

SUPPLY-SIDE OPTIMIZATION: MAXIMIZING ABSORPTIVE RATES

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... Pooh and Piglet walked home thoughtfully together in the golden evening, and for a long time they were silent.

"When you wake up in the morning, Pooh," said Piglet at last, "what's the first thing you say to yourself?"

"What's for breakfast?" said Pooh. "What do you say, Piglet?"

"I say, I wonder what's going to happen exciting today?" said Piglet.

Pooh nodded thoughtfully.

"It's the same thing," he said.

A. A. Milne
The World of Pooh

INTRODUCTION

The complexities of feeding behavior extend far beyond the simple priorities of life in The Hundred Acre Wood. Vermeij (1987), for example, has suggested that predator-prey relations have continually escalated as predators and prey co-evolved. A consequence of such escalation is that prey defences and predator weapons against them both continue to become more effective. The ultimate source of the material and energy for this escalation in heterotrophs with digestive tracts is absorption across the gut wall. Thus it is arguable that the lowest common denominator in foraging theory should be absorption of digestive products; the ultimate evolutionary escalation must be in rate of gain from food. Most foraging theory, however, focuses on choice of diet and feeding location (Stephens and Krebs, 1986) and stops with prey acquisition and pre-ingestive handling -- despite the fact that digestive handling times often far exceed pursuit and ingestive handling times.

We have adapted a body of theory within chemical engineering aimed at the analysis and design of chemical reactors to analyze the process of digestion in animals possessing guts (Penry and Jumars 1986, 1987; Jumars and Penry 1989). In so doing, we address the scale on which optimization of foraging behavior must ultimately take place: that of anabolic supply to

fuel life's activities. For example, the most frequent pattern of digestive processing seen in animals is the combination of plug flow (little axial mixing in the gut) with enzymatic digestion that follows Michaelis-Menten kinetics. Penry and Jumars (1987) demonstrated within the context of chemical reactor theory that this combination of digesta mixing and reaction kinetics should maximize rate of production of digestive products. With this combination of characteristics, they noted, digestive product formation rate rises continuously with ingestion rate; given Michaelis-Menten kinetics, increasing residence time of material in the gut decreases substrate concentration and thus decreases overall reaction rate. Penry and Jumars (1987) also suggested that optimal throughput rates arise as increasing gross gains with increasing feeding (and thus digestion) rate become offset by steeply-rising costs that are also proportional to feeding rate. The need to invoke ill specified and thus unmeasurable costs has been a chronic problem in optimal foraging theory. Further, digestive costs measured to date are apparently too small to be the prime factors limiting the rate at which material is moved through guts (e.g.: Bohrer and Lampert, 1988; Taghon, 1988). Further still, Phillips (1984) noted that physiological limitation of an animal's capacity for assimilation could confound predictions from simple cost-benefit optimization of the ingestion process alone.

We have continued to develop and modify chemical reactor theory for application to heterotrophy because our prior applications have stopped short of the key step of absorption. Our continuing work on digestion has been inspired in large measure by the evocative graphical arguments of Sibly (1981, Fig. 5.2) and can be viewed as an attempt to quantify the arguments inherent in his graphical procedure. Our primary purpose in this paper is to derive a coupled model of digestion and absorption and to give preliminary results from it. A summary of notation used in this derivation appears in Table 1. What we realized when we progressed to the stage of modeling absorption of digestive products is that maximization of absorption rate sets an optimal ingestion rate. Faster feeding produces digestive products at a greater rate, but one that results in undigested food and digestive products being defecated without being used. Bayne et al. (1987) recognized this trade-off in assimilation efficiency versus ingestion rate in their experiments with the suspension-feeding mussel *Mytilus edulis*. Moreover, an ingestion rate below optimal yields an incremental absorptive rate not worth the incremental time required to obtain it relative to what could be realized with infusion of new food substrate at a slightly faster ingestion rate. The implicit trade-offs in digestive product formation rate and absorption rate thus prove to be special cases of the principle of lost opportunity (Stephens and Krebs, 1986). Below the optimal ingestion rate an animal loses the opportunity for greater gut-averaged absorption rate that is driven by concentration of digestive products, that is, ingesta is over utilized, while above the optimal ingestion rate an animal loses the opportunity to absorb products because undigested and digested materials are under utilized. Given the ability to predict an optimal absorption rate, it is possible for us to predict an optimal absorption

TABLE 1 Notation used in the model of coupled digestion and absorption. In addition, the subscript $_0$ refers to input (feed or time 0) values, while the subscript $_f$ refers to final (output or fecal) values, and (with the exception of ER') dimensionless quantities that we derive are indicated with a subscripted asterisk (*). Because of its common prior usage in chemical engineering, however, we use X without the subscripted asterisk. Energy can be substituted for mass by converting mol to their equivalents in cal throughout.

<u>Notation</u>	<u>Meaning</u>
A	absorbed digestive products (mol)
AR	absorption rate (mol volume ⁻¹ time ⁻¹)
AR*	AR/W _{max}
C _F	input concentration of food resource or digestive substrate (mol volume ⁻¹)
C _F *	C _F /K _m
C _P	concentration of digestive product (mol volume ⁻¹)
C _P *	C _P /M _m
∂C _F	incremental change in C _F (mol volume ⁻¹)
∂C _P	incremental change in C _P (mol volume ⁻¹)
∂V	incremental change in volume (volume)
ER*	egestion ratio, OM output/OM input
ER'	renormalized egestion ratio = C _{Pf} /M _m + (C _{Ff} /K _m)/(C _{F0} /K _m)
F	input or feed (mol)
K _m	half-saturation constant for digestion (mol volume ⁻¹)
M _m	half-saturation constant for absorption (mol volume ⁻¹)
n ₁	conversion rate exponent
n ₂	absorption rate exponent
OM	organic matter, F + P (mol volume ⁻¹)
P	intermediate digestive products (mol)
q ₀	volumetric input flow rate (volume time ⁻¹)
r _{FP}	rate of F to P conversion (mol volume ⁻¹ time ⁻¹)
r _{PA}	rate of product absorption (mol volume ⁻¹ time ⁻¹)
s	specific dynamic action coefficient (0.0 ≤ s ≤ 1.0)
τ	throughput time (time)
τ*	τV _{max} /K _m
V _{max}	maximal digestive rate (mol volume ⁻¹ time ⁻¹)
W _{max}	maximal absorptive rate (mol volume ⁻¹ time ⁻¹)
X	fractional conversion of F to P

efficiency. We show that explicit application of the principle of lost opportunity to digestion and absorption has many additional uses.

One controversial implication of our applications of the principle of lost opportunity to digestion and absorption is that increasing weight-specific respiration with decreasing absolute weight is more a function of anabolism than catabolism. Small organisms *can* have a higher weight-specific metabolic demand because they can have a higher weight-specific rate of metabolic gain. Since measured demand (O_2 utilization) is based on prior gain, it should be more obvious than it has been that anabolism determines catabolic potential, not vice versa. Less controversial but no less important are implications for mass and energy flow in ecosystems. There is increasing realization that many empirically determined characteristics of communities are direct consequences of individuals acting in a manner that maximizes individual fitness (Huston et al., 1988; Jumars et al. 1989). Material cycling in aquatic systems is especially sensitive to the fraction of digestive substrates and products released in dissolved form because solutes are rapidly dispersed by physical mechanisms in streams, lakes and oceans, while particulate remains can follow very different pathways.

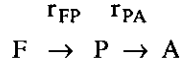
A MODEL FOR PLUG-FLOW DIGESTION AND ABSORPTION

Simple relationships

Here we extend the earlier treatment of digestion as an optimized process (Penry and Jumars 1986, 1987; Jumars and Penry, 1989) to predict trends in gut throughput rates, throughput compositions, and egesta compositions associated with maximal absorptive rates as food resources and reaction kinetics vary. In development of the model presented here we assume that an animal can and will modify its feeding behavior (i.e., throughput rate) instantaneously and that digestion and absorption proceed as a single two-step reaction series with each step showing saturation kinetics. We further assume that food encounter rate does not limit the rate of ingestion. The latter assumption has two clear benefits: It allows us to characterize food simply via the concentration of some growth-limiting component, and it is easily relaxed. We treat this concentration together with the kinetics of digestion and absorption as the determinants of food quality. If encounter rate does limit ingestion rate (food quantity), then it is a simple procedure (easily carried out by the reader in the graphs we present) to bound the optimization with the encounter rate-limited ingestion rate.

Digestion of proteins and complex carbohydrates in a raw feed occurs by way of enzymatic conversion to intermediate products such as small peptides, free amino acids, and monosaccharide sugars. These smaller molecules, in turn, are taken up at the gut wall by carrier-mediated transport (Karasov and Diamond, 1988). Within the simple tubular gut of

many animals, such reactions can be considered to occur in an ideal plug flow reactor (PFR; Fig. 1). Aspects of PFR performance are discussed in considerable detail in Levenspiel (1972). In short, a PFR is characterized by equal residence time for all mass elements passing through the vessel; that is, there is no mixing along the flow path. We assume that there is perfect mixing of digestive (= conversion) products, however, across the flow path to facilitate absorption (= assimilation) at the gut wall. Because reactions continue along the flow path, concentration gradients in both food substrate and intermediate product are established, and a mass balance must be defined for a differential element of volume ∂V . The problem thus becomes one of performance in an ideal PFR that hosts the single two-step reaction series,



(representing enzymatic conversion of food F to product P at rate r_{FP} , and absorption of P across the gut wall at rate r_{PA}). Enzymatic conversion can be described by the mass balance within ∂V :

accumulation of F + disappearance of F by conversion to P = input of F - output of F.

Absorption of P across the gut wall can be described by the mass balance within ∂V :

accumulation of P + production of P from F + absorption of P across gut wall =
input of P - output of P

We assume for this initial analysis that absorptive sites are uniformly distributed along the entire length of the gut, just as we assume that digestive kinetics are uniform along the entire length of the gut (i.e. C_F and C_P are changing due to digestion and absorption, but rate parameters from relevant reaction rate equations are invariant with location). We set $C_{P0} = 0$ for all the model runs presented here. Under steady state, accumulation rates of both F and P are equal to zero, and reactor performance can then be described in terms of mass balances per unit of time in the differential volume ∂V (referring to the notation summarized in Fig. 1 and Table 1):

$$(-r_{FP})\partial V = q_0 C_F - q_0(C_F + \partial C_F),$$

disappearance rate of F by conversion to P =
(volumetric flow rate) (input of F - output of F),

$$(r_{FP} - r_{PA})\partial V = q_0 C_P - q_0(C_P + \partial C_P),$$

production rate of P from F + absorption rate of P across gut wall =
(volumetric flow rate) (input of P - output of P).

With some rearrangement,

$$\frac{\partial V}{q_0} = \frac{\partial C_F}{r_{FP}} = \frac{\partial C_P}{r_{PA} - r_{FP}} \quad (1)$$

where C denotes the concentration of F or P and q_0 is volumetric flow rate. Note that r_{FP} and r_{PA} are positive in the direction of digestion and absorption. This notation has been modified

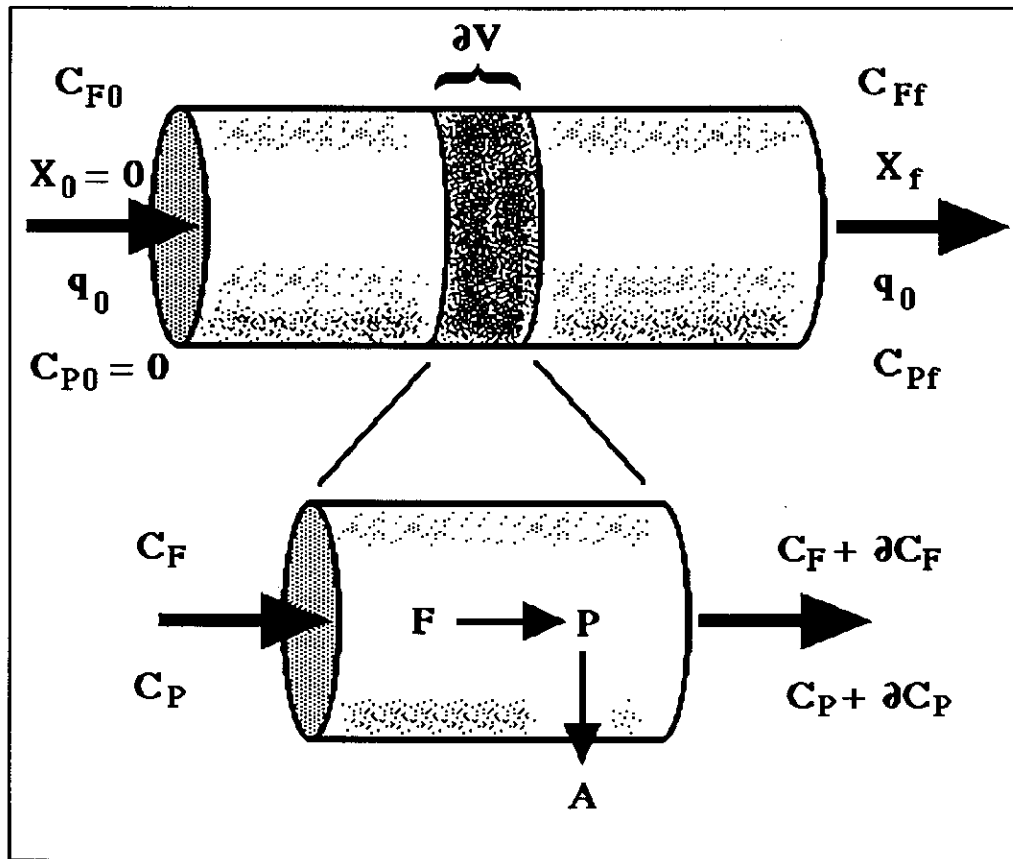


FIGURE 1. Schematic of digestion and absorption in a plug-flow gut. See text and Table 1 for explanation and notation.

from Penry and Jumars (1986, 1987) to accommodate the additional terms needed to describe absorption.

Treating absorption as a seemingly homogeneous reaction in the fluid phase is not unrealistic in the presence of perfect radial mixing. With perfect mixing, a fluid element in any unit of length of gut is in contact instantaneously with the same unit of length of gut lining. Thus a given areal concentration of absorptive sites on the gut lining is readily converted to a volumetric concentration of absorptive sites simply by dividing the number of absorptive sites per unit of length of gut by the volume of digesta per unit of length of the gut. The presence of villi or other ramifications of the gut wall is easily incorporated into this interpretation as well.

The two leftmost terms of Eq. 1 describe the relationships governing the fate of food resource F . In constant-density systems $C_F = C_{F0}(1-X)$, where X is the fraction of F converted to intermediate product P . Accordingly, $-\partial X = \partial C_F / C_{F0}$, and the two leftmost terms can be

integrated over reactor volume to calculate throughput time, τ , required for final conversion X_f at either a fixed throughput flow rate q_0 or specified reaction rate r_{FP} :

$$\tau = \int_0^V \frac{dV}{q_0} = \int_{C_{F0}}^{C_F} \frac{dC_F}{r_{FP}} = C_{F0} \int_0^{X_f} \frac{dX}{-r_{FP}} \quad (2).$$

For constant-volume, constant-density systems, distance along the gut can be expressed in terms of τ . We explicitly assume that digestion causes no appreciable change in volume or density of digesta. This assumption can be relaxed fairly easily, but it is more widely applicable than one might suppose. We work primarily with deposit feeders, the bulk of whose ingested food is completely indigestible. Moreover, in terrestrial animals (e.g., *Homo sapiens*) solid food often is of order of 10% of gut throughput, with the rest being added fluids that are resorbed in the hindgut (e.g., Drasar and Barrow, 1985).

The two rightmost terms in Eq. 1 can be rearranged to yield the relationship:

$$\frac{\partial C_P}{\partial C_F} = \frac{r_{PA}}{r_{FP}} - 1 \quad (3).$$

Eq. 3 represents the steady-state balance between production and absorption of digestive product P. Not surprisingly, Eq. 3 indicates that this balance is a function of the ratio of absorption rate to conversion rate. For example, a small decrease in food resource concentration C_F due to conversion to product P will result in a net increase in product concentration C_P if the ratio of absorption rate to conversion rate is less than unity (i.e., new P is produced more rapidly than it is absorbed). Conversely, a small decrease in C_F due to conversion will result in an incremental decrease in C_P if the ratio of absorption rate to conversion rate is greater than unity. To evaluate PFR performance as well as optimal absorption rate and distributions of food and digesta through the gut, Eq. 3 must be solved to evaluate C_P as an explicit function of C_{F0} and r_{PA}/r_{FP} .

Absorption in an ideal series-reaction PFR is evaluated by noting that over the entire reactor volume V a steady-state mass balance requires that:

$$\text{total absorption} = \text{amount of P produced} - \text{amount of P egested} = V(C_{F0}X_f - C_{Pf}).$$

Thus the gut-averaged absorption rate per gut volume is:

$$AR = \frac{\text{total absorption}}{(\text{volume})(\text{throughput time})} = \frac{C_{F0}X_f - C_{Pf}}{\tau} \quad (4A).$$

Costs of digestion can be incorporated into this approach as well. For example, increasing throughput rates could result in increased mechanical costs of material handling to the animal. The rate at which these costs are incurred may be expressed as a fraction of substrate throughput

$$\text{rate or: rate of mass loss due to digestion} = \frac{sC_{F0}}{\tau}, \quad 0 < s < 1.$$

Thus net absorption rate is:

$$AR = \frac{\text{total absorption}}{(\text{volume}) (\text{throughput time})} = \frac{C_{F0}(X_f - s) - C_{Pf}}{\tau} \quad (4B).$$

A non-zero s establishes a minimal conversion factor X_{\min} for net positive absorption rate.

Utilizing Eq. 2 and 3 to evaluate Eq. 4 for $0 < X < 1$ enables us to predict distributions of component F and product P though the gut, throughput rates (τ^{-1}) and relative amounts of unconverted F and unabsorbed P egested at optimal absorption rates for given input concentrations of F and P, cost coefficient s , and specified digestive reaction kinetics.

Kinetics of digestion and absorption

Hydrolysis of ingested organic material by digestive enzymes falls into a class of saturation-limited, catalytic reactions whose rates can be described by the Michaelis-Menten equation (Briggs and Haldane, 1925):

$$-r_{FP} = \frac{V_{\max} C_F}{K_m + C_F} \quad (5A),$$

where V_{\max} is the maximal attainable conversion rate at saturation and K_m is the concentration yielding conversion rates of $1/2(V_{\max})$. [Note that $-r_{FP} = 0.5V_{\max}$ at $K_m = C_F$; $-r_{FP} = V_{\max}$ for $K_m \ll C_F$; and $-r_{FP} = V_{\max}/K_m$ for $K_m \gg C_F$.] A modified form of the Michaelis-Menten equation to accommodate conversion-absorption rates that are other than first order is

$$-r_{FP} = \frac{V_{\max} C_F^{n_1}}{K_m^{n_1} + C_F^{n_1}} \quad (5B).$$

Although the form of Eq. 5B is somewhat arbitrary, it conveniently preserves the physical meaning of reaction rate at saturation, V_{\max} , and half-saturation concentration, K_m , while allowing characterization of more complex reactions at low C_F .

Reactions governing uptake of small-molecular intermediates at the gut wall occur at rates given by a similar form (e.g. Fisher and Parsons, 1953; Wilson, 1962; Davenport, 1972):

$$-r_{PA} = \frac{W_{\max} C_P}{M_m + C_P} \quad (5C),$$

where W_{\max} and M_m are analogous to V_{\max} and K_m as noted above. Again, a modified form of the Michaelis-Menten equation for reactions of varying order in C_P is

$$-r_{PA} = \frac{W_{\max} C_P^{n_2}}{M_m^{n_2} + C_P^{n_2}} \quad (5D).$$

Digestive or absorptive kinetics may differ from simple Michaelis-Menten form (Fig. 2) for many reasons. Exponents n_1 and n_2 less than one cause the curve of reaction rate versus substrate concentration to deviate from the classic Michaelis-Menten hyperbola by being more nearly linear. Exponential values less than unity are thus used to represent either of two relatively common situations. One is incorrect identification of the limiting nutrient. Measurements may be made of some bulk ingesta constituent whose concentration is correlated inversely with that of the rate-limiting ingredient; one might, for example, measure total organic carbon, while the ingredient driving the digestive reaction is some much more labile component that is proportionately scarce in foods characterized by high total organic carbon. The other situation is passive absorption of products (e.g., of volatile fatty acids in ruminants). Exponents n_1 and n_2 greater than one, on the other hand, give the curve of reaction rate versus substrate concentration greater nonlinearity than the hyperbolic form, making it sigmoidal. By analogy with electromagnetic resistance laws, exponents greater than one are appropriate in description of overall kinetics controlled by parallel two-step reaction series involving multiple food substrates and digestive products. This description would appear the most generally compatible with the energy maximization premise when rate of energy gain limits growth and energy is extracted from a wide array of food molecules. Alternatively, the comparatively slow reaction rate at low concentration (Fig. 2) for these higher exponents could be used to represent either a reaction that shows diffusional rate limitation when food is of low quality and the high bulk restricts diffusion or a situation in which enzyme is induced in proportion to substrate concentration. The latter case would be treated more accurately by varying V_{\max} or W_{\max} , but our simpler formulation gives some insight nonetheless into the kinetic consequences. We thus give results with varying n as a sensitivity analysis and to achieve generality.

Governing equations for optimal PFR deposit feeding behavior

Substitution of Eq. 5B into Eq. 2 and performing the integration yields throughput time (τ) as a function of input substrate concentration (C_{F0}) and final conversion fraction (X_f):

$$\tau = \frac{C_{F0}}{V_{\max}} X_f - \frac{K_m}{V_{\max}} \ln(1 - X_f) \quad n_1 = 1.0 \quad (6A)$$

and

$$\tau = \frac{C_{F0} X_f}{V_{\max}} - \frac{K_m^{n_1}}{V_{\max}} \left[\frac{(C_{F0}(1-X_f))^{1-n_1} - (C_{F0})^{1-n_1}}{1-n_1} \right] \quad n_1 \neq 1.0 \quad (6B).$$

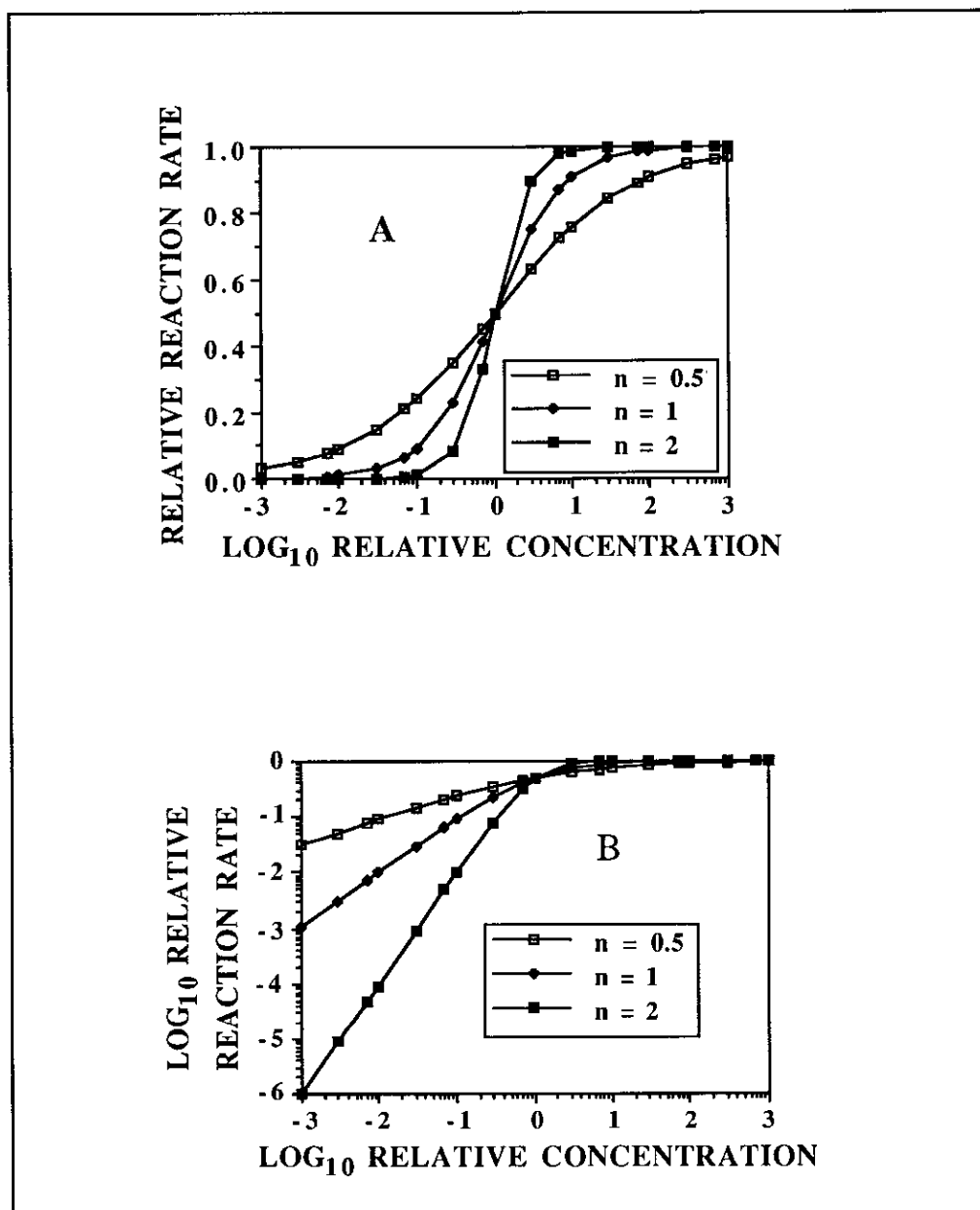


FIGURE 2. Proposed saturation-limited kinetics (r/r_{\max}) vs relative reactant concentration (C^*) for n^{th} order digestive and absorptive reactions; $n = 0.5, 1.0$ and 2.0 . (A) Semi-log plot and (B) log-log plot to demonstrate strongly nonlinear behavior.

Eq. 6A and 6B, in turn, can be rearranged to calculate relative throughput time:

$$\tau_* = \frac{\tau V_{\max}}{K_m} = C_{F0*} X_f \cdot \ln(1 - X_f) \quad n_1 = 1.0 \quad (6C),$$

and

$$\tau_* = C_{F0*} X_f \cdot \frac{(C_{F0*}(1-X_f))^{1-n_1} - (C_{F0*})^{1-n_1}}{1 - n_1} \quad n_1 \neq 1.0 \quad (6D),$$

where $C_{F0*} = C_{F0}/K_m$. Defining relative throughput time in this way is helpful in predicting PFR performance under different input conditions. For example, under very low concentrations of substrate in the ingested food ($C_{F0*} \ll 1.0$), τ_* approaches $[-\ln(1-X_f)]$ when $n_1 = 1$, and throughput time is relatively independent of input substrate concentration (C_{F0}). Moreover, at low relative feed concentrations ($C_{F0*} \ll 1.0$) throughput time required for feed conversion X_f is a function of conversion rate order as well (Fig. 3). Under these food quality-limiting conditions, relative throughput time required for conversion X_f increases with increasing conversion rate order (n_1). At or near saturation levels of input concentration ($C_{F0*} \gg 1.0$), however, throughput time becomes linearly dependent on input concentration and can become quite long at relatively high conversions. This trend is not reaction-order dependent (Fig. 3). Substitution of Eq. 5B and 5D into Eq. 3 yields:

$$\frac{\partial C_P}{\partial C_F} = \frac{W_{\max}}{V_{\max}} \frac{C_P^{n_2} (K_m^{n_1} + C_F^{n_1})}{C_F^{n_1} (M_m^{n_2} + C_P^{n_2})} - 1 \quad (7A).$$

Solutions obtained for Eq. 7A can be made general by multiplying both sides of the equation by K_m/M_m and factoring K_m and M_m out of the terms in parentheses. The dimensionless form of the equation then becomes:

$$\frac{\partial C_{P*}}{\partial C_{F*}} = \left(\frac{W_{\max}}{V_{\max}} \frac{C_{P*}^{n_2} (1 + C_{F*}^{n_1})}{C_{F*}^{n_1} (1 + C_{P*}^{n_2})} - 1 \right) \frac{K_m}{M_m} \quad (7B),$$

where as above $C_{F*} = C_F/K_m$ and $C_{P*} = C_P/M_m$. As with throughput time, expressing in this way the balance between production and absorption of product P is helpful in analysis of PFR performance under food concentration-limiting conditions and saturated, rate-limiting conditions.

Substitution of Eq. 6C and 6D with solutions for Eq. 7B into Eq. 4B enables direct calculation of relative absorption rate:

$$AR_* = \frac{AR}{W_{\max}} = \frac{V_{\max}}{W_{\max}} \frac{(C_{F0*}(X_f - s) - C_{Pf*} \frac{M_m}{K_m})}{\tau_*} \quad (8),$$

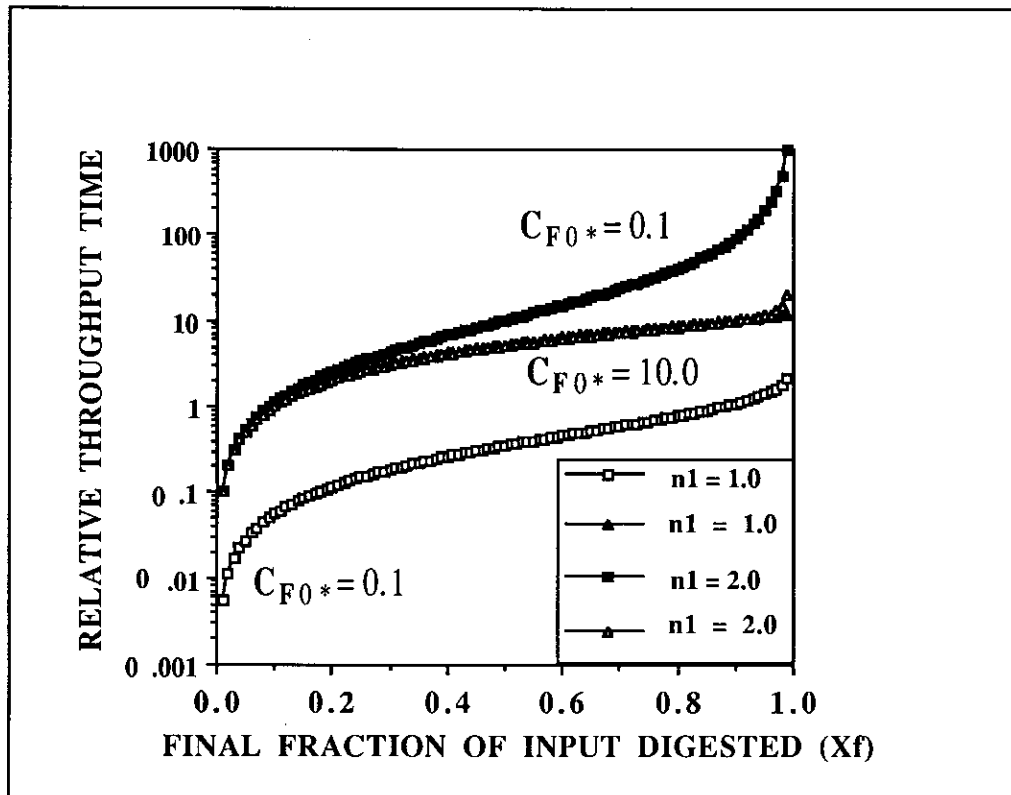


FIGURE 3. Predicted relative throughput times (τ_*) required to convert fraction X_f of initial relative food resource concentrations ($C_{F0^*} = 0.1, 10$) by conversion to digestive product C_P for varying reaction order ($n_1 = 1.0, 2.0$). Note the near overlap in τ_* near saturation ($C_{F0^*} \geq 10$) for both reaction orders in contrast to the increase in throughput time with reaction order at sub-saturating food input concentrations.

where $0 < AR^* < 1.0$ and as above $C_{F^*} = \frac{C_F}{K_m}$, $C_{P^*} = \frac{C_P}{M_m}$. Marginal analysis of this function

suggests that optimal absorptive rates exist for the condition $\frac{\partial AR^*}{\partial \tau_*} = 0$, or with differentiation

of Eq. 8 and rearrangement:

$$(AR^*)_{opt} = \frac{V_{max}}{W_{max}} \frac{\partial \left\{ C_{F0^*} [(X_f)_{opt} - s] - (C_{P^*})_{opt} \frac{M_m}{K_m} \right\}}{\partial (\tau_*)_{opt}} \quad (9).$$

Eq. 9 indicates that optimal gut-average absorptive rate is achieved when gut-average absorptive rate just equals the marginal gain in absorption at the end of the gut. The situation is analogous to the application of the Marginal Value Theorem to duration of stay in food patches (Stephens and Krebs, 1986). This condition thus defines the optimal throughput rate: Shorter throughput times result in under-utilization of available food resource; longer throughput times suffer "diminishing returns" that, while increasing the total amount absorbed, serve to decrease gut-average absorptive rate.

To recapitulate briefly, our approach treats the digestive process as a single two-step reaction series in which conversion of input substrate to intermediate, small-molecular weight products and subsequent absorption of those products each is governed by spatially uniform rate equations of Michaelis-Menten form. The equations governing gut performance are derived from steady-state mass balances and are made dimensionless with respect to Michaelis-Menten parameters. A variety of potential digestive and absorptive reaction orders are incorporated to assess robustness of model predictions over a broad range of input food concentrations and reaction rates. To calculate substrate and product distributions through the gut as well as relative absorption rates for varying input substrate concentrations, Eq. 7B is solved numerically with a fourth-order Runge-Kutta algorithm for varying relative input food concentrations (C_{F0}^*), for varying degrees of food conversion ($0 < X_f < 1$), and for specified reaction orders (n_1, n_2) and kinetic coefficient ratios ($W_{max}/V_{max}, M_m/K_m, s$). Errors incurred in solutions for C_{Pf} are within about 1% or less of analytical solutions obtained for linearized forms of Eq. 5 under end-member conditions (i.e., $C_{Ff}^*, C_{Pf}^* \ll 1$; $C_{Ff}^*, C_{Pf}^* \gg 1$).

Relative absorption rate, AR^* , for varying input substrate concentrations is then evaluated from Eq. 8. Next, optimal absorption rate, $(AR^*)_{opt}$, its associated optimal throughput rate, $(\tau^{-1})_{opt}$, and optimal egestion ratio, $(ER^*)_{opt}$, are calculated. ER^* can be considered as (1 - absorptive efficiency) and is calculated from:

$$ER^* = \frac{OM \text{ output}}{OM \text{ input}} = \frac{\text{unconverted feed} + \text{unabsorbed intermediate}}{\text{input feed}} =$$

$$\frac{C_{Ff} + C_{Pf}}{C_{F0}} = (1 - X_f) + \frac{C_{Pf}^* M_m}{C_{F0}^* K_m}$$

Enzymatic secretions into the gut could be added to the numerator to the extent that they are not subsequently resorbed. We do not add this complication but do note that with its addition ER^* values greater than one are possible (Bayne et al., 1987). We also evaluate the distribution of throughput components under the optimal operating strategy and do so for a range of input conditions (C_{F0}^*) and reaction orders (n_1, n_2). To demonstrate relatively robust trends in digestive and absorptive behavior of simple, tubular guts, only results for rate coefficient ratios ($W_{max}/V_{max}, M_m/K_m$) of unity and zero digestive costs (s) are shown. With information available on a given species, it would be straightforward to tailor the results further.

RESULTS

"Performance" curves (Fig. 4) reveal that possible digestive-absorptive alternatives do exhibit maximal rates of absorption per gut volume. The curves all show maxima, but those maxima are sharper for lower input food concentrations (C_{F0^*}) and higher reaction order (n). We caution that the plots are log-linear and thus understate the sharpness of the optima. Relative absorption rate, not surprisingly, approaches saturation with increasing degree of digestive saturation (i.e., food substrate concentration) for any digestive-absorptive reaction order (Fig. 5A). For digestive kinetics of first order or less, relative throughput rates are predicted to be decreasing monotonically with increasing degree of digestive saturation (Fig. 5B). Optimal relative throughput rates, however, exhibit maxima at intermediate degrees of digestive saturation for digestive reaction kinetics of order greater than unity (Fig. 5B), even when absorption kinetics are of simple Michaelis-Menten form ($n_2 = 1$). Similar trends are observed for other values of W_{\max}/V_{\max} , M_m/K_m , and C_{P0^*} . Of particular interest in microbial and detrital food webs is the fraction of organic matter predicted to be passed without absorption (Fig. 6).

Total ER* in Fig. 6A represents the quantity (organic matter out)/(organic matter in) vs. degree of digestive saturation and thus represents the quantity (1 - absorption efficiency), with areas under respective curves indicating relative importance of undigested food input (C_{Ff}) and unabsorbed digestive product (C_{Pf}). Somewhat counter-intuitively, absorptive efficiency is predicted to increase with increasing degree of digestive saturation; the reason is that there is no marginal gain from gut passage when the material contained in the gut is still capable of saturating absorption kinetics. While presentation of absorptive efficiency is useful in the context of the published literature, Fig. 6A can be misleading because it represents a plot of $(1/C_{F0})$ vs C_{F0} . An alternative presentation (Fig. 6B; $ER' = (C_{Pf}/M_m + C_{Ff}/K_m)$) leaves the ordinate independent of food resource concentration. Increasing total ER' with increasing degree of digestive saturation reflects, not surprisingly, the effects of the quality "richness" of food resources available; rate of organic matter egestion in feces clearly rises with food richness (C_{F0}). Inspection of both Figures 6A and 6B suggests that unutilized digestive product P can make up a significant fraction of the egesta. Without the explicit model it would not be obvious that optimal rate of absorption by an animal coincides with behavior that increases both digestive efficiency (%) and egestion rate ($\text{mol volume}^{-1} \text{time}^{-1}$) of undigested food and unabsorbed product with increasing degree of digestive saturation (C_{F0^*}). Relatively higher throughput rates and concentrations of unabsorbed digestive product at low C_{F0^*} may seem counterintuitive, but are necessary to sustain optimal absorptive rates via maintenance of C_p gradients across the gut wall in the face of dilute food resources.

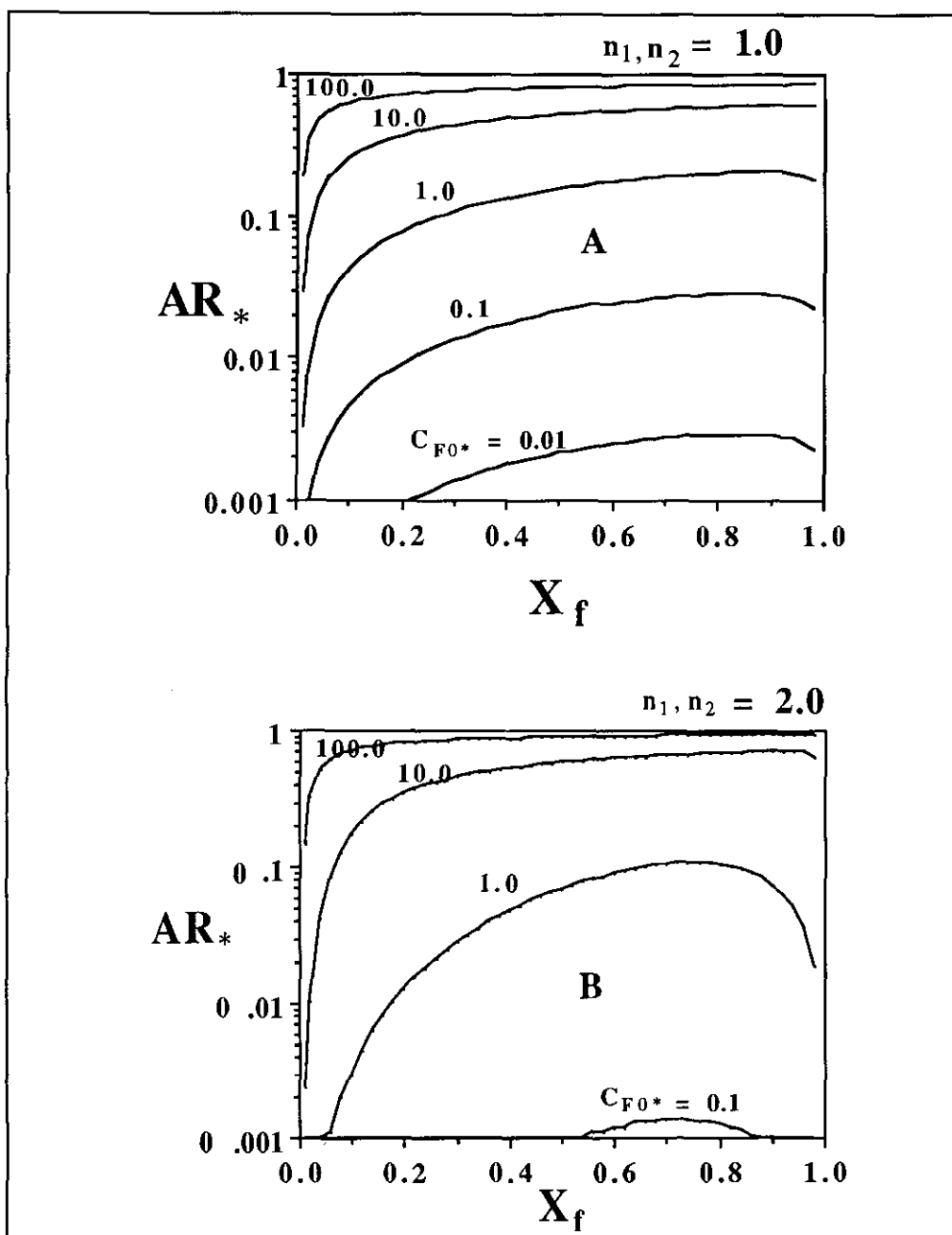


Figure 4. Predicted gut-averaged relative absorption rate (AR_*) as a function of final conversion fraction (X_f) and of varying initial food concentration (C_{F0^*}), where $W_{max}/V_{max} = M_m/K_m = 1$ for uniformly (A) first-order and (B) second-order kinetics. Patterns are similar for other values of W_{max}/V_{max} and M_m/K_m .

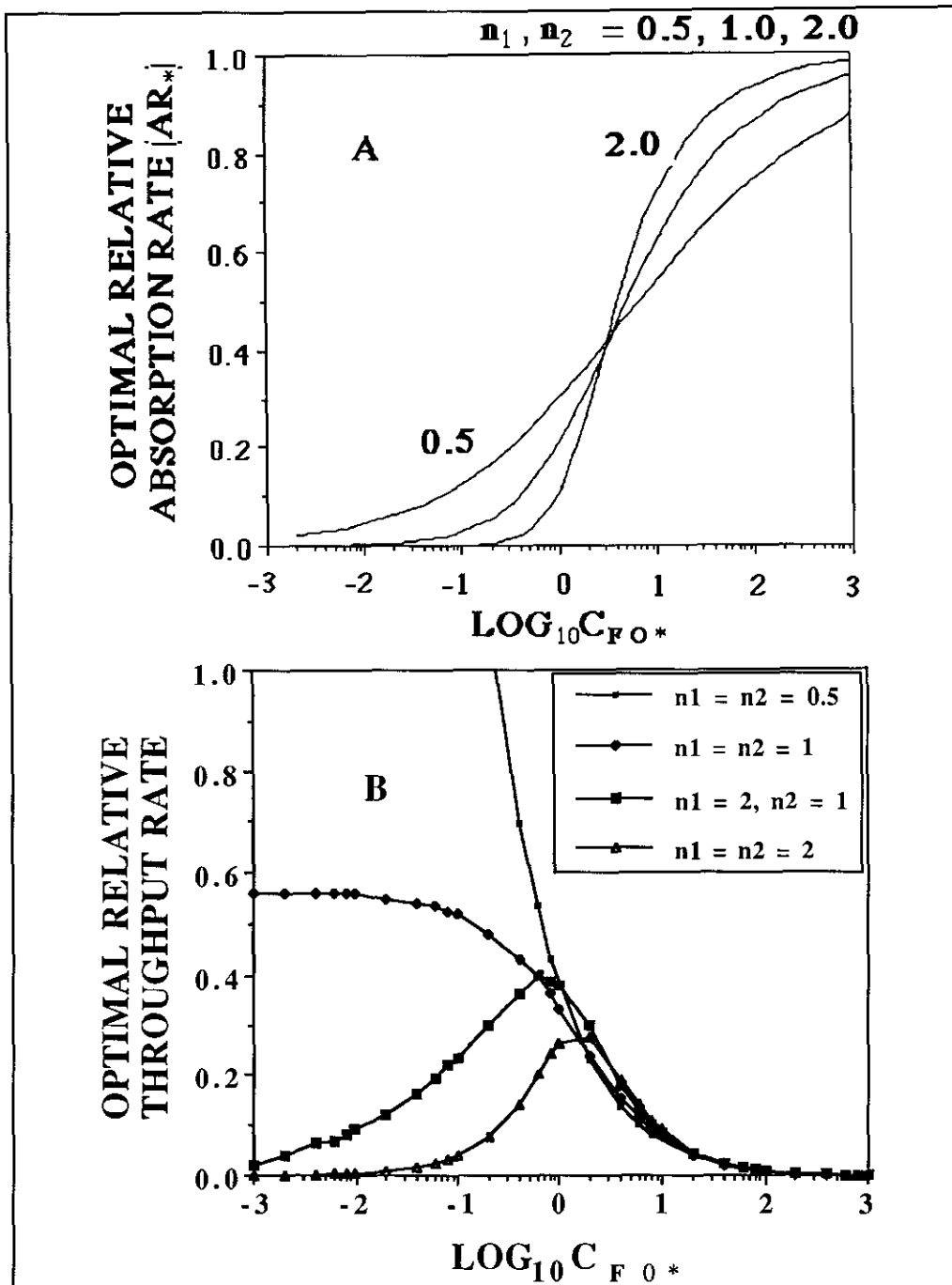


FIGURE 5. Predicted trends in optimal absorption (A) and throughput (B) rates versus C_{F0^*} for reactions of varying orders. $W_{\max}/V_{\max} = M_m/K_m = 1.0$, but patterns are similar for other values. Optimal relative throughput rate $= 1/\tau^*_{\text{opt}}$.

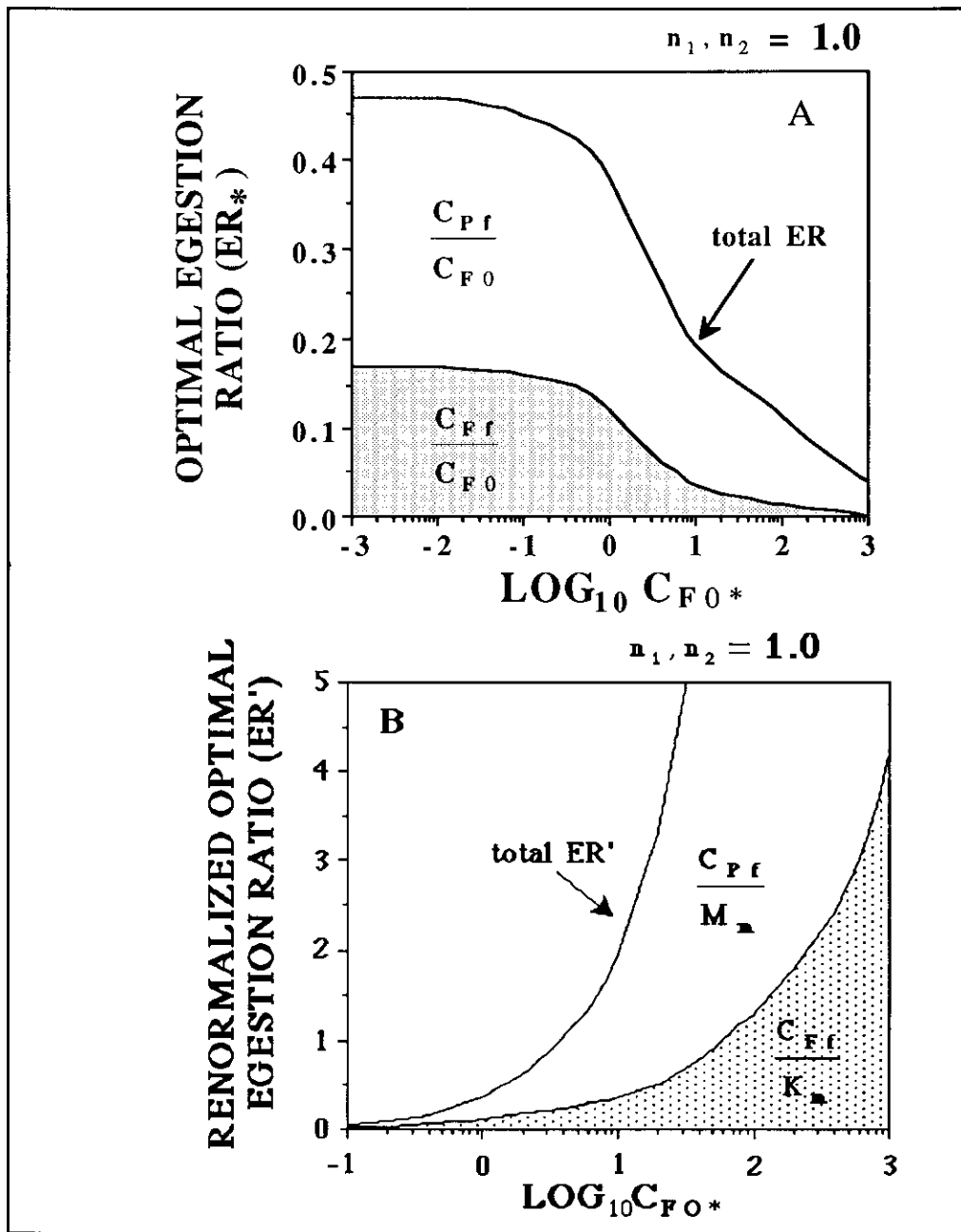


FIGURE 6: (A) Optimal egestion ratio (ER*) and (B) renormalized egestion ratio (ER') vs. relative food resource concentration (C_{F0} *). Similar trends are observed for varying reaction-rate order, W_{max}/V_{max} , and M_m/K_m .

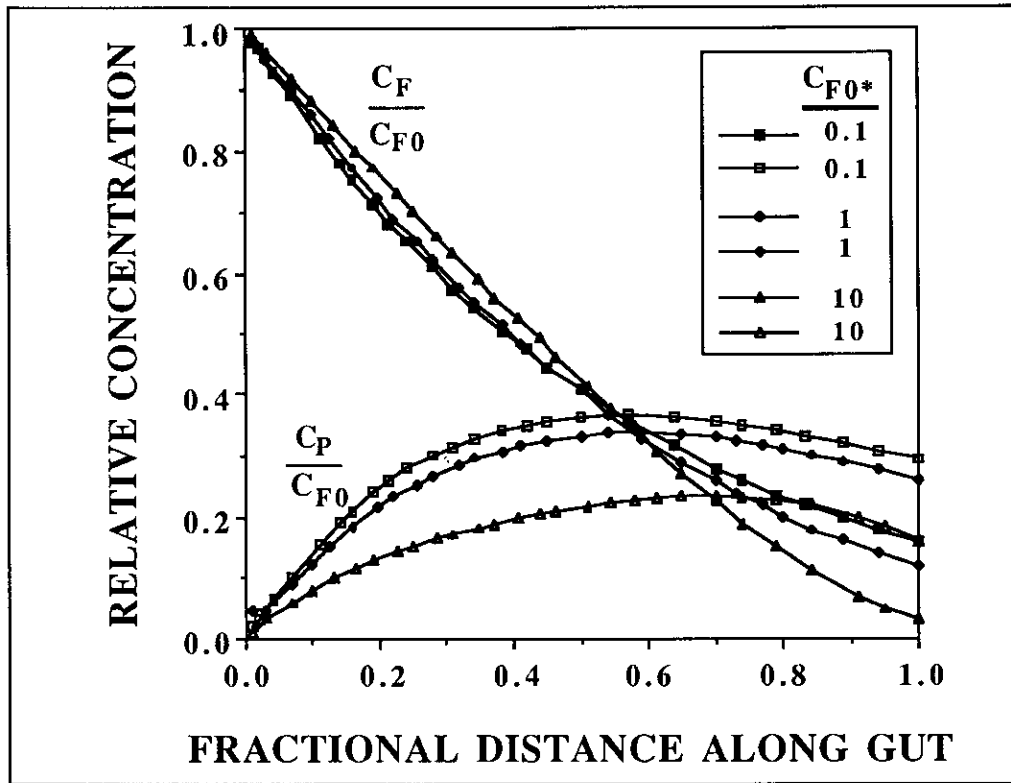


FIGURE 7: Predicted distribution of relative concentration of unconverted substrate (C_F/C_{F0}) and unabsorbed product (C_P/C_{F0}) for various input food concentrations (C_{F0*}) under the optimal operating policy (maximal absorption rate) as a function of fractional distance along the gut for $W_{\max}/V_{\max} = M_m/K_m = 1.0$, $n_1 = n_2 = 1.0$. Similar trends are observed for varying reaction rate constants and order.

The axial pattern of relative concentrations of unconverted food resource and unabsorbed digestive product through the gut under the optimal operating policy (Fig. 7) are not as surprising; relative concentrations of food resource are predicted to diminish with distance through the gut, while undigested products peak in concentration before the end of the gut is reached. As with egestion ratios, similar trends are observed for varying reaction rate constants and orders.

DISCUSSION

Relationships to prior processing rate models and observations

This coupled digestion-absorption model is the logical extension of optimal digestion approaches to predict aspects of feeding behavior (Penry and Jumars 1986, 1987; Jumars and Penry, 1989). For a range of input food concentrations (C_{F0}), Jumars and Penry (1989) solved the easier problem of predicting conversion (X_f) and throughput times (τ) needed to maintain a fixed rate of digestive product formation. For standard ($n_1 = 1$) Michaelis-Menten kinetics, optimal digestion modeling led to the conclusion that shorter throughput times always yielded greater digestive production rates. Thus Jumars and Penry (1989) were forced to conclude that throughput rate in an animal acting to maximize net rate of gain must be set at some optimum by unidentified costs that rise rapidly above some as yet undetermined rate of material processing. The present approach circumvents the unsatisfying conclusion that unknown costs determine throughput-time by allowing the balancing kinetics of digestion and absorption, coupled through the concentration of digestive products, to set the optimal rate of material processing. This approach thus represents an important extension of the intuitive arguments of Phillips (1984), in which limitations to assimilation were invoked within the context of a cost-benefit balance in feeding behavior.

Kofoed et al. (1989) started at the other end of the digestion-absorption couple. Their model includes linear absorption kinetics, but it does not include digestion. Thus they implicitly assumed that either food is ingested in a form that can be absorbed directly without conversion or that the kinetics of digestion are so much faster than those of absorption that digestion can be ignored kinetically. Consideration of their experimental protocol suggests that this assumption is true for the experimental conditions provided but that it may not be true in nature. In their experiments Kofoed and coworkers gave the animal pure, rich foodstuffs (bacteria or diatoms) to conduct absorption measurement; this would place the animal under high C_{F0}^* in terms of the digestion-absorption model; hence the kinetics of both digestion and absorption would be saturated, and the implicit assumption that digestion kinetics are unimportant would hold. Thus their protocol might provide a valuable, non-destructive alternative to the techniques of Karasov and Diamond (1983) for getting at maximal absorption rate (W_{max}) freed of the effects of digestive kinetics. The form of the equation that Kofoed et al. (1989) used further implicitly assumed that the entire volume of the gut operates as a continuously stirred tank reactor (or CSTR in the treatment by Penry and Jumars, 1987). We suspect that plug flow is the more frequently accurate representation of digesta mixing (Penry and Jumars, 1987), especially in the absorptive portions of animal guts, and that Michaelis-Menten kinetics more accurately represent absorption (Davenport, 1977) than do linear absorption coefficients. Kofoed et al.'s (1989)

preliminary results do fall on curves compatible with their model, but the trends could also be fitted with plug flow and Michaelis-Menten kinetics.

In contrast to the absorption focus of Kofoed et al. (1989), it might be reasonable to do the opposite and focus on digestion alone if absorption were never rate limiting. The presence of an optimum in the coupled model, however, suggests that natural selection will drive ingestion rate away from either extreme. There is an optimum precisely where neither digestion nor absorption rate can be ignored. The coupled digestion-absorption model, however, clearly needs the scrutiny of tests with full closure on the kinetic parameters of digestion and absorption. Net absorption rate is the key measurement and whether it is maximized at the ingestion rates observed under *ad libitum* food supply is the key question. Fortunately, reasonably artifact-free methods for characterizing absorption kinetics have been developed (Karasov and Diamond, 1983).

At first sight the existence of an optimal gut retention time without the need for inclusion of explicit costs appears suspicious. Implicit costs -- the lost opportunity to absorb digestive products at a greater rate -- are exceedingly important ones, however. They represent true costs in evolutionary terms: reductions in the ability to respond to the pressures of natural selection. The search for explicit costs of digestion, moreover, has found them to be small in comparison with the subsequent costs of constructing new molecules from digestive products, the so-called "specific dynamic action" (Kjørboe et al., 1985; Bohrer and Lampert, 1988; Taghon, 1988). Rather than conclude that a more thorough search for explicit digestive and absorptive costs is needed, we suggest instead that evolution is likely to have acted to poise animals at the processing-rate optima we have identified. What needs evaluation in order to test this idea is whether explicit costs, e.g. of enzyme production, are large or trivial in comparison with potential gains lost in small departures from the otherwise optimal processing rates.

Our model adds fuel and some light to the controversy over whether volumetric ingestion rates should decrease or increase with increasing food quality (Cammen, 1989; Taghon, 1989). Specifically, it demonstrates that an animal operating to maximize its rate of absorption may uniformly decrease feeding rate with increasing food quality if the digestive reaction shows simple Michaelis-Menten kinetics. If, on the other hand, digestion consists of a number of reactions in parallel, each described by hyperbolic kinetics ($n_1 > 1$), then a peak feeding rate at intermediate food quality is to be expected. Therefore measurements of feeding rate against some measure of food quality alone (e.g., Taghon and Jumars, 1984) are not sufficient to determine whether an animal is processing ingested material in a manner that maximizes rate of gain from absorption. Taghon and Jumars' (1984) findings of higher volumetric ingestion rate with higher food protein content to be consistent with the maximization of absorption would imply (cf. Fig. 5B) that $n_1 > 1$ and $C_{F0} < 1$ for the protein ingested as bovine serum albumin. In any event, neither their nor our present results are easily reconciled with the idea of digestive homeostasis (Calow, 1982; Cammen, 1989). An animal seeking to

achieve a constant rate of absorptive gain at any fixed C_{F0}^* would be faced with the quandary of having two alternative solutions at any rate below the maximal achievable AR^* (Fig. 4).

The coupled model does help to refine the concept of food quality. Information on quality is contained within C_{F0} as well as within all four kinetic parameters of the digestive and absorptive reactions (V_{max} , W_{max} , K_m and M_m). This five-parameter definition of food quality is consistent with the observation that animals select against foods that they do not have the enzymatic capability to digest or absorb (Martinez and Stevens, 1989) Penry and Jumars (1987) point out that physical form and diffusional constraints may complicate the kinetics of digestion, and they certainly can complicate absorption as well. Before testing of the present model, however, we hesitate to add this degree of complexity. Some degree of phase heterogeneity in the reactions and some degree of diffusional control of kinetics can be accommodated in the Michaelis-Menten parameterization without serious violation of its interpretation.

Quantity of food enters the model most directly as throughput rate, q_0 , which can be converted easily to τ in a fixed-volume system: $\tau = (\text{gut volume})/q_0$. Throughput time also is directly related to X_f (Eq. 6). If the quantity of food available is unlimited, then optimization would argue for the solutions depicted in Fig. 4. Solving for the optimal processing rate under an ingestion rate set lower than the food quantity-unlimited optimum is a simple matter of truncating the range of q_0 , τ , and X_f over which the maximal AR is sought. Just as simple intuition would suggest, food shortage should drive τ and X_f up; intuition, however, might not predict the degree of nonlinearity shown above $X_f = 0.9$ (Figs. 3 and 4).

Whether or not the details of this model hold up under scrutiny, the focus it provides on net absorption rate as the determinant of growth potential suggests a critical re-appraisal of fundamental metabolic scaling arguments. The observation that net growth of animals scales with body mass raised to an exponent between $2/3$ and 1 is usually explained as indicative of decreased metabolic demand per unit of body weight with increasing body weight. We find this explanation inconsistent when metabolic components are placed in their logical sequence. Prior gain clearly determines whether an animal has material to oxidize at present; present oxidation much less clearly indicates future gain (e.g., Kristensen, 1989). There are many ways to reduce metabolic demand, especially in small individuals (spores, seeds, resting stages); in heterotrophs there are no ways to oxidize material that was not absorbed. The very fact that smaller animals show more rapid population growth (e.g., Fenchel, 1974) is inconsistent with the overriding importance of metabolic "demand." Since they supposedly have a higher weight-specific metabolic demand, smaller organisms should fare more poorly.

The greater growth potential of smaller organisms is far more consistently explained by the supply side of metabolism. The data clearly demonstrate that smaller organisms can grow faster, not that small organisms must grow faster. Isometric growth increases absorptive sites only as body volume raised to a power of $2/3$. Allometries such as increasing gut length in

proportion to volume or increasing ramification of gut linings with animal size can raise the exponent to some extent, but the diffusion advantage of small individuals in gaining nutrients at a greater rate is physically irrevocable. At some point further ramification of absorptive sites into the gut must displace gut contents to an extent that decreases net rate of gain. For these reasons we hope to see the approaches of Karasov and Diamond (1988) extended to examine the issue of the scaling of absorption rate with body size within species.

Model extended

That we work on deposit feeders helps explain many of the assumptions of the model. These animals characteristically spend most of their time feeding and appear far more rarely limited in growth potential by food quantity than are most other trophic groups. They also are incapable of digesting much of their food on a volumetric basis.

Our reasons for not starting out, say, with the more complicated and possibly more generally applicable assumption that volume of gut contents changes significantly during digestion goes beyond a predilection for animals that eat sand and mud. Volume reduction during digestion can have two important effects. One is to permit input rate to the gut to exceed output rate ($q_0 > q_f$) from the gut by a significant amount; thus a gut of a given size can allow greater ingestion rate when a significant fraction of the volume ingested can be digested and absorbed away (e.g., Lehman, 1976). A more subtle but possibly equally important effect of volume change during digestion and absorption will be to vary the concentration of digestive enzymes and thereby V_{max} . Both effects are reasonably straightforward to model, but are likely to be highly species specific and diet specific in magnitude. Here we have endeavored to provide a template for the parts of the system that are common to most species with the hopes that it will be modified as applications demand. Specifying the extent to which a food parcel can be digested and absorbed further allows one to use the digestion-absorption theory and the principle of lost opportunity to set an upper bound on selection costs that an animal should bear. Such costs should be no larger than the added rate of absorptive gain stemming from selection.

Along similar lines, our assumption that digestion and absorption kinetics are constant along the full length of the gut need to be modified for applications to particular species. In several kinds of invertebrates, however, digestive and absorptive functions are broadly distributed axially (e.g.: Michel, 1988; Féral, 1989). A useful and fairly general elaboration of the model might divide the gut into three segments with successive functions of primarily digestion (foregut and stomach), digestion plus absorption (midgut and hindgut), and neither (rectum). The purely digestive portion may be treated with the equations of Penry and Jumars (1987). The intestine may be treated with the present equations by modifying the input stream to have a non-zero C_{p0} determined by output from the foregut. Digestion could be allowed to

continue beyond the actively absorbing midgut by taking the midgut's output as input for the digestive equations. Modifying the equations in this way requires specification of gut geometry and thus is less general than the template we provide, but it raises the very exciting possibility of determining an optimal geometry of digestion and absorption, linking the study of histology and internal morphology with the ecology of foraging. Another interesting complication would be to calculate an optimal retention time and diet choice for a mixture of food items varying in quality. An obviously needed further addition is to allow digestive and absorptive kinetics to vary with time -- with adaptive state of the individual (e.g., Karasov et al., 1983)

An added benefit of these extensions would be to better define the chemical environment of an animal's gut and the chemical output from it. The latter has obvious advantage in studies of material processing (e.g., Jumars et al., 1989). The former provides a context for interpreting the results of past observations of microbial growth in animal guts (e.g.: Deming and Colwell, 1982; Drasar and Barrow, 1985; Plante et al., 1989) and for designing new experiments. Our demonstration that a certain amount of digestive inefficiency is optimal in terms of the gut owner's absorptive rate of gain explains the existence of hindgut and fecal resources for microbial growth and for utilization by detritivores.

To extend the essence of Poo's comment to Piglet beyond the joy of throughput, there are many aspects of feeding that can be exciting. The model presented here is for us a truly exciting advance in ongoing efforts to understand and to predict the influence of digestive and absorptive processes on foraging behavior. Indeed, the insight of supply-side optimization has whetted anew our appetite for inquiry into the ecology of feeding.

SUMMARY

We extend a model of optimal digestion to the step of absorption by way of a generalized performance analysis of guts behaving like continuous, plug-flow chemical reactors hosting series reactions at steady state. The model predicts an optimal rate of ingestion or gut residence time without inclusion of explicit costs. Costs are included implicitly via the principle of lost opportunity: processing faster or slower than the optimum leads to lesser rates of absorption. This criterion for optimality can be evaluated explicitly by noting that maximal absorptive rates of digestive products in simple tubular guts are achieved when marginal gain in absorption at the end of the gut just equals gut-averaged absorptive rate. In simple tubular guts hosting classical Michaelis-Menten digestive and absorptive kinetics, optimal throughput rates of food in unlimited quantities are predicted to decrease with increasing food quality. Higher-order digestive reaction kinetics, however, lead to throughput rate maxima at intermediate food qualities. Animals acting to maximize individual rates of absorption of digestive products are predicted to egest substantial components of undigested food and unabsorbed digestive

products, with the efficiency of absorption and rate of egestion of usable organic matter both rising with food quality. Perspectives advanced by this model highlight the role of digestion-absorption reaction kinetics in foraging behavior.

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ORAL DISCUSSION – P.A. Jumars

Q. (Real) How would you go about measuring the kinetic parameters in your model ?

A. The tough one in our system, because of the small sizes of the animals, is knowing the characteristics of the digestive enzymes in situ. The usual techniques of grinding whole animals release stored enzymes and so cannot be used to infer activities in the gut lumen. Karasov and Diamond's technique, on the other hand, is a straightforward way of estimating the absorption kinetics. It might be possible from net changes plus absorption kinetics to back out digestive kinetics.

Q. (Hobbs) Have you examined the effects of gut fullness ?

A. In the model as written, there is no change in gut fullness due either to uncoupled variations in ingestion and egestion or to absorption. In deposit feeders such changes are minimal. I have modeled (separately from the present text) the effects of absorptive change in volume; as you would expect absorption of a significant volumetric fraction of the digesta effectively increases the ingestion rate that a gut of given volume can accommodate.

Q. (Hobbs) What is the meaning of the exponent, n , in the hyperbolic model ?

A. Values of n less than one indicate more nearly linear kinetics of uptake and values of n above one indicate more sigmoidal uptake kinetics (more nonlinear) than the classic Michaelis–Menten form. Values of n less than one are suggestive of measurement artifacts or of passive absorption (e.g. of volatile fatty acids in ruminants). Values of n above one may be quite common in nature if digestion and absorption are rate limited by reactions running in parallel.

Q. (DeMott) Can you offer the animal two different particles of different digestibilities ?

A. Your question can be rephrased in two different ways that both can be addressed with the present model by changing its boundary conditions: How much is selection worth (in absorption rate per time) and what is the optimal gut retention time for an animal constrained to eat a mixture of two food types of differing kinetics ? Both are very interesting questions well worth pursuing.