and a limited ability to seek out new food patches, then varying gut passage times and ingestion rates as a function of the available food's nutritional quality would appear to be the principal remaining method of maximizing net rate of energy intake.

Over the past several years two schools of thought have arisen on the effects of food quality on ingestion rate. One group reports that ingestion rates vary inversely with food quality (e.g., Calow 1975a; Streit 1978; Cammen 1980), which would act as a mechanism for maintaining constant intake rate of some food component, such as energy (Calow 1975b). Conversely, others find ingestion rates to be positively related to food quality (e.g., Frankenberg and Smith 1967; Hylleberg 1975). Cook and Cockrell (1978) developed an optimal ingestion rate model for macrophages. However, their model relates ingestion rate of the predator to intercatch interval, a measure of prey density, not to any measure of food quality. Here I present a simple model to predict an animal's optimal ingestion rate as a function of the nutritional quality of its food. It is tailored specifically to microphages, allowing considerable simplification over models for animals with greater opportunities for food item selection. For example, pursuit time, handling time, and intercatch interval are not as crucial for organisms which handle their food items in bulk. The model's basic prediction is that an optimal ingestion rate exists for any given quality of food, and that this optimal ingestion rate should increase as food quality increases for the microphage to maximize its net rate of gain.
THE MODEL

For the model’s currency (sensu Schoener 1971) let $E$ represent any component of the animal’s food that is requisite for life and successful reproduction; $E$ could thus be energy, essential amino acids, organic nitrogen, trace elements, etc. It is, perhaps, easiest to think of $E$ in energy terms such as calories. Then, considering the feeding process only,

$$ E_n = E_t - E_c $$

where $E_n$ is the net time rate of energy intake (cal/t), $E_t$ the time rate at which energy is gained from ingestion and absorption of food (cal/t), and $E_c$ the time rate at which energy is expended to collect, ingest, and process that food (cal/t). Now,

$$ E_i = E_i \text{ (ingestion rate, energy content of food, efficiency of energy absorption)} $$

and

$$ E_c = E_c \text{ (ingestion costs, digestion costs, search costs, handling costs).} $$

The model to be developed assumes the costs of feeding ($E_c$) are the same for all food types; that is, at a given ingestion rate, it costs the same to feed on a “high quality” as on a “low quality” food. This assumption seems realistic for such microphages as aquatic deposit feeders but may be unrealistic for those situations in which physical differences among food types can correlate with nutritional quality and might affect the animal’s ingestion costs (e.g., Belovsky 1978; Milton 1979). In addition, the model assumes that ingestion rate depends only on food quality and that a given food type is supplied at a rate which keeps its availability constant. The terms “quality” and “quantity” may appear to be ambiguous in this context. For example, one phytoplankter will be of higher quality than a second individual if it has a higher carbon content; however, it can also be described as having a greater quantity of carbon. To remove this ambiguity, let quantity refer to the volume or numerical abundance of food items available to a microphage and food quality to some measure of the food’s nutritional worth per unit volume or per item. For example (given constant size of the individual items), the concentration of algal cells or number of sediment particles available would be a measure of food quantity and the carbon content per cell or per particle would be a measure of food quality.

For a microphage, (3) can be reduced to

$$ E_c = E_c \text{ (ingestion costs, digestion costs),} $$

since handling costs can be considered part of ingestion costs for a bulk feeder, and search costs are either often inseparable from costs associated with general locomotion (e.g., a herbivorous zooplankter) or effectively zero (e.g., sessile suspension or deposit feeding benthos). Ingestion costs include the costs of physical activities associated with movement of feeding structures during capture and ingestion of food, while digestion costs cover the biochemical costs of ab-
sorbing the ingested food. For simplicity, these costs will be combined and expressed as a function of ingestion rate during subsequent model development. Then

\[ E_n = I E_f A_e - K_1 I^x \]  

(5)

where \( I \) is ingestion rate (food items/h); \( E_f \) is energy content of the food ingested (cal/food item); \( A_e \) is the animal's absorption efficiency on the food ingested (dimensionless, varies from 0 to 1); \( K_1 \) is a positive constant transposing \( I^x \) into units of calories per unit time; and \( x > 0 \). It seems reasonable that for microphages which spend most of their time feeding (Croll and Smith 1978; LaTouche 1978; Taghon, personal observations), the costs of feeding should be a function of the rate at which feeding takes place. Power functions of ingestion rate to represent the costs of feeding have been used, with good results, in other models dealing with microphage feeding dynamics (Lam and Frost 1976; Lehman 1976). For the exponent of this model, the limiting case, \( x = 0 \), results in a constant cost of feeding regardless of the magnitude of the ingestion rate and is clearly unreasonable. While it might be preferable to restrict \( x \) to \( x \geq 1 \), it is possible that bulk handling of food particles may result in disproportionately small increases in \( E_c \) as \( I \) increases. For this reason, \( x \) was permitted to take on values less than 1 in the model, even though such values may be unrealistic.

Three cases for absorption efficiency were also investigated. In case 1, absorption efficiency did not vary with ingestion rate but was constant (Conover 1966; Corner et al. 1972; Schindler 1971). Other studies have shown that ingestion rate and absorption efficiency are inversely related (Calow 1975a; Schindler 1971; Widdows 1978; Dallinger and Wieser 1977), in support of the idea that absorption of food nutrients is more efficient when food passes slowly through the gut. Accordingly, in case 2 absorption efficiency decreased linearly with ingestion rate, and in case 3 the decrease was exponential.

\section*{RESULTS}

\textit{Case 1.}—To solve for optimal ingestion rate, take the derivative of (5) with respect to \( I \) where absorption efficiency is constant and positive,

\[ \frac{dE_n}{dI} = E_f A_e - x K_1 I^{x-1}. \]  

(6)

To solve for the critical ingestion rate, \( I^* \), set (6) equal to zero,

\[ I^* = \left( \frac{E_f A_e}{x K_1} \right)^{\frac{1}{x-1}}. \]  

(7)

The \( I^* \) then represents the ingestion rate where \( E_n \), the net time rate of energy gain, will be maximal or minimal depending on the sign of the second derivative of (5). \( I^* \) is not the ingestion rate at the critical food concentration referred to in zooplankton feeding studies [e.g., McMahon and Rigler 1963].

\[ \frac{d^2E_n}{dI^2} = -x(x - 1)K_1 \left( \frac{E_f A_e}{x K_1} \right)^{\frac{x-2}{x-1}}. \]  

(8)
For $x > 1$, $d^2E_n/dI^2$ is always negative, therefore $E_n$ reaches a maximum at $I^*$. From (7), $I^*$ increases directly with $E_f$, the nutritional value of the food. Therefore, an animal for which $x > 1$ should increase its ingestion rate on higher quality foods to maximize its net rate of gain. It is in this sense that $I^*$ represents the "optimal" ingestion rate.

When $0 < x < 1$, (8) becomes a positive quantity, and now $E_n$ is at a minimum at $I^*$. The exponent in (7) becomes negative, and (7) is better rewritten as

$$I^* = \left( \frac{xK_1}{E_f A_e} \right)^{\frac{1}{1-x}}. \quad (9)$$

Now, as food quality increases, $I^*$ will decrease. However $E_n$ is now minimized at $I^*$, so $E_n$ will, by definition, be greater for $I$ values both greater and less than $I^*$. $I = 0$ will always be less than $I^*$ since from (9), $I^*$ is a positive number. From (5), $E_n = 0$ at $I = 0$. Therefore, for $E_n$ to be minimized at $I^*$ it must be negative. An animal must adjust $I$ to be greater than $I^*$ under these conditions to maintain a positive $E_n$. Indeed, for any $E_f$ the animal should maintain its maximum possible ingestion rate if it falls in this category (constant absorption efficiency, $0 < x < 1$), but only if $E_n$ can be made positive by doing so. Otherwise, it would be preferable to cease feeding until, for instance, food quality increased to a level where $E_n$ became positive.

For the remaining possibility, $x = 1$, (7) cannot be evaluated. Returning to (5),

$$E_n = I \left[ E_f A_e - K_1 \right]. \quad (10)$$

As long as the bracketed quantity is greater than 0, the animal again should maintain its maximum possible ingestion rate to maximize $E_n$. If the bracketed term is 0 or less, a deficit in $E_n$ exists for any $I$; as above, feeding should cease until food quality increases sufficiently to insure a positive net rate of energy gain.

Case 2.—For a linear decrease in absorption efficiency with increased ingestion rate, (5) becomes

$$E_n = IE_f \left[ (A_e)_{0} - K_2 I \right] - K_1 I^x \quad (11)$$

where $(A_e)_{0}$ is the maximum absorption efficiency; $0 < (A_e)_{0} < 1$ and $0 < K_2 \leq (A_e)_{0}/I_{\text{max}}$, where $I_{\text{max}}$ is the maximum ingestion rate the animal is capable of maintaining. Differentiating (11) with respect to $I$ gives

$$\frac{dE_n}{dI} = E_f (A_e)_{0} - 2K_2 E_f I - K_1 x I^{(x-1)}, \quad (12)$$

such that

$$I^* = \frac{E_f (A_e)_{0}}{2K_2 E_f + K_1 x I^{(x-2)}}, \quad (13)$$

The second derivative, evaluated at $I^*$ is

$$\frac{d^2E_n}{dI^2} = -2K_2 E_f - K_1 x (x - 1) I^{(x-2)}, \quad (14)$$

which is always negative in sign for $x \geq 1$. Therefore, $E_n$ is maximal at $I = I^*$. 


From (13) it is not immediately apparent how \( I^* \) varies with \( E_f \). From (12) another expression for \( I^* \) can be obtained:

\[
\frac{K_1 x I^*(e^{-1})}{E_f(A_e)_0} + \frac{2K_2 I^*}{(A_e)_0} - 1 = 0. \tag{15}
\]

By inspection, we see that as \( E_f \) increases \( I^* \) will asymptotically approach \((A_e)_0/2K_2\). That \( I^* \) is monotone nondecreasing as food quality increases was confirmed by solving (15) iteratively over a wide range of parameter values.

Data from Richman's (1958) classic study on the energetics of *Daphnia pulex* and from Lehman's (1976) subsequent use of Richman's results in his feeding model can be used to evaluate the equations derived in this section. Richman used four different concentrations of algae during his feeding experiments, ranging from 25,000 to 100,000 cells/ml, and found a constant filtering rate (thus an increasing ingestion rate assuming constant filtration efficiency) and an approximately linear decrease in assimilation with increasing cell concentration. Comparison of Richman's experimental results with model predictions (table 1, case 2) shows the optimal ingestion rates predicted by the model are quite reasonable.

The sign of (14) could become positive for \( 0 < x < 1 \), depending on the magnitude of the other equation parameters. If this occurs, \( E_n \) would now be

<table>
<thead>
<tr>
<th>Food Concentration ( (\text{cells/ml}) )</th>
<th>( I^* ) ( (\text{cells/min}) )</th>
<th>( E_n ) ( (\text{cal/min}) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>25,000</td>
<td>43</td>
<td>( 1.3 \times 10^{-5} )</td>
</tr>
<tr>
<td>50,000</td>
<td>88</td>
<td>( 1.1 \times 10^{-5} )</td>
</tr>
<tr>
<td>75,000</td>
<td>130</td>
<td>( 1.3 \times 10^{-5} )</td>
</tr>
<tr>
<td>100,000</td>
<td>147</td>
<td>( 1.4 \times 10^{-5} )</td>
</tr>
</tbody>
</table>

**TABLE 1**

**COMPARISON BETWEEN RICHMAN'S (1958) DATA ON DAPHNIA PULEX FEEDING AND PREDICTIONS FROM THE OPTIMAL INGESTION RATE MODEL**

<table>
<thead>
<tr>
<th>( (A_e)_0 ) ( (\text{cells/min}) )</th>
<th>( I^* ) ( (\text{cells/min}) )</th>
<th>( E_n ) ( (\text{cal/min}) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>.25</td>
<td>74</td>
<td>( 1.2 \times 10^{-5} )</td>
</tr>
<tr>
<td>.50</td>
<td>148</td>
<td>( 4.8 \times 10^{-5} )</td>
</tr>
<tr>
<td>.75</td>
<td>222</td>
<td>( 1.1 \times 10^{-4} )</td>
</tr>
<tr>
<td>1.0</td>
<td>297</td>
<td>( 1.9 \times 10^{-4} )</td>
</tr>
</tbody>
</table>

† Data are averages for Richman's pre-adult *Daphnia* (0.7 and 1.3 mm size classes). Ingestion rate \( I \) calculated as food concentration times filtering rate, assuming 100% filtration efficiency. Net rate of energy gain \( E_n \) calculated as energy consumed times percent assimilated.

‡ For parameters in equations (11) and (13), \( E_f = 1.3 \times 10^{-6} \text{cal/cell} \), \( K_2 = .00167 \text{min/cell} \) (Richman 1958); \( K_1 = 2.4 \times 10^{-11} \text{cal/min/cell}^2 \), \( x = 2 \) (Lehman 1976). Values of \( x < 2 \) result in very small increases in \( I^* \) and \( E_n \). The maximum assimilation efficiency Richman found was .24.

§ Parameters for equations (16) and (17) same as in case 2, except \( K_2 = 100 \), assuming \( (A_e)_0 = .5 \) and \( I_{\text{max}} = 147 \text{cells/min} \). As in case 2, values of \( x < 2 \) result in very small increases in \( I^* \) and \( E_n \). When \( K_2 = 50 \), \( I^* \) and \( E_n \) are half of those tabled, while letting \( K_2 = 200 \) results in doubling of the tabled values.
minimized at $I^*$, just as it was when $0 < x < 1$ in case 1. The argument presented previously is valid now as well. Thus, if (14) is positive, the net time rate of energy gain ($E_n$) will be negative when the animal is feeding at $I^*$. If the animal cannot maintain a positive $E_n$ by increasing its ingestion rate above $I^*$, as in case 1, the best strategy would be to stop feeding until food quality increased to a point where (11) became positive for some $I$. The point here is that ingestion rate will never increase on lower quality food if the net rate of energy gain is being maximized. When in fact $x$ was allowed to become less than 1 and the model run using Richman’s data, (14) was always negative in sign, and the tabled values of $I^*$ and $E_n$ varied little as $x$ changed. Therefore, the $I^*$ values in table 1 result in maximal $E_n$ values, and both sets of numbers are in good agreement with Richman’s experimental results.

Case 3.—When absorption efficiency exponentially decreases with ingestion rate, (5) can be written as

$$E_n = I E_f [(A_e)_0 e^{(-K_2I)}] - K_1 I^x. \tag{16}$$

$K_1$ and $K_2$ are positive constants, $K_2 \geq I_{max} \ln (A_e)_0$ where $I_{max}$ is again the maximum ingestion rate the animal is capable of maintaining and $(A_e)_0$ is the maximum absorption efficiency, $0 < (A_e)_0 \leq 1$.

$$\frac{dE_n}{dI} = E_f [(A_e)_0 e^{(-K_2I)}] - \frac{K_2 e^{(-K_2I)}}{I} - K_1 I^{x(\times - 1)} \tag{17}$$

and

$$\frac{d^2E_n}{dI^2} = -\frac{K_2 e^{(-K_2I)}}{(I^*)^3} - K_1 x(1 - 1)(I^*)^{(x-2)}. \tag{18}$$

Equation (17) can be solved by iterative methods for $I^*$ as a function of $E_f$. Figure 1 shows this relation for several values of $K_2$, holding all other parameters constant, and figure 2 shows the results of letting only $x$ vary. Again $I^*$ is monotone nondecreasing with $E_f$, as in previous results.

Richman’s (1958) data on *Daphnia* energetics can once more be used to see if these equations result in biologically reasonable predictions of ingestion rates (table 1, case 3). Again, the agreement between predicted and observed values is good.

For $x \geq 1$, (18) is always negative, so the ingestion rate–food quality relations shown in figures 1 and 2 result in maximal values of $E_n$. If $x < 1$, (18) could become positive, which would lead to minimal values of $E_n$ when the animal was feeding at $I^*$. However, as in case 2, (18) was always negative for $x < 1$ when parameter values corresponding to Richman’s (1958) results were used in the model, and optimal ingestion rate increased with food quality.

**DISCUSSION**

These simple models show the existence of an optimal ingestion rate which maximizes the net time rate of energy gain and is a function of the quality of food available to microphagous feeders. Generally, the models predict that an opti-
Fig. 1.—The optimal ingestion rate ($I^*$), which maximizes the net rate of energy gain to an animal, as a function of food nutritional value ($E_f$), for case 3 of the model (see text). Units are arbitrary. $x = 2, K_1 = 1, (A_v)_0 = 1$, while $K_2$ was permitted to vary.

Fig. 2.—The optimal ingestion rate ($I^*$), which maximizes the net rate of energy gain to an animal, as a function of food nutritional value ($E_f$), for case 3 of the model (see text). $K_1 = K_3 = 1; (A_v)_0 = 1; x$ variable.

mally feeding animal should increase its ingestion rate as food quality increases. An examination of experimental studies on ingestion rate–food quality interactions reveals no clear tests of the models presented here. As mentioned earlier, empirical results fall into two general categories: Ingestion rate decreases with increased food quality, or it increases. Among the former studies, Cammen (1980) and Monakov (1972) found that ingestion rate is inversely correlated with the organic matter content of sediment for a variety of aquatic deposit feeders, but correlated factors such as sediment texture were not considered. Gordon (1966) also found that a deposit-feeding polychaete reworks sediments at a rate inversely proportional to sediment pigment concentrations, but the relationship between pigment concentration and nutritional value is not clear. A negative relationship between absorption efficiency and ingestion rate exists for a gastropod (Calow 1975b) and an oligochaete (Streit 1978); however, the relationship (if any) between food
quality and absorption efficiency is unknown. Freshwater invertebrate herbivores feeding on different leaves have lowest ingestion rates on those leaf types that lead to greatest weight gains (Barlocher and Kendrick 1973; Iverson 1974; Barbosa and Greenblatt 1979). Again, the effects of texture and composition (e.g., structural carbohydrates, secondary plant metabolites) on ingestion rate are not easily separated from the effects of nutritional value. Himmelman and Carefoot (1975) for a chiton and Vadas (1977) for sea urchins reported that ingestion rates correlate inversely with caloric content of food, but since several food types were used in these studies, the possibility of variables other than caloric content influencing ingestion rate again cannot be dismissed.

Studies otherwise similar to those reviewed above have shown the opposite trend of increased ingestion rate on higher quality food. The same ambiguities exist. Thus, Hylleberg (1975) observed that a deposit-feeding polychaete decreases its feeding rate when given sediments which had been ignited to oxidize all organic matter; changes in other sediment parameters as the result of ignition are unknown. Cadée (1976) found a positive correlation between rate of feces production in a deposit-feeding polychaete and the primary production rate of benthic microalgae; both these parameters are correlated with temperature as well, making any food quality–ingestion rate relationship less clear. Doyle (1979) showed that a deposit-feeding crustacean increases its ingestion rate as more natural sediment floc is added to a sediment floc-glass bead mixture, but sediment composition variations again could have an effect. Frankenberg and Smith (1967), in their classic study of coprophagy, found that a variety of marine animals have ingestion rates positively correlated with carbon and nitrogen content of the feces fed them. Since these feces came from a variety of other animals, interspecific differences in the texture and other characteristics of the feces cannot be excluded as factors in determining the observed trends in ingestion rate. Hargrave (1970) found a positive relationship between absorption efficiency and ingestion rate for a deposit-feeding amphipod, but again the relationship with food quality is unclear. Pechenik and Fisher (1979) found that a snail has the highest ingestion rate on the alga that produces the greatest rate of growth in the snail, but palatability effects are unknown. Freshwater stream invertebrates increase their ingestion rates as their leaf foods become more “conditioned” by microorganisms (Kaushik and Hynes 1971; Cummins et al. 1973; Anderson and Graffius 1975; Graffius and Anderson 1979) and hence more valuable nutritionally, but this effect could also be the result of physical degradation of the leaves over time, allowing easier ingestion.

The disparate trends illustrated by the above studies may be caused by these various uncontrolled variables which may make the animals unable to rank their food items along a one-dimensional axis (sensu Gray 1979) of food quality. Nor can the limited selective abilities of microphages be ignored. The fact that food of higher quality is presented does not guarantee that food of higher quality is ingested. Tentaculate deposit feeders, for example, mechanically select particles of lower submersed weight even when no differences exist in the relative food values of the particles (Self and Jumars 1978). To test the model predictions for ingestion rate, all food variables (such as concentration, composition, size, shape,
ease of ingestion, etc.) should be kept constant and only food quality (as expressed, e.g., by caloric, carbon, or nitrogen content) be allowed to vary. Care should also be taken to provide food in abundances below those which become either physiologically or mechanically limiting. If this limiting abundance is reached, no alteration of ingestion rate with food quality may be observed (Frost 1972). Controlled experiments to separate the effects of food quality, structural components, toxins, etc., will elucidate the dominant factor or factors affecting ingestion rate and need to be performed.

In short-term field or laboratory experiments, constant food availability can reasonably be maintained; however, in the natural environment shortages of food, whatever its quality, can occur. Specifically considering deposit feeders, if rate of food renewal as determined by microbial recolonization of sediment particles is a factor (e.g., Levinton and Lopez 1977) and is not constant over time, an animal may well adjust its feeding rate to complement the long-term average food renewal rate. Such a feeding rate may be suboptimal from the viewpoint of short-term energy maximization. In addition, external food inputs can occur. For example, water currents can transport allochthonous food materials to benthic microphages on a constant or pulsed, cyclic basis; even in the deep sea, seasonal inputs of food are suspected (Deuser and Ross 1980). Whether and how a microphage adjusts its rate of feeding to the rate of food supply and whether the rate of food supply varies appreciably over temporal and spatial scales pertinent to foraging strategy are largely unknown and need future study.

While this paper emphasizes microphages, the model can be applied to the ingestion phase of macrophagous feeding as well. Once a food item has been selected and captured by a macrophage, given that all other food item-related parameters are the same, the macrophage should feed at a faster rate on higher quality food items to maximize $E_n$, its net rate of gain. Time minimizers (sensu Schoener 1971) should behave similarly. Varying feeding rate in response to food quality will assure the least expenditure of time spent feeding to obtain a given energy requirement for those animals whose feeding behavior incurs a high risk of predation (e.g., Levinton 1971; S. A. Woodin, personal communication).

Finally, if an animal regulates its ingestion rate so that, for example, rate of energy intake is kept constant (the idea of homeostasis [Calow 1975a]), then a decrease in ingestion rate on foods of higher energy content can occur. Unless such homeostasis increases long-term energy gain or positively affects fitness in some more complex and as yet undocumented way, it seems an unlikely behavioral response. The success of optimal foraging models to date (Pyke et al. 1977) supports this contention.

SUMMARY

A simple model based on microphagous feeders (animals which process their food items in bulk with little chance of selecting food items on an individual basis) has been developed to predict how ingestion rate should vary with food quality if the net time rate of gain of some measure of food quality, say energy, is to be maximized. Three variants of the model were considered, in which absorption
efficiency (1) was constant, (2) decreased linearly with increased ingestion rate, or
(3) decreased exponentially. The optimal ingestion rate, which maximized the net
rate of energy gain, depended on food quality and increased on higher quality
foods. For certain parameter values, constantly maintaining the maximum inges­
tion rate resulted in maximal net energy gain. Experimental results from the
literature on a variety of animals are not in consistent accord with these predic­
tions. It seems likely that uncontrolled and confounding variables, such as food
composition or palatability, may obscure the effects of food quality on ingestion
rate.

ACKNOWLEDGMENTS

I thank P. A. Jumars, B. W. Frost, T. W. Schoener, C. H. Peterson, J. E.
Eckman, R. F. L. Self, and two anonymous reviewers for criticisms of early
versions of this paper. I especially thank S. Shetye for providing a computer
program of the bisector method for solving equations and L. Ross for typing the
manuscript. This work was supported by DOE contract DE-AT06-76-EV-75026
(DE-EV-75026-85) to G. C. Anderson. This paper is contribution no. 1207 from
the Department of Oceanography, University of Washington.

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