

The Tau of Continuous Feeding on Simple Foods

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ABSTRACT

Chemical reactor theory under the premise of maximization of net rate of nutrient absorption has been used to predict throughput time, τ , of digesta in animals. Animals that feed on hexoses, such as many vertebrate fruit and nectar eaters, are of central interest in testing reactor theory because they use no hydrolysis before absorption and, hence, should provide valuable, simplified test cases. Graphical methods based on batch reactors and used to make such predictions in the past can give optimal gut throughput times (τ_{opt}) identical with predictions from continuous plug-flow reactor models derived here: in animals with passive, linear uptake alone, τ_{opt} should decline as hexose concentration of food increases. If saturating active uptake is involved, however, a minimum in τ_{opt} (maximum in ingestion rate) is predicted at intermediate hexose concentration, the exact location of this minimum depending on costs of ingestion as well as on uptake kinetics. That is, τ_{opt} first falls to a minimum with increasing hexose concentration and then increases. Optimal throughput time rises as uptake sites become saturated because there is little gross gain and no net gain from increased ingestion rate when uptake already is nearly saturated. It also rises with increasing costs of ingestion. The continuous-time analytic solutions provided here further make the novel and very general prediction of high sensitivity to decreasing τ below τ_{opt} .

Introduction

Ingestion rate is a functional response that directly influences individual growth and that connects individuals with popula-

tion and ecosystem processes through its consequences for predator-prey interaction, population growth, and nutrient cycling. Penry and Jumars (1987) identified the analogy between chemical reactors and animal guts as an aid to understanding the relationship between ingestion rate and downstream digestive processes. Dade et al. (1990) and Martínez del Río and Karasov (1990) extended the approach to include both hydrolysis and absorption and to predict the ingestion rate that maximizes net rate of absorptive gain to the animal. Both sets of authors explicitly treated gastrointestinal systems with plug flow. In plug flow, food items enter and exit in roughly the same order and flow through the reactor continuously, with little axial mixing relative to the axial transport rate. Plug-flow reactors (PFRs) are also known as tubular reactors (e.g., Fogler 1992) because a tubular shape favors this flow pattern. Sugar digestion and absorption occur in the vertebrate intestine and invertebrate midgut, which presumably show little axial mixing, and therefore plug flow has been used to model sugar assimilation in nectar- and fruit-eating animals (Martínez del Río and Karasov 1990).

In most animals and for most substrates, digestion comprises two steps, hydrolysis into smaller molecules and absorption across the gut wall. Both steps can be nonlinear in concentration of food and hydrolysate, and, in general, the resulting coupled equations have no analytic solutions. Therefore, animals for which simplifications of the equations are possible provide valuable test beds for both the description of a gut as a chemical reactor and for the optimization premise, i.e., that net rate of gain is maximized. Martínez del Río and Karasov (1990) seized on nectarivores and frugivores as such valuable test cases, and the theoretical framework that they provided has been used by experimentalists at a recently accelerating pace (Karasov and Cork 1996; Downs 1997; López-Calleja et al. 1997; McWilliams and Karasov 1998; Levey and Martínez del Río 1999). The general conclusion of these empirical studies is that results do not appear to match predictions of reactor theory under the optimization premise and hence that the reactor-theory description of reaction kinetics and mixing, the cost function, and/or the premise must be incorrect.

Some confusion has resulted from the divergent optimization methods used by Martínez del Río and Karasov (1990) versus those used by Dade et al. (1990). Martínez del Río and Karasov (1990) explicitly discussed continuous plug flow, but they used graphical solutions for optimal gut retention time that apply explicitly to batch reactors. In an ideal batch reactor (BR), flow is discontinuous: the gut is filled and kept well mixed (both axially and radially) for a given holding time, t , before emptying.

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Equivalence in performance equations between PFRs and BRs is well established (Levenspiel 1972; Penry and Jumars 1987). It holds because the entire volume in a BR follows the same time course as does a single volume element in a PFR. Equivalence of solutions for digestion in an animal, however, requires that costs as well as gains be treated comparably, and application of BR solutions to PFRs requires conversion from the discontinuous per-batch solution of a BR to the continuous processing of a PFR. Some conventions do not apply to both reactor types. For example, PFR throughput time (τ , which in a PFR is identical to both mean and individual volume-element residence time) often is equated with gut volume, G , divided by volumetric ingestion, or throughput, rate v_0 (vol time⁻¹). Because a BR has discrete episodes of filling and emptying, its volumetric ingestion rate cannot be defined in the same steady fashion, and its characteristic timescale of reaction (in this case, absorption) is the holding time, t , between bouts of filling and emptying. Idle time and thus overall BR performance are not characterized by this t . Therefore, whereas τ and t have similar uses in reactor theory for each kind of reactor, they cannot be defined or manipulated identically for both continuous and discontinuous operation. This separate treatment and care in conversion is not peculiar to reactor theory but also is essential in other more familiar ecological applications such as population dynamics, where discrete-time and continuous-time models both are used.

Our primary purpose here is to revisit reactor-theory predictions for nectarivores and frugivores to reconcile predictions from these two rather different approaches. Dade et al. (1990) did not treat the simple cases (absorption without hydrolysis) explicitly, and, hence, differences from their approach and results of Martínez del Río and Karasov (1990) have not been apparent. Rather than simplify from the more general case of coupled hydrolysis and absorption treated by Dade et al. (1990)—in order to give access to intermediate equations and analytic solutions where available—we derive in a manner comparable to Dade et al. (1990) the two simplest PFR solutions for animals feeding on hexoses. A key point in the derivations is that all the equations are continuous in time, as befits a PFR.

Material and Methods

Linear, Nonsaturable Uptake Rates

The simplest possible case is an animal eating pure hexoses (hence, requiring no hydrolysis) and absorbing food entirely through passive, nonsaturable processes (Karasov and Cork 1996). The only reaction is absorption, and its rate ($-r_{pA}$, shorthand for conversion of product to absorbate in mol vol⁻¹

time⁻¹) is characterized by a first-order coefficient, a (time⁻¹), operating in linear proportion to product concentration (C_p , mol vol⁻¹):

$$-r_{pA} = aC_p. \quad (1)$$

Because Equation (1) gives the rate of change of product concentration, its integral reveals the product concentration as a function of time in the reactor or of position down the gut (Fig. 1A), the two being interconvertible linearly in a PFR (Levenspiel 1972; Penry and Jumars 1987):

$$C_p = C_{p0}e^{-a\tau}. \quad (2)$$

The second subscript refers to the initial (time-zero or ingested) concentration, and τ is throughput time (which only for an ideal PFR equals both mean and individual volume-element residence time) in the reactor. The same solution was used by Alexander (1991) to approximate hydrolytic kinetics in grazers. If one knows throughput or holding time (τ) in the gut, and volume of gut contents does not change, gross rate of absorptive gain over that interval can be obtained by taking the difference between incoming and outgoing concentration. Rate of absorption from the whole gut, J_A , no matter what kind of reactor or reaction kinetics, so long as volume does not change, can be calculated simply as the difference between input and output concentrations multiplied by the volumetric throughput rate ($G\tau^{-1}$):

$$J_A = (C_{p0} - C_{pf})G\tau^{-1}. \quad (3)$$

Here the second subscript f refers to “final” concentration and G is luminal or “gut” volume. For the case of pure absorption (no hydrolysis), G most appropriately should be taken as the volume of the absorptive segment of the gut alone, as C_p cannot change elsewhere, and, hence, flow and mixing patterns elsewhere do not influence reactor performance.

To give more insight into more complicated cases and to allow direct comparison, however, we go through several intermediate steps that parallel the approach of Dade et al. (1990) and illustrate how this simplest possible digestive PFR should operate. In the case of linear kinetics, local absorption rate (W) mirrors the local concentration (Fig. 1A–1B), and whole-gut absorption (mol vol⁻¹) approaches 100% of the incoming food at long throughput times (Fig. 1C). Because of the fact that the longer that material remains in the gut, the more depleted in hexose the lumen becomes, gross absorption rate or gross rate of gain (J_A , the total moles absorbed in Fig. 1C divided by the throughput time required to absorb them, yield-

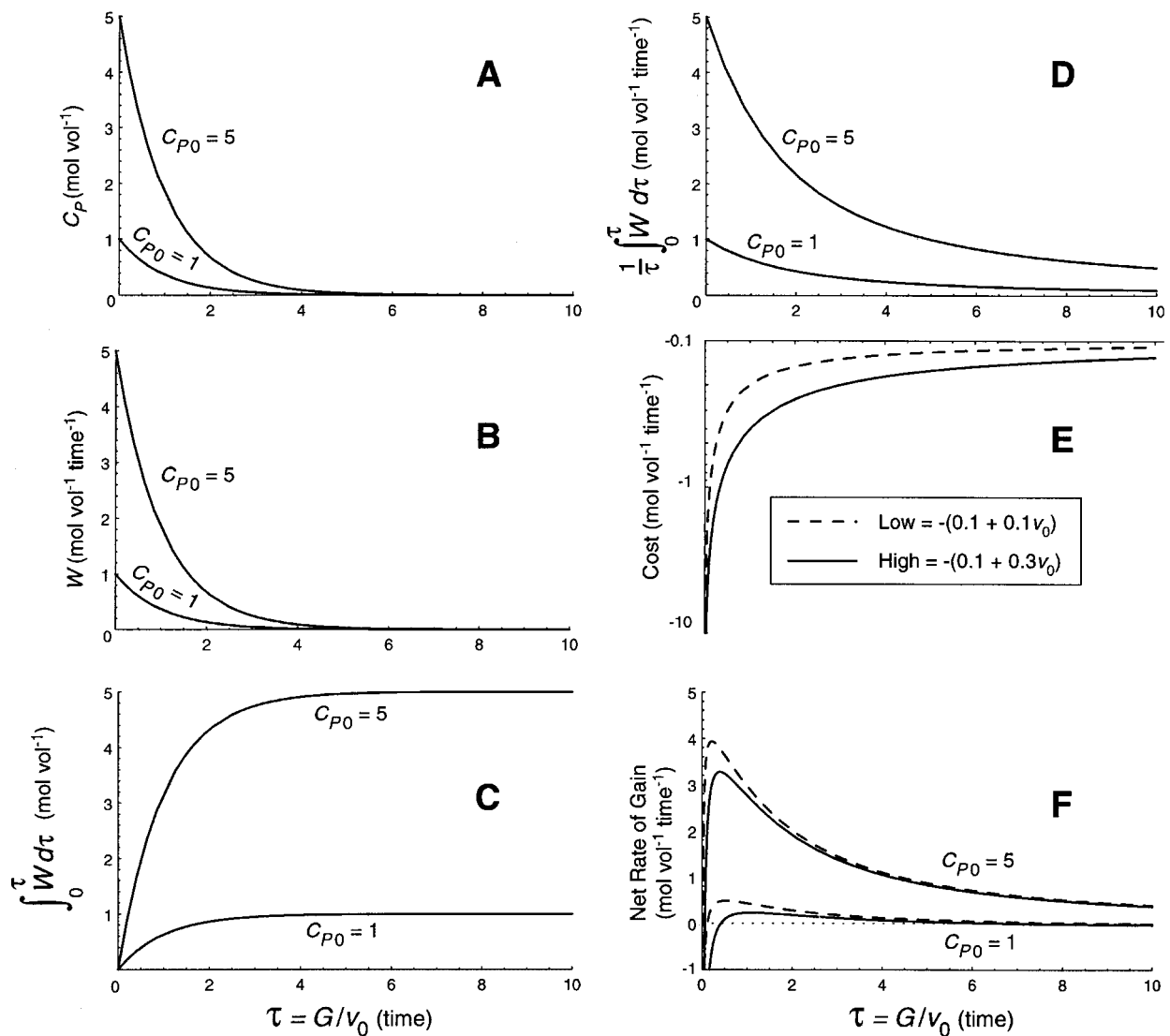


Figure 1. Performance as a function of gut residence time, τ , of a hexose feeder modeled as an ideal plug-flow reactor (PFR) with purely passive absorption at two hexose concentrations (1 and 5 mol vol⁻¹). Gut volume (G) and the absorption rate constant (a) are both set to unity for simplicity of illustration. In a PFR, time and axial position are interconvertible linearly. Concentration curves (A) can be interpreted as egested concentrations after the indicated residence time (C_p), and the values at all shorter times then show the axial profile of concentration along the gut. Local uptake rate (B) is obtained by inserting this local concentration into the rate Equation (1) for absorption. That curve is integrated over the entire residence time to give total gain (C), and the integral is divided by τ to obtain uptake rate per unit of time (D). Adding gross rate of expenditure (E) to the latter function gives net rate of gain (F), which reveals that optimal retention time increases as hexose concentration decreases and cost of obtaining food increases. Dashed lines indicate lower costs.

ing Fig. 1D) decreases with τ . For the case of linear uptake without hydrolysis, then, no local optimum occurs in ingestion rate without including explicit costs: Maximal gross absorption rate occurs at infinite ingestion rate ($\tau = 0$; Fig. 1D) because depletion of luminal contents by a finite rate of absorption then is ineffectual, and luminal concentration throughout the gut equals C_{p0} .

For a truly continuous feeder (i.e., a PFR), feeding costs as

well as gains must be continuous. Many animals have reservoirs (stomachs or crops) that, among other functions, provide continuity of flow through the absorptive, plug-flow sections of their guts (e.g., Levey and Duke 1992). Even morphologically simple animals without reservoirs, such as sea cucumbers, can have surprisingly constant throughput rates and times (e.g., Self et al. 1995). Other continuous cost functions could be used, but the simplest that we can devise that has some realism is to

posit fixed costs (per unit of time) and costs that are proportional to volumetric ingestion rates (v_0):

$$R = -(x + yv_0), \quad (4)$$

where R is the total rate of loss (mol time⁻¹), x is the nonfeeding whole-animal utilization rate (mol time⁻¹), and y is the cost of ingesting a unit of volume of food (mol vol⁻¹). This choice of a cost function (Fig. 1E) is not accidental; it is the continuous-time analog for a PFR of the BR description of costs used by Martínez del Río and Karasov (1990).

To avoid proliferation of dimensions and units and to keep the example more transparent, we retain the reactor-theory convention of focus on mole balance (Fogler 1992) and write all gains and costs in molar equivalents of hexose. It is more conventional ecologically to estimate R in units of energy per unit of time and to convert the gain function to these dimensions as well, and it would be straightforward to do so through the number of joules per mole of hexose.

Saturable Uptake Rates

Adding an active uptake component for hexose adds some complexity. Following Dade et al. (1990), we describe Michaelis-Menten or hyperbolic kinetics of absorption as

$$-r_{PA} = (W_{\max}C_p)/(M_m + C_p), \quad (5)$$

where W_{\max} and M_m are, respectively, the maximal rate and half-saturation (Michaelis-Menten) constants for absorption. Concentration down the gut or with time then is (Fig. 2A)

$$C_p = M_m \text{ Product Log} \left(\exp \{(-\tau W_{\max}/M_m) + \ln [C_{p0} \exp (C_{p0}/M_m)]\} \right), \quad (6)$$

where the solution comes by setting the rate of change of concentration equal to the right side of Equation (5) and applying the solve function of Mathematica 3.0 (Wolfram 1996). The product log is a generalized exponential function that is the solution for w in $z = w \exp(w)$ (Wolfram 1996). Costs were unchanged from the case of linear uptake. Up- or down-regulation of absorptive sites is not considered here, as absorption over the timescale over which the animal is exposed to differing food concentrations (C_p) is assumed to be characterized by a constant W_{\max} and M_m .

Results

Using Equation (4) as a cost function and combining it with gains yields the prediction for animals not requiring hydrolysis and employing strictly passive uptake that optimal throughput time increases as costs (y) increase and food (product) concentration decreases (Fig. 1F). Because throughput time in a

PFR is related reciprocally to volumetric ingestion rates (i.e., $\tau = G/v_0$), the model predicts rising volumetric intake rate with increased hexose concentration in nectar.

Using Equation (6) to find the gut's performance, however, produces some important differences from Figure 1 due to saturation of uptake (Fig. 2A–2F). Here and for all other comparisons with strictly linear uptake, we compare hyperbolic kinetics against linear kinetics only for the special case where a of Equation (1) equals W_{\max}/M_m of Equation (5), i.e., the linear equation that gives the solution to Equation (5) as $C_p \rightarrow 0$. Under this condition, $-r_{PA}$ from Equation (1) is always equal to $-r_{PA}$ from Equation (5) for any value of C_p . Notably, at C_{p0} well above M_m , concentration drops off less steeply with throughput time or distance into the gut (Fig. 2A), local uptake stays below its saturated rate rather than simply reflecting concentration (Fig. 2B), and whole-gut uptake rate, J_A , is much lower and less peaked at high food concentration (Fig. 2D).

Unlike the strictly linear case, τ_{opt} under saturating kinetics depends on hexose concentration of food (C_{p0}). For concentrations well above M_m , optimal throughput time rises with concentration because there is no net gain from displacing gut contents with incoming food when rates already are near saturation levels. Thus, a negative relationship between hexose concentration in food and intake rate is expected. Because Equation (5) becomes linear for $C_p \ll M_m$ (i.e., $-r_{PA} = [W_{\max}/M_m] C_p$), its predictions must then converge to those of Figure 1 at low C_{p0} . In consequence, τ_{opt} first falls to a minimum with increasing hexose concentration and then increases. The hexose concentration at which the relationship between optimal τ and C_{p0} changes direction is located near M_m and depends on the costs of feeding. For example, for the low- and high-cost cases of Figure 2, minima in τ_{opt} occur at $C_{p0} = 0.81$ and 1.12, respectively. Analogously, there must be a similar minimum at some product (food) concentration for predicted ingestion rate when uptake is described as the sum of linear and saturating functions (Martínez del Río and Karasov 1990), and so no simple monotonic predictions are possible for expected direction of change in ingestion rate with food concentration when saturating functions are involved. As with the cases illustrated in Figure 1, however, increasing costs of feeding (y) must drive τ_{opt} higher (Fig. 2F).

Discussion

Martínez del Río and Karasov's (1990) graphical method gives the same prediction with respect to effects of food quality and ingestion costs and finds the identical optima in τ (Fig. 3). A graphical method is prevalent in analysis of batch reactors for two reasons: costs (e.g., of filling and emptying the reactor) and gains are often sequential in batch reactors, and the graphical approach provides an easy way of dealing with this discontinuity of process (e.g., Aris 1965; Penry and Jumars 1986).

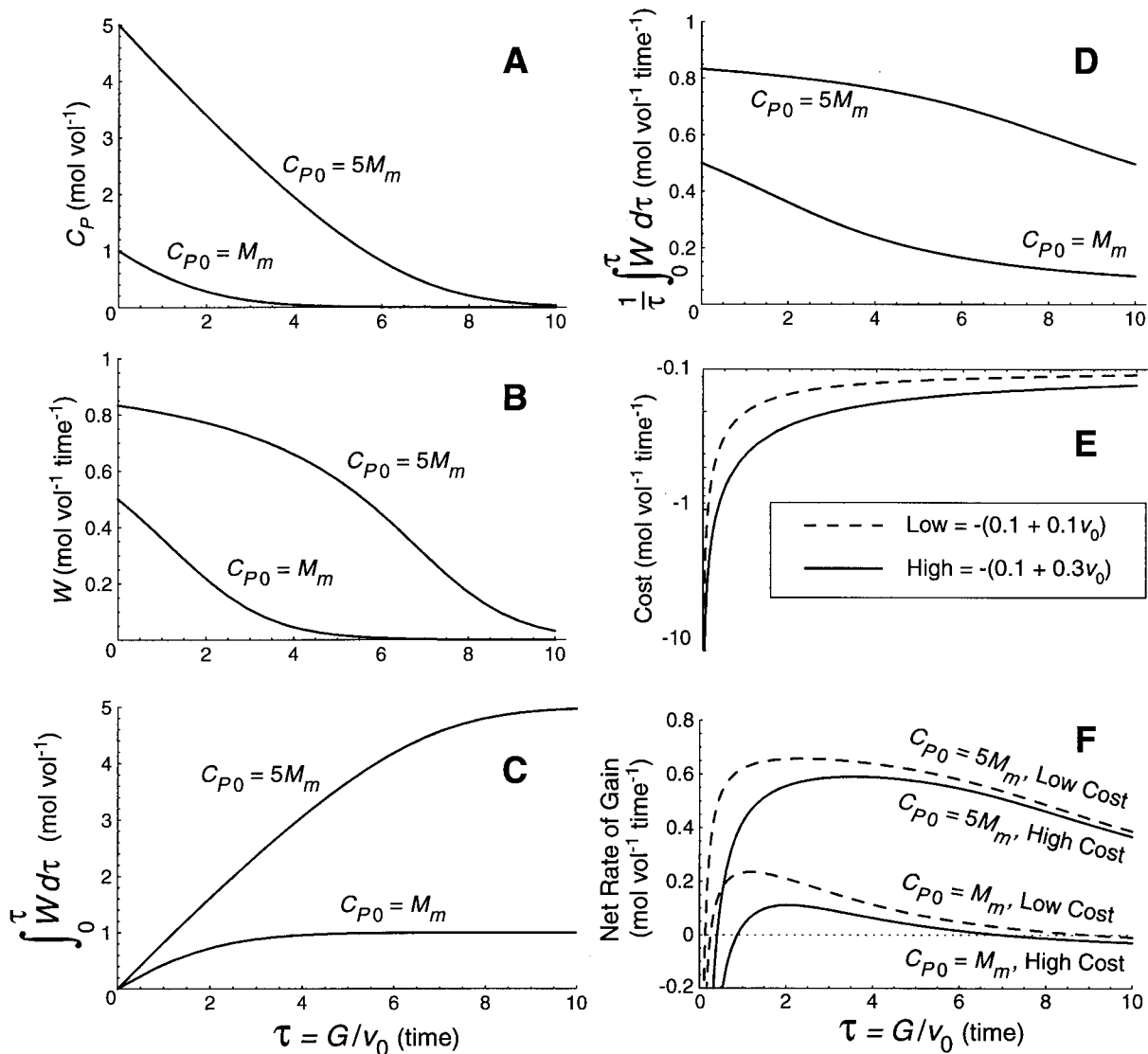


Figure 2. Performance as a function of gut residence time, τ , of a hexose feeder modeled as an ideal plug-flow reactor (PFR) with hyperbolic kinetics of absorption at two hexose concentrations (1 and 5 mol vol⁻¹). W_{\max} , M_m , and G all are set to unity for simplicity and ease of comparison with Figure 1 and with previous nondimensional plots (Dade et al. 1990); readers comfortable with nondimensionalization can substitute C_p/M_m and W/W_{\max} for C_p and W , respectively. In a PFR, time and axial position are interconvertible linearly. Concentration curves (A) can be interpreted as egested concentrations after the indicated residence time, and the values at all shorter times then show the axial profile of concentration along the gut. Local uptake rate (B) is obtained by inserting this local concentration into the Michaelis-Menten Equation (9) for absorption. That curve is integrated over the entire residence time (C), and this integral is divided by τ to obtain uptake rate per unit of time (D). Adding gross expenditure (E) to the latter function gives net rate of gain (F), which reveals that optimal retention time increases both with hexose concentration above M_m and with cost of obtaining food.

Martínez del Río and Karasov (1990) assumed ingestion costs to be instantaneous, formally making their cost function discontinuous and explaining the negative intercepts of the net gain curves (Fig. 3). The downturn of the net gain curve at long retention times reflects continuous metabolic costs that accumulate linearly with time (i.e., resting metabolic rate). To apply Martínez del Río and Karasov's (1990) model to animals

with PFR-like processes requires a few accommodations. The net gain curve shown in Figure 3 must be considered as costs and gains per batch and τ as the time devoted to processing a single batch. Batch size, in order for the batch-reactor performance equations to apply to this PFR, must be one gutful (of the absorptive PFR section alone, for reasons noted previously).

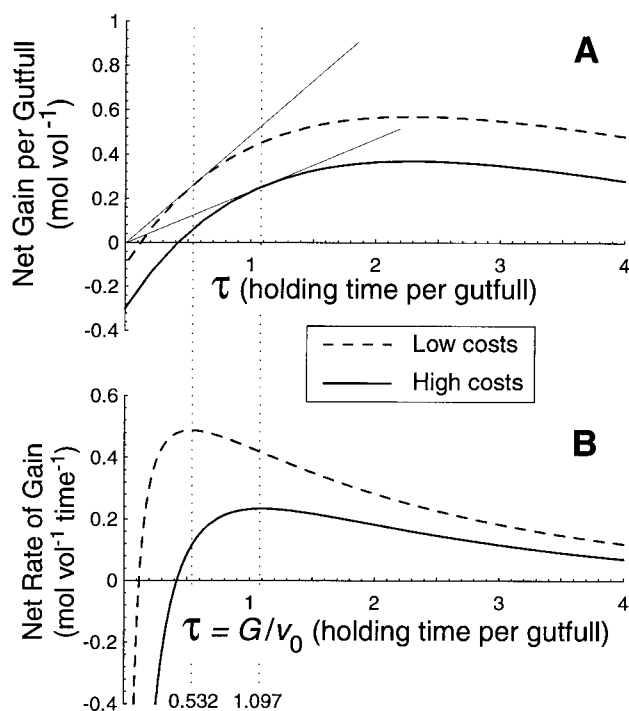


Figure 3. Direct comparison of the batch-reactor solution (A) of Martínez del Río and Karasov (1990) and the PFR solution (B) of Figure 1 for optimal gut residence times at a product concentration of 1 mol vol⁻¹. Note that the abscissa in A is not G/v_0 because in a batch reactor inflow is not continuous. Net gain shown in A is per batch. The slope of the tangent to the curve from the origin in A is the maximal rate of gain achievable per τ but must be multiplied by the number of gutfulls ingested per unit of time to yield the net rate of gain per unit of time shown in B. Note that B explicitly plots net rate of gain and incorporates the costs of continuous feeding described in Equation (4).

The graphical method of finding τ_{opt} as the point at which a line through the origin is tangent to the net gain curve identifies the holding time that maximizes the rate of gain per batch holding time, t . To convert gains per batch holding time to gains per unit of time in continuous feeding requires multiplication of gain per batch by the number of batches processed per unit of time, which is inversely proportional to t . That transformation yields Figure 1F. Equation (4) represents this conversion of the cost to fill a gut once (C_0 of Eq. [5] of Martínez del Río and Karasov [1990], p. 625) to the number of gut fillings per unit of time at the specified t and the addition of constant costs unrelated to the rate of ingestion. That is, Martínez del Río and Karasov's (1990) estimate of the energy required to fill the gut simply can be divided by the volume of the absorptive, PFR section of the gut, G , to yield y of Equation (4). Failure to account for the modifications that need to be made to apply the batch-inspired model of Martínez del Río and Karasov (1990) to continuous feeders can lead to erroneous predictions, however.

That their graphical cost function should not be applied to a PFR without considering the number of batches processed per unit of time is seen most easily in the limits (Fig. 4). When feeding slows to zero (large τ), their costs still include a single

gut filling, whereas only x of Equation (4) is important. Conversely, when ingestion rate goes toward infinity ($\tau \rightarrow 0$), their function approaches the costs of filling the gut once, whereas the gut must be filled many times per unit of time, and the only important costs are in the second term on the right side of Equation (4). The need for the conversion is not obvious when the unit of time employed is close to a single throughput time, as it was for Martínez del Río and Karasov (1990; τ of order 1 min), because at $\tau = 1$ (and only there), results for the two cost functions converge (Fig. 4).

Explicit solution for net rate of gain as a function of gut throughput time (Fig. 1F) has the added advantage of revealing the shape of the net gain curve and hence the anticipated resistance of the individual to displacement from its optimal retention time. It is apparent, for example, that with our simple cost function (Eq. [4]), net rate of gain falls off more steeply below the optimal retention time than above it and that the optimum is sharper at higher food concentrations. Working with the continuous function in the primary currency of foraging theory (net rate of gain) also reveals that constant costs per unit of time (x of Eq. [4]; Fig. 1E) can have no effect on location of the optimum, although they clearly do determine the magnitude of net gain. For example, exposing a homeo-

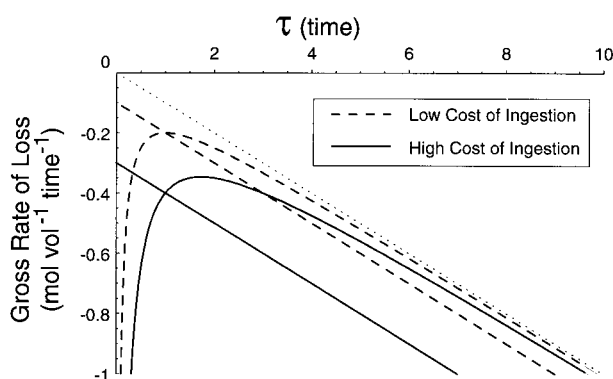


Figure 4. Comparison of costs per gutful as posited by Martínez del Río and Karasov (1990) for graphic, BR solution, and costs of continuous plug-flow reactors feeding as posited by Equation (4). Costs per gutful are the straight lines with intercepts that correspond to the cost of filling the gut once and then holding the digesta for the specified time, whereas the costs of continuous feeding are shown as smooth, solid and dashed curves that accommodate smoothly varying ingestion rates. The dotted line through the origin represents fixed costs per unit of time, to which both smooth curves asymptote as feeding rate approaches 0. The two kinds of cost functions match only at $\tau = 1$ because at that point the number of gutfuls processed per unit of time is 1.

therm to low temperature (as McWilliams and Karasov [1998] did to help assure that rate of energy gain was important to the animal) should not change retention time under the optimization premise. Increasing the cost of acquiring food (γ in Eq. [4]), however, leads to increased τ_{opt} (Fig. 1F).

Net gain curves show broader peaks with less distinct optima under saturating kinetics, implying less disadvantage in feeding more slowly and retaining digesta past τ_{opt} , and optimal retention times are longer than for the unsaturated case (Fig. 2F). Because feeding often exposes an individual to hazard from predation (Fraser and Gilliam 1992; Anholt and Werner 1995) and gross rate of gain falls off so slowly with increasing throughput time, throughput times higher than those based on maximizing gross rate of gain from absorption should be expected.

It is evident from these two simple examples (Figs. 1 and 2) that no sweeping generalization about direction and magnitude of change expected in ingestion rate with food concentration should be made for all hexose feeders. Even for animals that feed on a single substrate that does not require hydrolysis, predicted change in feeding rate hinges very critically on the cost function and on the extent to which uptake is saturated. For the complex but realistic case of animals with both active and passive uptake (Martínez del Río and Karasov 1990), if the kinetic parameters are known, predictive plots analogous to those of Figures 1 and 2 can be produced numerically (Dade et al. 1990) for comparison with data.

Our particular formulation of costs (Eq. [4]), in turn, is equivalent to assuming a specific dynamic action (including both mechanical and enzymatic costs of food processing in digestion as well as costs of chemosynthesis from digestive products) proportional to volumetric ingestion rate—no doubt an oversimplification. One alternative for which there is some

experimental support (e.g., Taghon [1988]) is proportionality of specific dynamic action to the molar ingestion rate of organic matter. For animals like hummingbirds (and the worms that Taghon [1988] examined for protein absorption) that show high and nearly constant assimilation efficiency, anabolic costs may well scale linearly to molar absorption rates of those substrates required for biosynthesis. Above some finite feeding rate or above some nectar viscosity (Kingsolver and Daniel 1983), mechanical inefficiency may set in, making costs increase nonlinearly with ingestion rate. Even without such steeply rising costs at higher feeding rates, Equation (4) gives total costs that initially fall rapidly with increasing τ and then asymptote to x as τ increases further (Fig. 1E).

For the more general case of digestion, hydrolysis and absorption both are involved. Even without an explicit cost function, the need to accomplish hydrolysis before absorption shifts maximal absorption rate to an intermediate ingestion rate (Dade et al. 1990). For hyperbolic kinetics typical of hydrolysis by feeders on disaccharides, such as hummingbirds (Martínez del Río 1990), optimal ingestion rates should vary inversely with concentration of disaccharide in the food, with the steepest drop near half-saturation values and costs that increase with ingestion rate again driving longer retention (Dade et al. 1990).

What Has Been Learned from Applying Guts-as-Reactors Models to Hexose-Feeding Birds?

Our attempt in this article is to clarify predictions from reactor theory regarding ingestion rates of simple substrates under the premise of maximization of net rate of absorption. It is not to

defend those predictions. A theoretical framework is useful to the extent that it spawns empirical work to test its predictions and that it allows interpretation of experimental results. Chemical reactor theory has been fertile at generating empirical research, but, as pointed out earlier, empirical research has led to the notion that the reactor-theory description of reaction kinetics and mixing, the cost function and (or) the premise must be incorrect for several combinations of species and foods.

Three observations seem to apply broadly to nectar- and fruit-eating birds feeding on hexoses. First, food intake decreases with increased sugar concentration. Second, assimilation efficiency of glucose is high (>90%) and appears to be independent of sugar concentration in food. Third, most studies also have reported relative constancy in net assimilation rate with varying hexose concentration in food (Karasov and Cork 1996; Downs 1997; Witmer 1998). An accurate model of gut function for hexose feeders must generate predictions consistent with these observations. For the case of linear absorption kinetics, it is plain from Equation (2) that absorption efficiency, $(1 - C_{pf}/C_{p0})$ will remain constant only if τ does, and therefore absorption rate will rise linearly with food (product) concentration. If the three empirical observations hold, then it is impossible that guts of nectar- and fruit-eating birds function as tubular reactors of constant volume in which hexose uptake takes place solely through passive processes, and in which retention time is modulated to maximize hexose uptake rate. Reactor theory has helped to clarify how the gastrointestinal systems of these animals do not function.

Seeger and Stubblefield (1996) suggest that optimization approaches to investigate biological phenomena often follow a cyclical process with three recurrent steps. First, a model that makes explicit assumptions is constructed. Second, an analysis of the model deduces optima as a function of the model's parameters. Third, an empirical test asks how well the model's assumptions and data agree. This process may cycle to the beginning in search of sets of assumptions that explain the biological process under investigation. Research on the digestive processes and ingestion rates of hexose feeders has followed this full cycle. Available data led to falsification of the predictions of a particular model and thus to reexamination of its assumptions.

Departures from predictions of a gut-as-reactor model can be due to inaccuracy of the descriptions of processing costs, reactant volumes, reaction kinetics or mixing or to inaccuracy of the optimization premise. A substantial body of research supports the notion that the kinetics of absorption in hexose-feeding birds takes place largely by passive and, presumably, paracellular processes (reviewed in Afik et al. 1997). The reaction kinetics assumed by the simple model appear to be correct, leaving the assumptions of constant gut volume, constant costs per unit of volume of nectar ingested, of insignificant axial mixing, and of absorption rate maximization as candidates for replacement. Costs per unit of volume of nectar ingested

may rise from increasing viscosity as sugar concentration of nectar increases (Kingsolver and Daniel 1983), and those complications are not included in Equation (4). Costs that rise with sugar concentration can overturn the simplest prediction that animals absorbing hexoses purely passively should feed faster on higher sugar concentrations. Such dependence of y of Equation (4) on food quality would yield an optimum for passive hexose absorbers and offset and sharpen optima for other cases. Under all these complicating scenarios, however, the conclusion that costs rise rapidly—and, hence, that net gains fall rapidly—with decreasing τ below τ_{opt} appears robust.

Conclusions

Animals clearly have numerous constraints that may compete with maximization of rate of gain from absorption in determining ingestion rates and might be parameterized as costs. Among them are the water-balance problems characteristic of life on land and in fresh water, with potentially very diverse solutions. Humans, for example, secrete several liters of fluid into 1 L of food each day and resorb the bulk of the water in the hindgut (Drasar and Barrow 1985). Water absorption can also be manipulated to raise product concentration in anterior absorptive sections as one potential means by which absorption rate can be kept high in animals feeding on very dilute foods (Dow 1981; Mayer et al. 1997). Conversely, there is evidence that birds feeding on hexoses at concentrations that exceed the osmolality of plasma dilute their incoming food with intestinal secretions (Chang and Rao 1994), presumably to avoid osmotic stress to cells of the mucosa, and nectar feeders in general may have hyper- or hypo-osmotic gut contents (Beuchat et al. 1990; Nicolson 1998). Secretion or extraction of significant fluid from the gut violates the assumption that volume is conserved (Penry and Jumars 1987; Dade et al. 1990; Martínez del Rio and Karasov 1990; the models here), and this secretion and subsequent extraction also take time that is not included in the simple formulations underlying Figures 1 and 2. This complication can be treated by maintaining mole balance not only on hexose but also on water and osmolytes in the lumen and tracking the costs and time involved. An important task in the future is to identify and quantify such other constraints on rate of ingestion and then to determine whether—under these constraints—ingestion rate can be predicted from optimization or from some other premise.

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