4-1-2000

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VOL. 155, NO. 4 THE AMERICAN NATURALIST APRIL 2000

Animal Guts as Ideal Chemical Reactors: Maximizing Absorption Rates

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Submitted November 30, 1998; Accepted November 22, 1999

ABSTRACT: I solved equations that describe coupled hydrolysis in and absorption from a continuously stirred tank reactor (CSTR), a plug flow reactor (PFR), and a batch reactor (BR) for the rate of ingestion and/or the throughput time that maximizes the rate of absorption (=gross rate of gain from digestion). Predictions are that foods requiring a single hydrolytic step (e.g., disaccharides) yield ingestion rates that vary inversely with the concentration of food substrate ingested, whereas foods that require multiple hydrolytic and absorptive reactions proceeding in parallel (e.g., proteins) yield maximal ingestion rates at intermediate substrate concentrations. Counterintuitively, then, animals acting to maximize their absorption rates should show compensatory ingestion (more rapid feeding on food of lower concentration), except for the lower range of diet quality for complex diets and except for animals that show purely linear (passive) uptake. At their respective maxima in absorption rates, the PFR and BR yield only modestly higher rates of gain than the CSTR but do so at substantially lower rates of ingestion. All three ideal reactors show milder than linear reduction in rate of absorption when throughput or holding time in the gut is increased (e.g., by scarcity or predation hazard); higher efficiency of hydrolysis and extraction offset lower intake. Hence adding feeding costs and hazards of predation is likely to slow ingestion rates and raise absorption efficiencies substantially over the cost-free optima found here.

Keywords: compensatory feeding, digestion, optimal foraging, reactor theory, symmorphosis.

Analogy between animal guts and idealized, simple reactors modeled by chemical engineers has provided a number of insights into animal digestion. Of the three kinds of ideal reactors modeled most frequently by chemical engineers, two operate continuously and one, discontinuously. In a continuously stirred tank reactor (CSTR, or backmix reactor), material flows through the reaction vessel steadily and is mixed in all directions instantaneously and continuously. In a plug flow reactor (PFR, or tubular reactor), material is mixed instantaneously and continuously in the radial direction but is not mixed axially to appreciable extent; items leave the tube in the same order that they entered. In the single variety of ideal, discontinuous reactor, the batch reactor (BR), material is mixed instantaneously and continuously after entry, but filling and emptying are discontinuous. Analogies have been made between each kind of ideal reactor and portions of digestive tracts of particular animals. Reactor theory has been especially useful heuristically in analyzing relationships among diets, gross morphologies of digestive tracts, and processing patterns of digesta. Mammalian herbivores have received the most detailed treatments (e.g., Penry and Jumars 1987; Hume 1989; Alexander 1991), but applications now extend broadly to other taxa (e.g., Horn and Messer 1992; Yang and Joern 1994). To give but two specific examples, reactor-theory analyses support the general superiority on low-quality forage of foregut fermenters with CSTR-PFR series (Penry and Jumars 1987; Alexander 1993*b*), and they quantify the advantage of coprophagy to hindgut fermenters (Alexander 1993*a*). Reactor-theory applications have also diversified beyond the physiology of digestion in individuals to other levels of the ecological hierarchy. They have been extended, for example, to analyze and to predict bacterial symbioses in animal guts (Plante et al. 1990; Ballyk and Smith 1999). At the ecosystem level, they have been used to predict and to test for "superfluous" or "luxury" consumption (Jumars et al. 1989; Nagata and Kirchman 1991) and to systematize studies of geochemical conversions accomplished during digestion (Mayer et al. 1997).

Reactor theory appears to have even broader potential for application to digestion and for understanding of its evolution, but several factors have impeded more systematic advance. Digestion in most animals comprises hydrolysis of food and absorption of products in series, but the focus of most reactor-theory applications to digestion has been on hydrolysis alone. This focus can be traced

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Am. Nat. 2000. Vol. 155, pp. 527–543.

back to the original application of reactor theory to animal digestion (Penry and Jumars 1986, 1987) and has been adopted with relatively few exceptions (i.e., Dade et al. 1990; Martínez del Rio and Karasov 1990). To avoid potential confusion, I should point out that hydrolysis and absorption occur in series, in the sense that no absorption is possible before hydrolysis, whereas the onset of absorption does not preclude further hydrolysis. If one were to choose either hydrolysis or absorption for detailed focus, however, absorption would clearly be the better choice for integration with foraging theory, as no gain can be declared until absorption across a cellular boundary is achieved. Most reactor-theory-based studies, and all those that have considered absorption in turn, have focused on PFRs. Although this focus is justifiable because some parts of nearly all metazoan guts—and in particular those portions with active absorption—appear to operate as PFRs, such focus can give little insight into the relative advantages of PFRs in the combined tasks of hydrolysis and absorption. For these reasons, I systematically compared each kind of ideal reactor's performance in hydrolytic and absorptive "reactions" in series. For the comparison, I made the explicit optimization assumption that the operating policy is to maximize the gross rate of absorption from the gut lumen. I found that indeed the PFR has major advantages in the coupled reactions, achieving a moderately higher absorption rate and doing so at a substantially lower ingestion rate. Less obviously, the CSTR also provides the basis for relaxing some idealizations of PFR behavior that are not strictly tenable in real guts (Jumars 2000, in this issue).

Perhaps the most important functional responses of heterotrophs from the collective standpoints of individual fitness, population dynamics, and ecosystem impacts are ingestion rates. Consequently, a great deal of productive effort over a long period has been expended to predict and to interpret shapes of ingestive functional responses (e.g., Real 1977). By contrast, in organisms more complicated than osmotrophs and protists (Fenchel 1987), comparatively little research has addressed the issue of what sets the inevitable plateau in those responses. I therefore used reactor-theory models to characterize the ingestion rates of animals dependent on various kinds and qualities of food, and I compared the predictions with empirical results. Model animals whose growth was rate limited by the acquisition of simple carbohydrates showed, in general, decreasing ingestion rates with increasing food quality, and animals whose growth rate was limited by protein acquisition showed peak ingestion rates at intermediate food quality (hydrolyzable protein concentration in the ingested food), which is consistent with observations of real animals. The results also reveal that an animal acting to maximize its rate of absorption will often show what loosely has been termed "compensatory feeding," that is, greater volumetric ingestion rate on lower-quality forage. Thus, observation of greater ingestion rate on lower-quality forage cannot be taken as evidence of failure of the optimality assumption or of success of an alternative assumption of homeostasis (Calow 1982), and testing optimality against competing assumptions will require explicit, quantitative predictions under each assumption to assess whether experiments can resolve the differences.

Methods

Coupling Hydrolysis and Absorption in a CSTR

The simplest possible case is a single CSTR with uniformly distributed absorptive sites (or uniform permeability to passive absorption) and linear kinetics of hydrolysis and absorption operating in series (fig. 1). For simplicity, here and throughout, I assume 1 : 1 stoichiometry of food conversion to product by hydrolysis; other stoichiometries can be accommodated by placing factors appropriately in the equations.

At steady state, the single CSTR of (luminal or gut) volume G (table 1) must balance inputs and outputs. I depart from the usual reactor-theory convention of using V for reactor volume because that symbol is often associated with kinetics of enzymatic hydrolysis. Food (F) enters at a known initial concentration (C_{F0}; mol vol^{-1}) and flow rate (v_0; vol time^{-1}) and is diluted immediately to its steady (final or outflow) concentration (C_{Ff}). Double subscripting does not correspond with matrix notation. The second subscript, following standard reactor-theory usage, refers to the position in time and/or in space, with 0 denoting initial values and f, final ones. Food disappears from the reactor by hydrolytic conversion to product at a volume-specific rate kC_{Ff} (mol vol^{-1} time^{-1}) and by an outflow from the reactor at a rate of $C_{Ff}v_0$ (mol time^{-1}):

$$C_{F0}v_0 = kC_{Ff}G + C_{Ff}v_0. \tag{1}$$

Dividing both sides of equation (1) through by C_{Ff} and rearranging yields

$$C_{Ff} = \frac{C_{F0}v_0}{v_0 + kG}. \tag{2}$$

Product appearance, in turn, is balanced by its disappearance via absorption at a rate aC_{Pf} (mol vol^{-1} time^{-1}) and by its outflow at a rate $C_{Pf}v_0$, where C_{Pf} is the concentration of product throughout the reactor:

$$kC_{Ff}G = aC_{Pf}G + C_{Pf}v_0. \tag{3}$$

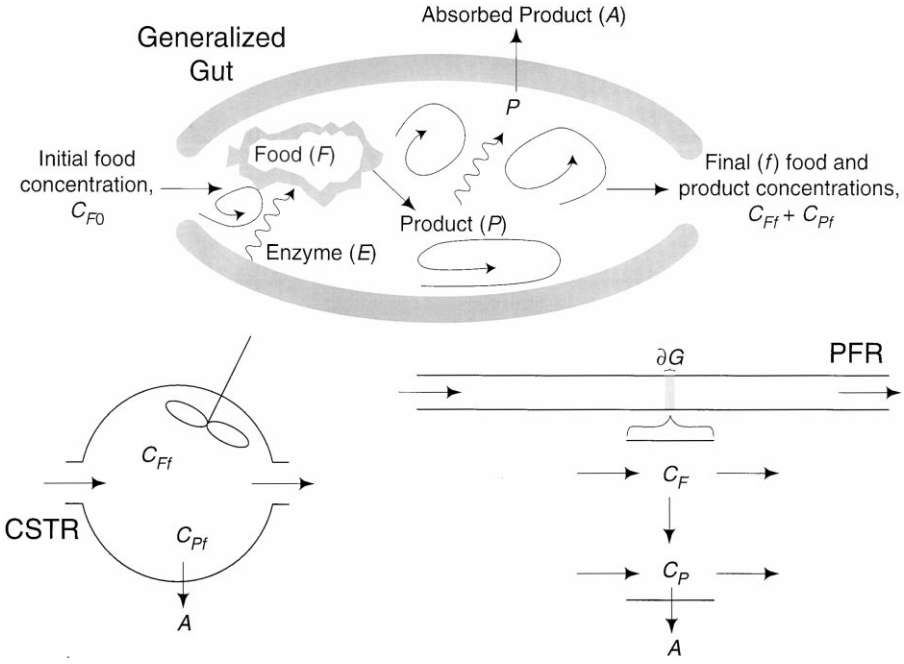

Figure 1: A generalized gut with continuously stirred tank reactor (CSTR) and plug flow reactor (PFR) idealizations. *Wavy arrows*, molecular diffusion. *Straight and coiled arrows*, advection (convection in engineering terms). Most animals use heterogeneous catalysis; solid phases include the food particles and the gut wall. The CSTR assumes perfect mixing, so mass balance is calculated over the whole reactor. The PFR assumes that axial mixing is absent, so mass balance is done either on the whole reactor or on a differential volume element, ∂G, and food and product concentrations vary axially. Other symbols are defined in the text and in table 1.

At steady state, the single input rate of food must also equal the sum of the three output rates:

$$C_{F0}v_0 = aC_{Pf}G + C_{Pf}v_0 + C_{Ff}v_0. \tag{4}$$

Substitution of the solution for C_{Ff} from equation (2) in turn gives

$$C_{Pf} = \frac{kC_{F0}v_0G}{(v_0 + kG)(v_0 + aG)}. \tag{5}$$

Total absorptive flux, J_A (mol time^{-1}), can then be calculated as $aC_{Pf}G$.

For these and any other typical absorption kinetics, absorption rate is a nondecreasing function of product concentration in the vessel from which absorption is occurring, so that the problem of maximizing absorption rate in a CSTR simplifies to one of maximizing product concentration. For the CSTR, C_{Pf} (which is also the concentration of product throughout the reactor) and, hence, J_A show maxima when ingestion rate is optimal ($v_{0\,opt}$). Differentiating equation (5) with respect to v_0 and setting the result equal to zero gives

$$v_{0\,opt} = \sqrt{ka}G. \tag{6}$$

The value of J_A at its maximum, $J_{A\,max}$, can be determined by substituting the right side of equation (6) into equation (5) and by multiplying both sides by the absorption coefficient:

$$J_{A\,max} = \frac{kaC_{F0}G}{(\sqrt{k} + \sqrt{a})^2}. \tag{7}$$

Many individual hydrolytic and absorptive reactions follow Michaelis-Menten kinetics instead of showing strict linearity in rate with reactant concentration. The disappearance rates of food into product ($-r_{FP}$) and of product into assimilant ($-r_{PA}$) can be written, respectively, as

$$-r_{FP} = \frac{V_{max}C_{Ff}}{K_m + C_{Ff}}, \tag{8}$$

$$-r_{PA} = \frac{W_{max}C_{Pf}}{M_m + C_{Pf}}, \tag{9}$$

where V_{max} and W_{max} are, respectively, the maximal rates

Table 1: Symbols used

Symbol	Meaning	Dimensions
a	Linear rate constant of absorption	time^{-1}
Subscript a	Absorption	…
C	Concentration	mol vol^{-1}
CSTR	Continuously stirred tank reactor (or backmix reactor)	…
Subscript F	Food	…
Subscript f	Final	…
Subscript FP	Hydrolysis of food to product	…
G	Volume of the gut lumen	vol
$-h_{\text{FP}}$	Rate of hydrolysis of food to product (arbitrary kinetics)	$\text{mol vol}^{-1}\ \text{time}^{-1}$
J_A	Total absorptive flux from the lumen	mol time^{-1}
K_m	Half-saturation constant for nonlinear hydrolysis kinetics	mol vol^{-1}
k	Linear rate constant of hydrolysis	time^{-1}
Subscript k	Hydrolysis	…
M_m	Half-saturation constant for nonlinear absorption kinetics	mol vol^{-1}
Subscript P	Product of hydrolysis from food	…
Subscript PA	Conversion of product to absorbate	…
PFR	Plug flow reactor (or tubular reactor)	…
$-r_{\text{FP}}$	Rate of hydrolysis of food to product (specified kinetics)	$\text{mol vol}^{-1}\ \text{time}^{-1}$
$-r_{\text{PA}}$	Rate of conversion of product to absorbate	$\text{mol vol}^{-1}\ \text{time}^{-1}$
τ	G/v_0; mean residence or throughput time of food in the gut	time
$V_{\max}$	Maximal rate of hydrolysis for saturating kinetics	$\text{mol vol}^{-1}\ \text{time}^{-1}$
v_0	Volumetric rate of ingestion	vol time^{-1}
$W_{\max}$	Maximal rate of absorption for saturating kinetics	$\text{mol vol}^{-1}\ \text{time}^{-1}$
Subscript 0	Initial (at time zero)	…

of hydrolysis and absorption and K_m and M_m are the food and product concentrations at which the respective rates are half maximal. Linearized versions of these equations are often invoked when substrate concentrations are well below their half-saturation constants ($C_{\text{F0}} \ll K_m$). For this case,

$$-r_{\text{FP}} = k = \frac{V_{\max}}{K_m}, \tag{10}$$

$$-r_{\text{PA}} = a = \frac{W_{\max}}{M_m}. \tag{11}$$

With these substitutions, the solutions are identical to the linear ones—if indeed $C_{\text{F0}} \ll K_m$—and optimal ingestion rate remains independent of food concentration although absorption rate at the optimal ingestion rate still rises linearly with food concentration (eq. [7]).

It is worth reemphasizing that here and throughout I equate optimal ingestion rate with the rate that maximizes the gross rate of absorption. My analysis includes neither induction or alteration of enzyme activity by changing food quality or quantity nor up- or downregulation of absorbers. That is, kinetics of both hydrolysis and absorption, in this analysis, are time invariant. The only variables are ingestion rate (v_0) and food quality (C_{F0}), and the animal can regulate only the former. Food quantity is assumed to be unlimited.

The usual simplification that at high-substrate concentration ($C_{\text{F0}} \gg K_m$) reaction rates equal their maximal value ($V_{\max}$) suffices to predict that absorption will go on at approximately its maximal rate, but it does not allow solution for the optimal ingestion rate: no matter how rich the food, it can be depleted over a sufficient retention time. A crude approximation of optimal throughput time ($\tau_{\text{opt}} = G/v_{0\,\text{opt}}$) for high C_{F0} is simply $C_{\text{F0}}/V_{\max}$. That is, there is little gross gain in conversion rate from increasing ingestion rate when conversion is already saturated, and both dilution of product with incoming food and egestion of product are real losses in terms of potential absorption rate, so there is good reason to avoid ingestion rates higher than barely sufficient to keep hydrolysis and absorption nearly saturated. Because of smoothly diminishing returns with increasing food concentration, optimal throughput rate under Michaelis-Menten kinetics must be $\leq v_{0\,\text{opt}}$ under the linear kinetics of equation (6).

The solution for luminal food concentration, which equals the exiting food concentration, generalizes from linear kinetics (eq. [2]) to arbitrary kinetics as

$$C_{\mathrm{Ff}} = C_{\mathrm{F0}} - \frac{h_{\mathrm{FP}} G}{v_0}, \tag{12}$$

where $-h_{\mathrm{FP}}$ is the conversion rate of food to product (mol vol^{-1} time^{-1}). Formally, the notation $-r_A$ of Penry and Jumars (1987) corresponds identically with $-h_{\mathrm{FP}}$ here, but the added subscript is necessary to track subsequent progress of the hydrolysate. The reader should not be confused by my reservation of the letter A (upper and lower case) for absorption versus Penry and Jumars's (1987) exclusive focus on hydrolysis and hence lack of distinction between hydrolysis and absorption. The expression C_{Ff} can also be obtained from the ideal CSTR performance equation (eq. [22] of Penry and Jumars 1987),

$$\tau = \frac{G}{v_0} = \frac{C_{\mathrm{F0}} X_{\mathrm{f}}}{-h_{\mathrm{FP}}}, \tag{13}$$

where X_{f} is the final conversion fraction, $1 - (C_{\mathrm{Ff}}/C_{\mathrm{F0}})$, of food to product.

Using Mathematica (Wolfram 1996), I substituted equation (8) into equation (12) to solve for food concentration. Then I substituted the solution for C_{Ff} into the analog of equation (4) under hyperbolic kinetics, with aC_{Pf} in the first term replaced by equation (9) to solve for C_{Pf}. By differentiating, I then solved for the ingestion rate, $v_{0\,\mathrm{opt}}$ at which C_{Pf} reached its maximum. The results given here were obtained with Mathematica 2.0 (Wolfram 1993) on a Macintosh Quadra 840AV and were spot checked in Mathematica 3.0 (Wolfram 1996) on a Power Macintosh 7300 and G3. The solutions are cumbersome algebraically, so I present them graphically.

When a finely dispersed, single, easily hydrolyzed nutrient limits growth rate and both its hydrolysis and uptake kinetics are hyperbolic, the coupled Michaelis-Menten equations for digestion and absorption should be accurate. What distinguishes more omnivorous animals with functional guts from most osmotrophs, however, is that they take in items that provide many, if not all, essential nutrients simultaneously (Tilman 1982). Consider, for example, protein acquisition. Proteins must be cleaved into pieces under 10 amino acids long before they can be absorbed, and these oligopeptides and individual amino acids have diverse carriers with varying specificities (Matthews 1991). In acquisition of the various essential amino acids, numerous reactions of hydrolysis proceed in parallel, as do those of absorption. If the individual reactions of hydrolysis and uptake are Michaelis-Menten in form, then the kinetics of nutrient acquisition comprising these reactions in parallel may be approximated by analogous equations of higher order. For the simplest case, two hyperbolic reactions (denoted by subscripts 1 and 2) proceed in parallel on the same substrate at concentration C. Their summed hydrolysis rates are

$$\frac{V_{1\max} C}{K_{1m} + C} + \frac{V_{2\max} C}{K_{2m} + C} = \frac{(V_1 + V_2)C^2 + V_1 K_2 + V_2 K_1}{K_1 K_2 + (K_1 + K_2)C + C^2}. \tag{14}$$

Dropping the linear terms yields (Dade et al. 1990)

$$-r_{\mathrm{FP}} = \frac{V_{\max} C_{\mathrm{Ff}}^2}{K_m^2 + C_{\mathrm{Ff}}^2}, \tag{15}$$

$$-r_{\mathrm{PA}} = \frac{W_{\max} C_{\mathrm{Pf}}^2}{M_m^2 + C_{\mathrm{Pf}}^2}. \tag{16}$$

Once again, for simplicity, I use only equations of second order. What is qualitatively different about any analogous equations with exponents >1 on the concentration terms, however, is that they are sigmoidal. In classical Michaelis-Menten kinetics dr/dC is greatest near $C_{\mathrm{F0}} = 0$, whereas, with equations (15) and (16), dr/dC reaches its peaks at C_{Ff} and C_{Pf} of $K_m/\sqrt{3}$ and $M_m/\sqrt{3}$, respectively. Reactions of this form yield absorption rates that are reduced dramatically over either the linear or the hyperbolic cases when $C_{\mathrm{F0}} \ll K_m$. As with hyperbolic kinetics, I used Mathematica (Wolfram 1996) to find solutions to the coupled equations analogous to equations (1), (2), and (4). Once again, results were obtained with Mathematica 2.0 (Wolfram 1993) and spot checked in version 3.0 (Wolfram 1996). I fixed C_{F0}, G, and v_0 before solving for C_{Pf}.

Many variants are possible, and I could not explore them all. Therefore, I chose a central case for detailed attention with nonlinear kinetics. This central case was $V_{\max} = W_{\max}$ and $K_m = M_m$, as it was for Dade et al. (1990). This choice is the simplest algebraically and is compatible with the concept and finding of "symmorphosis," that is, that ingestion, hydrolysis, and absorption rates should be, and often are, balanced (Diamond 1991; Diamond and Hammond 1992). There are many reasons, however, why either affinities, maximal rates, or both should sometimes differ between hydrolysis and absorption in real animals (e.g., effects of secondary compounds in the diet on hydrolytic activity or far greater costs of production or maintenance of absorptive sites than of hydrolytic enzymes). I therefore experimented with deviations from the central case. I do not present the results here because the primary difference is that when the two rates diverge radically the slower of the two processes (rather than both) limits the rate of absorption, and the approach of Penry and Jumars (1987) can be applied to the slower reaction of the pair. If the two sets of Michaelis-Menten parameters are known, however, the task of finding solutions to the coupled equations becomes easier and clearly gives greater accuracy than the more general case treated here. Recognizing that food qual-

ity cannot be defined independently of digestive ability and to collapse all results onto a small set of curves, I defined it partially as the nondimensional concentration C_{F0}/K_m. Value of food to the animal also depends on rate of hydrolysis relative to its maximum: similarly, I nondimensionalized reaction rate as V/V_{max}.

Other variants that I could not explore systematically in a treatment of this length are various combinations of the kinetics analyzed here. For example, some animals show a high apparent proportion of passive uptake for some nutrients (e.g., Afik et al. 1997), especially when digestive products are small or hydrophobic (Self et al. 1995). Adding a linear component to otherwise hyperbolic or sigmoidal kinetics would produce a behavior intermediate between linear and saturating kinetics but without true saturation. It is difficult to imagine, however, an animal digestive system that would not saturate substantially at some rate of intake and food concentration; utilization and synthesis show lags (leading to buildup of intermediates and slowing of absorption), and animals are containers of finite sizes.

Coupling Hydrolysis and Absorption in a PFR and BR

The simplest PFR is inherently more complex than the simplest CSTR because its contents are not spatially uniform. It is possible to construct equations for a plug flow reactor analogous to equations (1), (3), and (4), but the mass balance is either for a small differential element of volume ∂G or for the reactor as a whole (Dade et al. 1990). I retained all the other simplifying assumptions that I made for a CSTR. I further assumed the distribution of digestive enzymes and absorptive sites to be uniform axially. Dade et al. (1990) described solutions for this case, to which I have made some minor simplifications (appendix).

Because the entire BR follows the same time course as does a volume element of a PFR, the same performance equations can be used to describe it (Levenspiel 1972; Penry and Jumars 1987). Intake and outflow are discontinuous, however, so v_0 is undefined and τ of equations (A5), (A11), and (A12) cannot be obtained as throughput time G/v_0. Batch-reactor holding time, t, is defined more simply as the time between filling and emptying. Also unlike the PFR, conditions in a BR at any one time are uniform spatially.

I do not distinguish between PFR and BR performance further because the differences are a result of variations in costs between steady and unsteady operation. I deemphasize costs here not for lack of importance but for lack of generality. When costs during times between gut filling differ substantially from costs during reactor operation, summing costs in series either algebraically or graphically (e.g., Penry and Jumars 1986) will be preferable. Batch reactors may require spectacular costs of setup (e.g., Secor and Diamond 1995) that nevertheless are repaid by the gains during the period of operation. The results presented here, however, involve no explicit costs, and so PFR and BR performance are quantitatively identical if filling and emptying are instantaneous. Because, by definition, the BR does not operate continuously, however, the PFR performance equations given in the appendix apply only during the period between filling and emptying of the reactor, and time-averaged performance must be reduced by accounting for the periods of emptying and filling and any "down" or idle time in between.

Results

Linear Kinetics At and Away from Optimal Ingestion Rates

The simplest case of a CSTR with linear kinetics of hydrolysis and absorption shows that, even without saturating kinetics of reaction and absorption and even without any explicit costs, there is an optimal retention time (fig. 2), that is, one that maximizes gross rate of absorption of product. This case gives intuition for the competing processes that lead to an intermediate optimum in flow rate of digesta. At lower ingestion rates, product concentration and absorptive flux are limited by the rate of supply of food; reaction and absorption in series are able to draw down product concentration. Because hydrolysis and absorption occur in series, the geometric mean of their two coefficients (eq. [6]) together with the mean residence time (set by G) determines the position of the maximum in C_{Pf} and hence in J. Greater gut volumes and higher geometric mean coefficients of digestion allow the maximum to occur at higher ingestion rates. At ingestion rates above the optimum, however, both dilution with incoming food and expulsion of product decrease product concentration and the absorptive flux that it drives. Marginal gains from further increase in ingestion rates vanish when the slope of the curve for egestion rate of product rises to that of the hydrolysis rate of food to product (fig. 2*C*). Beyond that ingestion rate, incremental increases in conversion rate of food to product are more than offset by incremental increases in egestion rate of product, so the concentration of product in the reactor begins to drop.

The nondimensional plot hides some interesting features that can be seen by inspecting the equations directly. For example, if efficiency of absorption were a consideration, as it might be if food were in short supply, equation (6) shows that the animal with the most nearly equal rates of hydrolysis and absorption would achieve the greatest efficiency of absorption, $1 - (C_{Pf} + C_{Ff})/C_{F0}$. Even when

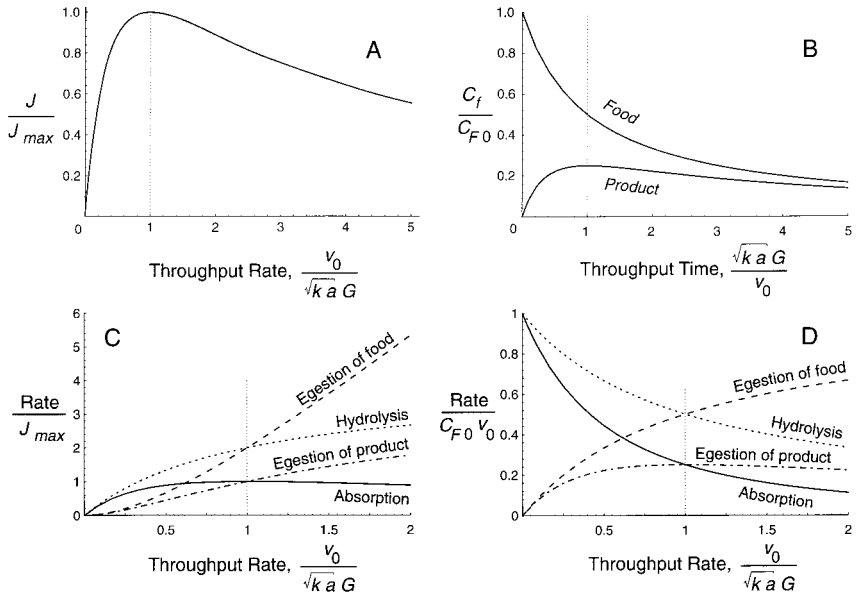

Figure 2: Ideal continuously stirred tank reactor (CSTR) performance under linear kinetics of hydrolysis and absorption. *Dotted vertical lines*, optima (*A–D*; maxima in absorption rates from the whole gut). *A*, Relative absorption rate (J/J_{max}) peaks at an intermediate nondimensional throughput rate. *B*, Nondimensional food concentration falls monotonically with increasing nondimensional throughput time, whereas product concentration shows an intermediate peak because hydrolytic production must precede absorption. *C*, Scaling flow and reaction rates against the maximal absorption rate (J_{max}) shows that beyond the optimal throughput rate potential gains from increased hydrolysis are more than offset by losses as egested food and product. *D*, Scaling rates against the molar inflow rate of food ($C_{F0}v_0$) shows that the CSTR is far from efficient at hydrolysis or absorption at even moderate ingestion rates. For hydrolysis and absorption in series, it suffers the serious design flaw that fractional egestion of product is greatest at the optimal ingestion rate.

hydrolysis and absorption coefficients are identical, however, this efficiency is still low (0.25) for a CSTR operating to maximize absorption rate, and its low value is surely one reason why no known gut operates entirely as a CSTR. The problem is an insurmountable one of CSTR performance: when absorption rate is maximized by having product concentration maximal, product at that concentration is also spilling out the exit of the reactor.

Under linear kinetics, some differences can be seen between PFR and CSTR performance in absorption. In the same nondimensional terms applied to a CSTR, differences in PFR performance at first appear subtle (fig. 2 vs. fig. 3). Among the most prominent is that food concentration falls off much more rapidly with nondimensional throughput time in a PFR, and product concentration, correspondingly, rises more quickly (fig. 2*B* vs. fig. 3*B*). Both conversion and absorption are more efficient in the PFR; by a nondimensional throughput time of 5, conversion and absorption are over 90% complete in the PFR, while roughly 1/5 of the food remains unhydrolyzed (let alone absorbed) in a CSTR.

Reactors Performing at Their Optima

In terms of absolute rate of absorption at its maximum, the PFR shows a 20% increase over that achieved by the CSTR at its maximum, given the same reactor volume. What is probably an even more significant advantage to an animal, however, is that the PFR achieves this higher rate of absorption at only 56% of the nondimensional ingestion rate required to maximize absorption rate in the CSTR. The animal operating at its maximal absorption rate, furthermore, jumps from a 25% rate efficiency of absorption (rate of absorption of product/rate of ingestion of food) in the CSTR to an efficiency of 54% in the PFR (or instantaneously filling BR).

The linear case also allows easy exploration of the effects of disparity in absorptive and hydrolytic rate constants, a and k, and the results are quite remarkable (fig. 4). By the time that their ratio reaches 100, the advantage of the PFR over the CSTR in enhancing absorption rate effectively is gone. Much of the drop is rapid, occurring below a ratio of 10. The qualitative reason is simple: the reactions occur in series, and as the disparity increases, the slower reaction

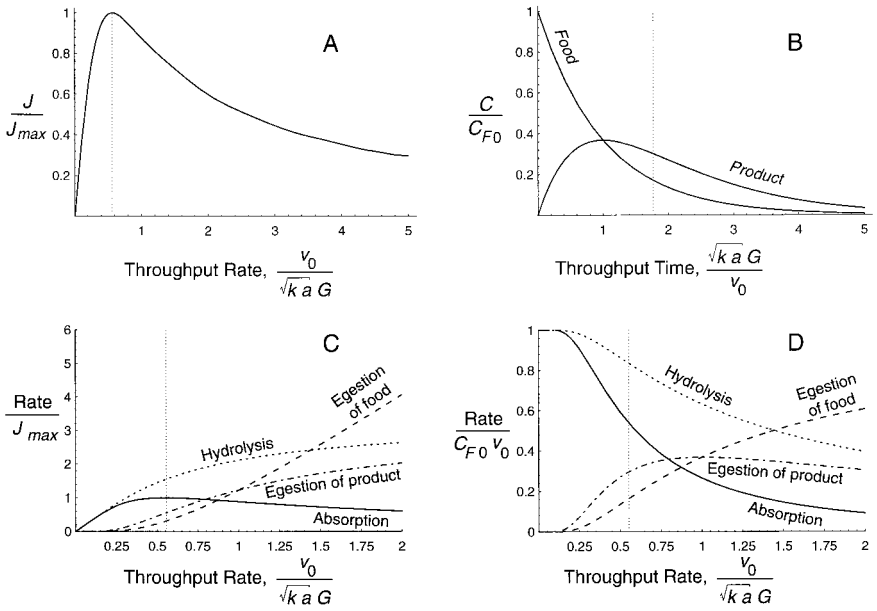

Figure 3: Ideal plug flow reactor (PFR) performance under linear kinetics of hydrolysis and absorption for comparison with the continuously stirred tank reactor (CSTR; fig. 2). *Dotted vertical lines*, optima (*A–D*; maxima in absorption rates from the whole gut). *A*, Relative absorption rate (J/J_{max}) peaks at a nondimensional throughput rate lower than that for the CSTR, and the maximum is sharper. *B*, Nondimensional food concentration falls faster with nondimensional throughput time, and product concentration rises higher without the axial mixing of a CSTR. *C*, Scaling flow and reaction rates against maximal absorptive flux shows that at its optimum, and well beyond in ingestion rate, the PFR loses much less undigested food and unabsorbed product than does the CSTR. *D*, Scaling rates against the molar inflow rate of food ($C_{F0}v_0$) shows marked superiority of the PFR to the CSTR in conversion and absorption efficiencies over a large range of ingestion rates below and near the optimum.

rate overtakes the mixing pattern in its influence on absorption rate. This effect is probably one driver of selection for "symmorphosis," that is, for close balance between hydrolytic and absorptive kinetics in digestion (Diamond and Hammond 1982). Unlike earlier symmorphosis arguments for respiratory systems (Weibel et al. 1991), the reason goes beyond simple waste in "overbuilding" one step of the process. Rate of absorptive gain and time spent foraging are first-order fitness determinants that hang in the balance.

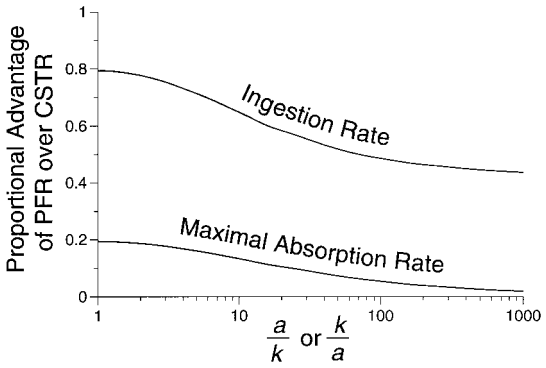

Figure 4: Relative advantages of plug flow reactor (PFR) performance over continuously stirred tank reactor (CSTR) performance fall when each operates at its maximal absorption rate, but the linear rate constants of hydrolysis (k) and absorption (a) diverge. Higher absorption rate and lower ingestion rate are considered advantageous.

Until this point in the text, ingestion rates for the CSTR and PFR have been implicitly synonymous with v_0. Better understanding of the underlying reasons for the behavior of each of the kinds of reactors is achieved, however, by distinguishing volumetric from molar ingestion rates, which differ in proportion to food concentration (C_{F0}). All results in this subsection treat reactors operating at the intake (ingestion) rate that maximizes absorption rate (mol time^{-1}). As expected, maximal absorption rate increases with food quality (fig. 5*A*). For saturating kinetics, either hyperbolic or sigmoidal, optimal volumetric and molar ingestion rates decrease from the linear case treated by equation (5) as saturation sets in (fig. 5*B*–5*D*).

Improving food quality in the range of $1 < C_{F0}/K_m < 10$ gives the most dramatic benefit in terms of both the maximal absorption rate and the decreased volumetric rate of ingestion needed to drive it. For both hyperbolic and sigmoidal kinetics, reduction in volumetric ingestion rate as a result of saturation becomes substantial as C_{F0} in-

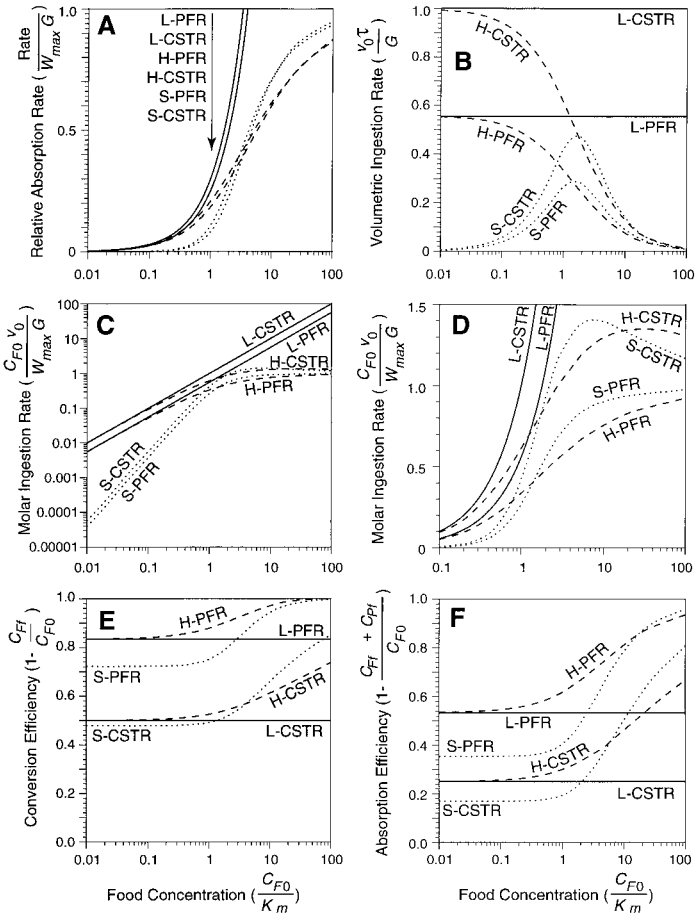

Figure 5: Ideal plug flow reactor (PFR) and continuously stirred tank reactor (CSTR) performance at their respective maximal absorption rates under linear (L), hyperbolic (H), and sigmoidal (S) kinetic alternatives as initial food concentration varies. All variables have been nondimensionalized so that they will apply to all cases where $V_{max} = W_{max}$ and $K_m = M_m$. Absorption rates (*A*) and therefore growth rates and fitness are expected to rise with food concentration. Volumetric ingestion rates (*B*) stay constant for linear kinetics but otherwise fall with food concentration, except for sigmoidal kinetics at low food concentrations. Molar ingestion rates (*C*, *D*) consequently increase with food concentration below K_m but asymptote to the saturation value at high food concentrations. The CSTR overshoots saturating ingestion rates (*D*) because of its inefficient conversion and absorption. Conversion (*E*) and absorption (*F*) efficiencies in general are low and constant below K_m but increase above it.

creases above K_m. Absorption rate and molar ingestion rate plateau at levels determined by V_{max} (fig. 5*A*, 5*C*, 5*D*). As food concentrations rise above K_m, volumetric ingestion rates fall (fig. 5*B*) because it takes decreasing volumetric input rates to hold hydrolysis and absorption rates near their saturation levels. Molar ingestion rates (fig. 5*C*) simplify the picture; all guts with saturating kinetics asymptote to the molar inflow rate, $C_{F0}v_0$, that will just balance the asymptotic rate of hydrolysis and absorption, W_{max} *G*. That is, at rate-saturating concentrations of food, ingestion rate drops in direct proportion to food concentration. It is easy to appreciate that as food quality rises for the general case of $V_{max} \neq W_{max}$, an animal acting to maximize its absorption rate should asymptote toward a molar ingestion rate that just maintains maximal gut-integrated absorption rate, $W_{max}G$.

Less intuitively, volumetric ingestion rates for both CSTRs and PFRs acting to maximize absorption rates should decrease monotonically under hyperbolic kinetics but show a peak near $C_{F0} = K_m$ for sigmoidal kinetics (fig. 5*B*). Very low hydrolysis rates at low food concentrations for sigmoidal kinetics constrain the animal to have long gut throughput times in order to achieve the product concentrations that yield the highest possible absorption rates, yet these rates are still low (fig. 5*A*). The peak in volumetric ingestion rate for sigmoidal kinetics is offset slightly to the right from $C_{F0} = K_m$ and slightly farther for the CSTR than for the PFR because the rate-determining concentration

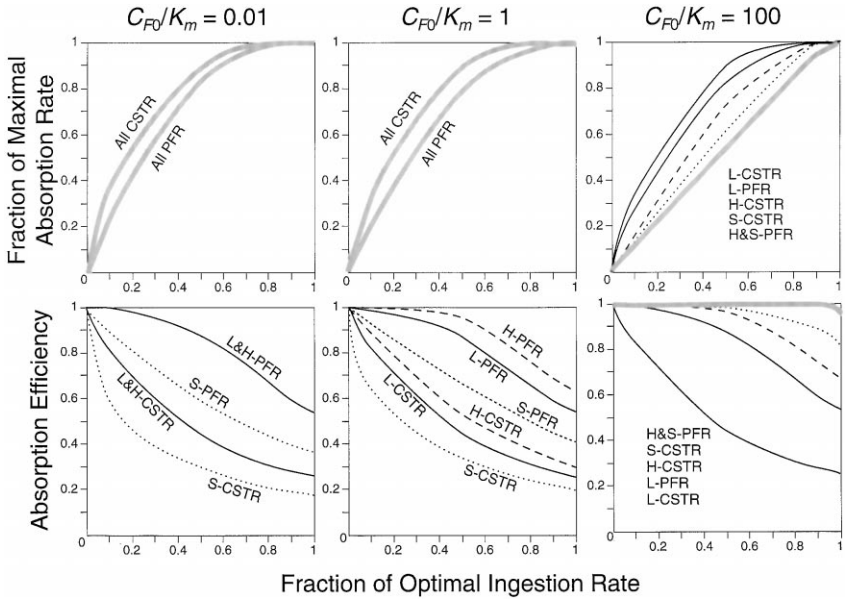

Figure 6: Performance (relative rates and efficiencies) of ideal reactors at ingestion rates at and below their optima. Linear (*L*), hyperbolic (*H*), and sigmoidal (*S*) kinetics are shown under three different food concentrations (poor to rich, going from left to right). Note that slowing of ingestion has little effect on gross gain from absorption (except at the highest food concentration) down to ingestion rates of about 0.6 times optimal because efficiency of absorption increases rapidly as ingestion rate slows below its cost-free optimum, offsetting the reduced ingestion and hydrolysis rates to maintain high absorption rates.

is that in the reactor rather than that of the incoming food, which is diluted to C_{Ff} immediately on entry into the CSTR.

Suboptimal Performance of Ideal Reactors

All the reactors under all the reaction kinetics considered so far for coupled hydrolysis and absorption show clear optima in ingestion rates when costs of processing are omitted: gross rate of gain, in terms of absorption rate from digestion, shows a peak at intermediate ingestion rate. I have stayed away from explicit costs because they vary widely among taxa and guilds of animals. Both Martínez del Rio and Karasov (1990) and Dade et al. (1990) showed how costs could be incorporated explicitly to assess net gains from hydrolysis and absorption, and more recently, Jumars and Martínez del Rio (1999) have explicitly treated the case of animals feeding on monosaccharides. As all these authors noted, any cost that increases with ingestion rate will slow ingestion rate below the one at which gross absorption rate is maximized. Costs can range from the mechanical ones of moving food through the gut, to those of producing enzymes and active absorptive sites, to fitness costs of exposure to predation while foraging. Because there can be no general treatment of specific costs, I have avoided important issues such as induction of hydrolytic enzyme secretion by ingestion of specific foods, variation of secretion rates with food quantity and quality (e.g., Langton and Gabbott 1974), and adaptation to diet by proliferation of absorptive sites (e.g., Karasov 1992). Adding more hydrolytic enzymes (raising V_{max}) or more absorptive sites (raising W_{max}) will raise absorption rate so long as there is substrate available for hydrolysis or absorption, respectively. Therefore, one cannot predict optimal policy for secretion of hydrolytic enzymes or adaptation via changing number of absorptive sites without specifying a cost per enzyme molecule or per absorber. If such a cost is specified, however, the optimal policy under steady feeding on food of a given quality is to increase enzyme secretion or absorber density until the marginal cost of secreting another enzyme molecule or adding another absorptive site fails to be returned as an added increment in absorption rate (e.g., as calculated by Jumars et al. [1993] for bacterial absorption).

The general answer to how much lower ingestion rate will be than the one that maximizes gross absorption rate, however, depends on peakedness of the plot of gross absorption rate against ingestion rate. Feeding rates above those that maximize gross rate of absorption should not be realized in the presence of any real costs. Absorption from the CSTR is slightly less sensitive in relative terms than from the PFR to ingestion-rate reductions below the

optimum (fig. 6), but it should be remembered that, under most conditions, the CSTR performs more poorly in terms of absolute rates of absorption. As ingestion rates slow, the two ideal continuous-flow reactors show remarkably little loss in gross rate of gain from absorption until ingestion rates (v_0) fall below approximately 0.6 times those that produce the maximum in gross absorption rate (fig. 6). Down to this point, the decrease in molar and volumetric ingestion rate is largely offset by increased absorption efficiency.

Discussion

Comparative Reactor Performance and Diet Choice

Plug flow reactors generally achieve higher absorption rates and do so at lower volumetric ingestion rates (fig. 5*A*, 5*B*) than CSTRs. A BR achieves these same relative gains in performance during reactor operation. The hazard of being eaten by a predator is often closely linked to time spent feeding (e.g., Fraser and Gilliam 1992; Anholt and Werner 1995), so this advantage of lower optimal ingestion rate is likely to be a major driving force behind the evolution of guts that operate as PFRs or BRs. This advantage in coupled hydrolysis and absorption extends the arguments made by Penry and Jumars (1986, 1987) for the prevalence of these two reactor types in nature. Reduced time spent feeding is also likely a major driver of diet choice; choosing richer foods not only raises absorption rate, but also lowers volumetric ingestion rate (time spent feeding). The effect is pronounced (large first derivatives of both absorption rate and volumetric ingestion rate, with respect to food concentration) over the range of intermediate food qualities near the half-saturation value for both kinds of saturating kinetics (fig. 5*B*).

Despite the simplicity of a single CSTR with linear digestive and absorptive kinetics and its continuous spillage of high product concentration under "optimal" performance, it may be a reasonable approximation for an important subset of real guts, that is, the fermentation chambers of animals eating low-quality forage and passively absorbing digestive products such as short-chain fatty acids (Alexander 1991). Rate of passive absorption is inherently linear in concentration, whereas restriction to low-quality forage is needed to keep the kinetics of food conversion to product in fermentative guts both roughly linear and a positive function of food concentration. For more accurate modeling of fermentation chambers, however, autocatalytic kinetics should be applied to the hydrolytic step (Penry and Jumars 1987).

Continuously stirred tank reactors and PFRs bound the limits of axial mixing from (respectively) complete to none, so the graphs of figure 5 can also be used to show the range in effects of the intermediate extent of mixing during gut passage. It is apparent that axial mixing has effects that are highly dependent on both shape of the reaction curves and food concentration. For example, axial mixing has the greatest effect on optimal ingestion rate (biggest difference between CSTR and PFR performance, with greatest advantage to the PFR) at low food concentration for hyperbolic kinetics but at intermediate food concentration for sigmoidal kinetics (fig. 5*B*).

Mixing styles and corresponding ideal models are often inferred from morphology. Interpretation from morphology alone is risky, however, because guts with a single opening may operate, nonetheless, in continuous flow and may maintain the along-flow chemical gradients characteristic of PFRs (Bumann and Puls 1997). Conversely, an isolated bolus passing down a tubular gut is better modeled as a batch.

Control of Ingestion Rate

A related issue of physiological and engineering control is the means by which an animal could adopt the optimal policy. Whether kinetics are linear or saturating, all that needs to be monitored to determine CSTR performance is the concentration of product anywhere in the reactor. If a change in ingestion rate increases C_{Pf}, then the new ingestion rate should be maintained or further change should occur in the same direction.

This simple control approach cannot work in a PFR, where product concentrations vary axially and maximizing product concentration at any one point may not maximize the axial mean concentration or the absorptive flux from the gut as a whole. It may be more practical for a PFR to monitor concentrations of absorbed products in internal body fluids, as both invertebrates and vertebrates are known to do, but adopting this means of determining gain entails some time lags in transport between the absorptive sites and the sensor. Potential for feedback instabilities appears to be ameliorated by chemoreceptors having more immediate contact with the input stream (e.g., Abisgold and Simpson 1988; Wallis et al. 1991). Some form of "satisficing" or adopting a simpler-than-optimal algorithm that achieves nearly optimal behavior may be more prevalent; humans, for example, slow down gastric emptying into the (PFR) duodenum in proportion to ingested fat concentration such that essentially all dietary fat is absorbed (Davenport 1982). Fats are often absorbed with linear kinetics because, in general, they can pass across hydrophobic cell membranes passively. One means to achieve high absorption efficiency (not necessarily maximal uptake rate) would be to sense uptake rate at the hind end of the absorptive section of the gut and to decelerate transport until absorption falls below a set threshold. Re-

sults for animals specializing on hexoses and showing largely linear kinetics of (PFR) absorption also suggest high, constant absorption efficiencies (Jumars and Martínez del Rio 1999) and perhaps a similar regulatory mechanism. For amino acids and sugars, the sensor may be integral to the absorber, detecting whether or not it is "busy."

Absorption Maximization versus Compensatory Feeding

One of the most commonly invoked ideas concerning ingestion rates is "compensatory feeding": Loosely, it is the idea that animals (must) eat faster on lower-quality forage and has been applied broadly to ingestion rates that vary inversely with food quality (e.g., Slansky and Wheeler 1991; Yang and Joern 1994). Implicit and sometimes explicit is the idea of an intake target or constant (rate of supply) requirement that must be met (e.g., Raubenheimer and Simpson 1993). Compensatory feeding would seem to be opposed to or at least distinct from absorption maximization, yet hyperbolic kinetics over the entire range of food quality and sigmoidal kinetics above $C_{F0}/K_m \approx 2$ under strict maximization of absorption rate show what could be called (incompletely) compensatory feeding (fig. 5*B*). All saturating kinetics converge at high food quality on a constant molar ingestion rate (fig. 5*C*) that equals the saturation level for hydrolysis and absorption. Absorption rate (fig. 5*A*) does not show saturation, however, until extremely high food concentrations are reached ($C_{F0}/K_m \approx 100$), and therein lies one means to distinguish the idea of operation to achieve constant intake versus the idea of operation to maximize absorption. Absorption rate continues to go up with food quality because absorption efficiency continues to rise as higher food concentration allows the digestive reactions to remain saturated at slower egestion rates.

Taghon and Greene (1990) carried out a suite of growth experiments with both natural and unnatural foods of varying protein concentrations on the marine lugworm *Abarenicola pacifica*. They found the predicted maximum in ingestion rates at intermediate protein concentration and, in the same individuals, found growth rates that continued to increase with food quality above the ingestion-rate maximum. This result is inconsistent with the idea of a constant intake target in this species but supports both the maximization premise and the idea that sigmoidal kinetics should apply well to protein digestion. Also, among polychaete annelids, Pandian and Marian (1985) found that absorption efficiency increases sigmoidally with nitrogen content of food, as predicted in figure 5 (fig. 5*E*, 5*F*), but their data combine experiments within and among species.

Many experiments have been performed with insects on diets varying in simple carbohydrate concentrations, and the general result is decreasing ingestion rate with increasing concentration (e.g., Bernays 1984; Simpson et al. 1989; Abisgold et al. 1994), as expected from figure 5. The same result has been obtained for nectarivorous birds (Downs 1997; López-Calleja et al. 1997) offered sucrose solutions of differing concentrations. More rapid growth on higher sugar concentrations (Abisgold et al. 1994) argues against maintenance of a set absorption rate as a valid description of operating policy, at least in aphids.

Experiments have been conducted with foods, both monosaccharides (Jumars and Martínez del Rio 1999) and amino acids (Abisgold et al. 1994), that require no hydrolysis before absorption. The predictions made here (fig. 5) assume a coupling of hydrolysis and absorption in producing an optimal ingestion rate. In the case of pure absorption of substrates that require no hydrolysis, a realistic optimum in ingestion rate cannot be found without including costs explicitly, but when such costs are included, they can easily lead to predictions of maximal ingestion rates at intermediate food concentration (Jumars and Martínez del Rio 1999).

Predicted versus Observed Absorption Efficiencies

Contrary perhaps to intuition, maximization of absorption rate leads to increased conversion and absorption efficiencies at higher food values under saturating kinetics (fig. 5*E*, 5*F*). Conversion efficiencies in the CSTR are chronically low but do increase at high food concentrations (fig. 5*E*). The PFR retains its well-known advantages over the CSTR in efficiency when the process of absorption is coupled to hydrolysis (fig. 5*F*). Absorption efficiencies for the PFR, especially at low food concentrations, still appear unrealistically low when compared against data (e.g., Downs 1997). Varying the extent of axial mixing cannot help this situation because, as I argued previously and have shown through simulations (Jumars 2000, in this issue), performance must fall between the bounds set by the CSTR (complete axial mixing) and PFR (no significant axial mixing).

These predicted absorption and conversion efficiencies should not be compared, however, against extant empirical results. Such data normally compare food against feces or estimate uptake from radiotracers. As Dade et al. (1990) noted, however, treating the entire gut as an axially uniform reactor is unrealistic. In both vertebrates and invertebrates, absorptive sites are concentrated in the midgut (vertebrate small intestine). This model deals with sections of the gut that perform both hydrolysis and absorption and so probably would best end with the midgut. In addition to a further continuous-flow portion of hindgut, a rectum may be present that allows discontinuous output

in the presence of more continuous input, just as a crop or stomach often can provide temporary storage for a more steady feed into these reactor sections (Bernays 1984).

This model does not include processes occurring in the hindgut. The layer of absorptive cells in midguts is replaced with remarkable frequency in both vertebrates and invertebrates (e.g., Altmann and Enesco 1967; Nott et al. 1985), presumably as an adaptation that restricts microbial fouling of critical absorptive surfaces. Microbial fermentation in the hindgut may act to recover a number of components that otherwise would be lost to the animal: material that was hydrolyzed but not absorbed in the time available before leaving the midgut, nitrogen in ablated absorptive cells or in endogenous digestive enzymes, carbohydrates used in mucous lubrication of digesta, and other chemicals impervious to the animal's enzymes but susceptible to bacterial attack. To be useful to the animal, this recovery mechanism must not require many additional active uptake sites, and microbial by-production of short-chain fatty acids is notable in this regard. Such a recovery mutualism is nearly universal in large animals with guts, where a 10% contribution to the animal's energy budget from short-chain fatty acids is typical (e.g., Bergman 1990). Microbial fermentation is not parameterized in this model, and the predicted efficiencies of conversion and absorption therefore would be compared most accurately against the difference between content of food entering the gut and content of food leaving the absorptive section of the midgut (vertebrate small intestine), hence requiring fistulation, intubation, or dissection for comparison with prediction. In other words, the efficiencies predicted here should underestimate efficiencies calculated by comparing ingested food with feces or measured by whole-body uptake of radiotracers, and the throughput times predicted here apply to only the hydrolytic and absorptive sections of the gut (with only those sections included as gut volume, G).

Adding both hindgut functions and real costs would drive predicted efficiencies up. Because of the insensitivity of absorption rate to decreased ingestion rate (fig. 6), however, even small costs (and predation hazards) of ingestion should drive ingestion rates down substantially from their cost-free optima. Hence, in general, it will be necessary to include species-specific feeding costs (and hazards) to predict ingestion rates that maximize net gain from absorption and to predict optimal absorption efficiencies. In short, ideal reactors with coupled hydrolysis and absorption provide some insights into the functions of real guts, and it is apparent where some differences between the predictions made here and observed ingestion rates and absorption efficiencies should arise.

Acknowledgments

This work was supported by NSF grant OCE 96-17701. R. Huey, C. Martínez del Rio, D. Penry, J. Schmidt, J. Travis, A. Woods, and an anonymous reviewer provided constructive criticism of earlier drafts.

APPENDIX

Coupled Hydrolysis and Absorption in a PFR (Modified from Dade et al. 1990)

Disappearance rate of food by conversion to product equals volumetric flow rate times the difference between input of food and output of food:

$$(-r_{FP})\partial G = v_0 C_F - v_0(C_F - \partial C_F). \tag{A1}$$

In addition, product formation rate from food plus absorption rate of product across the gut wall must equal volumetric flow rate times the difference between inflow and outflow of product:

$$(r_{FP} - r_{PA})\partial G = v_0 C_P - v_0(C_P + \partial C_P). \tag{A2}$$

With rearrangement,

$$\frac{\partial G}{v_0} = \frac{\partial C_F}{r_{FP}} = \frac{\partial C_P}{r_{PA} - r_{FP}}. \tag{A3}$$

The last two terms can be rearranged further to yield (Dade et al. 1990)

$$\frac{\partial C_P}{\partial C_F} = \frac{r_{PA}}{r_{FP}} - 1. \tag{A4}$$

The latter result is particularly useful because this equation can be solved analytically for simple reaction-rate functions and numerically for many others, and it proves useful for displaying the pattern of product concentration along the gut.

Mass balance must also hold over the entire gut as well as over these individual volume elements. The two leftmost terms of equation (A3) can be integrated over the entire reactor volume to yield the throughput time, τ, required for a final conversion, X_f, where X is the fraction of food converted to product ($= 1 - [C_F/C_{F0}]$):

$$\tau = \int_0^G \frac{dG}{v_0} = \int_{C_{F0}}^{C_{Ff}} \frac{dC_F}{r_{FP}} = C_{F0} \int_0^{X_f} \frac{\partial X}{-r_{FP}}. \tag{A5}$$

Total absorption, in turn, must equal the amount of product formed minus the amount of product egested, making gut-averaged absorption rate per unit of volume, $\overline{A}$, calculable as

$$\overline{A} = \frac{C_{F0}X_f - C_{Pf}}{\tau}. \tag{A6}$$

As a general approach that works with nonlinear as well as linear kinetics, one can note that food concentration is affected by digestive reaction rate alone and, therefore, is far easier to analyze or to predict than is product concentration. Time and axial location can be interchanged through equation (A5), fractional down-gut position (relative to the hindmost coordinate) and fractional time (relative to τ) being equal in a constant-volume, constant-density PFR. With the same linear kinetics used for the CSTR,

$$\frac{\partial C_F}{\partial t} = kC_F. \tag{A7}$$

Integrating this expression shows that concentration of food decreases exponentially with time or distance down gut:

$$C_F = \frac{C_{F0}}{e^{kt}}. \tag{A8}$$

For linear kinetics of hydrolysis and absorption, with the further stipulation that $a = k$, equation (A5) can be solved to give

$$C_P = C_F \ln C_{F0} - C_F \ln C_F. \tag{A9}$$

With this profile of product down gut or in time, one can multiply the local concentration of product times the concentration-specific rate of absorption to get the local rate of absorption, integrate axially to find the total rate of absorption, and divide by total length or time to get a mean absorption rate, $\bar{A}$. The retention time that maximizes $\bar{A}$ is optimal and corresponds with the point where marginal gain from further retention equals 0, that is, where local rate of absorption at the rear of the gut equals the mean for the whole gut (Dade et al. 1990). This solution for $a = k$ satisfies the equation

$$k^3\tau^2 + k^2\tau + k = e^{k\tau}. \tag{A10}$$

Optimal retention time, τ_{opt}, then simplifies to $1.79(ka)^{-1/2}$, and maximal absorption rate, to $0.298C_{F0}(ka)^{1/2}G$.

For the more general linear case where $a \neq k$, equation (A5) yields

$$C_{\mathrm{P}} = \frac{C_{\mathrm{F0}}^{(1-a/k)}\left(C_{\mathrm{F0}}^{a/k} - e^{k\tau}\left(\frac{C_{\mathrm{F0}}}{e^{k\tau}}\right)^{a/k}\right)k}{e^{k\tau}(a-k)}. \tag{A11}$$

An analog of equation (A10) for this case can be obtained by the same method of finding the maximum in gut-averaged absorption rate as a function of retention time but is too algebraically cumbersome to reproduce here.

For the hyperbolic case, equation (A5) gives

$$\tau = \frac{C_{\mathrm{F0}}X_{\mathrm{f}}}{V_{\max}} - \frac{K_m}{V_{\max}}\ln(1 - X_{\mathrm{f}}), \tag{A12}$$

whereas, for the sigmoidal case, it yields

$$\tau = \frac{C_{\mathrm{F0}}X_{\mathrm{f}}}{V_{\max}} - \frac{K_m^n}{V_{\max}}\left(\frac{[C_{\mathrm{F0}}(1 - X_{\mathrm{f}})]^{1-n} - C_{\mathrm{F0}}^{1-n}}{1-n}\right), \tag{A13}$$

where n is the order of the reaction. The only case that I treat here is $n = 2$, but I give the general solution derived by Dade et al. (1990; their eq. [6B] = my eq. [A13]) for all $n \neq 1$. Because time and position are interchangeable in a PFR at steady state, equations (A12) and (A13), together with the definition of X, can be used to calculate food concentration as a function of time ($C_{\mathrm{F}}(t)$) or position in the gut.

Analytic solutions for optimal throughput time under nonlinear hydrolysis and absorption kinetics are not available. Therefore I used interpolating functions to solve first-order differential equations ("NDSolve" function in Mathematica) for C_{Pf} as a function of C_{Ff}, that is, equation (A4) with the boundary conditions $C_{\mathrm{Pf}}(C_{\mathrm{F0}}) = 0$ and $C_{\mathrm{Pf}}(0) = 0$. The former of these two boundary conditions is obvious; no product can exist before food has been converted. The latter is less obvious; because hydrolysis causes roughly exponential decrease in food concentration, only at infinite throughput time will all the food be gone, and then all the product will have been absorbed as well. I next substituted the interpolating function into either equation (A12) or (A13) to get $C_{\mathrm{P}}(t)$. I took local absorption as equal to local product concentration times the concentration-specific absorption rate. I integrated over the whole gut and divided by gut throughput time to give mean absorption rate and found iteratively the ingestion rate (v_0) for which this mean was maximal. I checked for numerical adequacy by halving time steps until no significant change occurred in the quoted results.

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Editor: Joseph Travis
Associate Editor: Raymond B. Huey