

# Chemical Reactor Analysis and Optimal Digestion

*An optimal digestion theory can be readily derived from basic principles of chemical reactor analysis and design*

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**F**oraging and digestion are two stages of a single process that determines an animal's net rate of energy and nutrient gain. According to the principles of dynamic programming, a method for formulating and solving optimization problems (Bellman 1957), the entire process is optimized only if digestion follows an optimal path constrained by the food items actually ingested. An animal feeding on a variety of foods should thus exhibit the flexibility to adjust digestion with respect to that range of food types. Conversely, the net rate of gain to an animal lacking such flexibility will be maximized over a restricted set of food types, making it a dietary specialist.

To test these general predictions and to formulate more specific ones, we must identify the operating variables for each stage. Many foraging theories exist (e.g., Charnov 1976, Orians and Pearson 1979, Pyke 1984, Schoener 1971), but there are only rudiments of an optimal digestion theory (Milton 1981, Sibly 1981, Taghon 1981, Troyer 1984). Without such a theory, studies of digestive systems (e.g. gut anatomy, histology, or enzymology) tend to be static, piecemeal, and most often nonpredic-

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tive. To date, for example, conspicuously few predictions and data exist on patterns and rates of material throughput.

Modeling the digestive process is a problem in chemical engineering. Given a chemical reaction and physical and economic constraints, a chemical engineer designs a reactor and an operating strategy that maximize the yield or yield rate of desired reaction products (Carberry 1976). Similarly, given the chemical reactions and the physical and energetic constraints of digestion, we try to discover how various gut configurations and digestive tactics may maximize an animal's net rate of energy and nutrient gain. The first step is descriptive: We must describe animal guts in terms of chemical reactor components and then use principles of reactor design to identify variables that characterize digestive strategies.

## Chemical reactor design

There are three general classes of reactors: batch reactors; steady-state flow reactors; and semibatch, or unsteady-state flow, reactors, which combine characteristics of the first two types (Levenspiel 1972). The batch reactor, as its name implies, processes reactants in discrete batch-

es. All reactants are loaded into the reactor and allowed to react; the resulting products are then removed. Composition of material within the reactor changes over time. In contrast, a steady-state flow reactor maintains constant flow of reactants into and products out of the reaction vessel. Composition at any point within the reactor is unchanged over time. Any reactor that cannot be classified as one of the first two types is a semibatch, or unsteady-state flow, reactor. Its operation may involve any or all of the following: intermittent flow of reactants into, or products out of, the reactor and density or volume changes of the material within the reactor.

Animals eating discrete meals can be classified as batch reactors and those that eat more or less continuously as steady-state flow reactors. Semibatch reactors may more realistically represent gut kinematics of animals that feed at irregular intervals, but these reactors are comparatively difficult to model (Levenspiel 1972). Understanding the gut kinematics of animals that approximate the easily modeled batch and steady-state flow reactors provides the basis for future consideration of semibatch guts.

Three ideal theoretical models—the batch reactor and two steady-state flow reactors (the plug-flow reactor and the continuous-flow, stirred-tank reactor)—form the basis of all chemical reactor design. These ideal reactor models differ principally in how reactants meet to react in the reaction vessel; for any given reaction, one of these three reactors usually represents

the best method of processing the necessary reactants. Industrial reactors are often designed so that their flow and mixing patterns approach these ideals (Levenspiel 1972).

In contrast with many industrial situations, temperature is approximately constant in an animal's gut, so we need consider only conservation of mass in developing reactor models for guts. For a given reaction rate equation, reaction extent and operating conditions in the reactor can be obtained by solving the appropriate mass balance equation. Comparing the detailed solutions for different reactor types enables us to identify the best reactor design for given reactions, for example, digestive reactions of specified kinetics.<sup>1</sup>

To identify their respective operating variables, we here introduce the basic considerations in the formulation of each ideal reactor model, including the reactor-specific mass balance equations (notation after Levenspiel 1972).<sup>2</sup> Examining these equations and the assumptions on which the derivations are based emphasizes the homology between animal guts and chemical reactors.

**Batch reactors.** In a batch reactor all reactants are initially loaded, then mixed thoroughly and allowed to react; the resulting product mixture is then completely removed. Changes occur only with respect to time; properties are assumed to be spatially uniform within the reactor. Since material neither enters nor leaves the reactor during reaction (input = output = 0), the mass balance consists of only two terms summing to zero: disappearance of reactant *A* by reaction and accumulation of reactant *A* in the reactor. The amount of *A* that disappears by reaction is a function of reaction rate ( $-r_A$ , in units of [amount of *A*/vol/time]), volume of reactants in the reactor (*V*), and the reactor holding time over which the reaction occurs (*t*). The amount of *A* that accumulates in the reactor is a

function of the amount of *A* initially added ( $N_{A0}$ ), and the fraction of *A* not converted to products ( $1 - X_A$ ), where ( $X_A$ ) is the fraction of *A* converted to products. The time required to achieve a conversion ( $X_{Af}$ ) in a batch reactor is

$$t = N_{A0} \int_0^{X_{Af}} \frac{dX_A}{(-r_A)V}$$

If we assume that each time an animal feeds it ingests enough food to fill the space available in its gut, then the reacting volume, measured by the volume of food initially ingested, equals reactor volume. But in contrast to the ideal batch reactor, the volume of the reacting mixture in an animal's gut decreases with increasing reaction time as products are removed through absorption. The ideal batch reactor model can be modified to describe this flow of products from the gut. In this initial exposition, however, we choose to neglect volume variations resulting from absorption of digestive products—a simplification that proves reasonable for animals such as deposit feeders and other detritivores, herbivores, and folivores with diets that normally include large quantities of inert or refractory materials like sediment grains, cellulose, or lignin. If the reacting volume does not vary significantly, *V* may be removed from under the integral.  $N_{A0}/V$  is the initial concentration of *A* ( $C_{A0}$ ), and the performance equation becomes

$$t = C_{A0} \int_0^{X_{Af}} \frac{dX_A}{-r_A}$$

This equation can be solved for the holding time *t* required to achieve a desired level of conversion  $X_{Af}$  of reactants to products ( $-r_A$  and  $C_{A0}$  specified) or for the reactor volume *V* required to achieve a given rate of production ( $-r_A$ ,  $C_{A0}$ , *t*, and  $X_{Af}$  specified).

Examining the reactor performance equation indicates that, for a given reaction rate expression, holding, or digestion, time is the important operating variable for animals with batch-reactor guts. We define an optimal operating strategy for any gut as the one maximizing net rate of energy or nutrient production from ingested foods. In determining an optimal operating strategy for a batch-reactor

gut under a given set of conditions, we must consider constraints on holding time, adding, for example, time between meals, when the gut may be idle. When we predict optimal operating policies for batch-reactor guts ( $X_{Af}$  specified), the quantity minimized should be the total time needed for a complete gut-reactor operating cycle—foraging, ingestion, digestion, and egestion.<sup>3</sup>

Since digestive reactions are, in general, first-order reactions or zero-order reactions shifting to first-order as reactant concentrations decrease, the extent to which ingested food materials are digested is completely determined by holding, or digestion, time. For maximum production rate, then, gut volume should be maximized so more food ( $C_{A0}$  constant) can be processed in the same holding time. However, the effectiveness with which enzymes and food particles come into contact decreases as gut volume and volume of material processed in each batch increase, resulting in less food converted per batch and placing upper bounds on gut volume. This decrease in effective contact among reactants may result both from a decrease in the effectiveness with which enzymes and food material can mix and, since enzymes are introduced from the gut wall, from a decrease in the gut's surface-to-volume ratio.

Animals that can be modeled as having batch-reactor guts include hydras, hydroids, jellyfish, sea anemones, and corals (Cnidaria), comb jellies (Ctenophora), brittle stars and starfish (Echinodermata), and some glycerid polychaetes (Annelida) that regurgitate their wastes (Ockelmann and Vahl 1970).

**Plug-flow reactors.** The plug-flow reactor (PFR) is characterized by a continuous flow of material through the reaction vessel. The flow pattern is orderly: material parcels enter and exit the reactor in the same sequence. Material is perfectly mixed radially, but mixing or diffusion along the flow path is negligible. Residence time in

<sup>1</sup>Penry and Jumars, manuscript in preparation.

<sup>2</sup>Since we are simply providing the descriptive basis for future theoretical and experimental analyses, deriving these equations here is unwarranted. Refer to chemical engineering texts (Levenspiel 1972, Smith 1981) for the derivations.

<sup>3</sup>A particular quantity (e.g., holding time or gut volume) is minimized or maximized both in the context of an optimization problem and in the broader evolutionary context of individual fitness (e.g., Townsend and Calow 1981).

the reactor is identical for all parcels—the necessary condition for plug flow (Levenspiel 1972). Under steady-state operation, changes occur only with respect to axial position within the reactor, and the mass balance is made over a differential volume element ( $dV$ ). The resulting equations relate reaction rate ( $-r_A$ ), reaction extent ( $X_A$ ), reactor volume ( $V$ ), and input rate of reactant  $A$  ( $F_{A0}$ , where  $F_{A0} = C_{A0} \times v_0$ , the product of  $A$ 's initial concentration and volumetric flow rate):

$$\frac{V}{F_{A0}} = \int_0^{X_A} \frac{dX_A}{-r_A}$$

or

$$\tau = \frac{V}{v_0} = C_{A0} \int_0^{X_A} \frac{dX_A}{-r_A}$$

The ratio of reactor volume ( $V$ ) to volumetric flow rate ( $v_0$ ) is the time ( $\tau$ , "space-time") required to process one reactor volume of material or, in biological terms, the ratio of gut volume to throughput rate is throughput time, the time required to process one gut volume of food. To maximize their energy and nutrient production rates, animals with PFR guts should process food to minimize throughput time required for any given conversion ( $-r_A$ ,  $C_{A0}$  specified). Gut volume and throughput rate are the important operating variables.

Many animals have guts that approximate plug-flow reactors. Examples include geese, corophiid amphipods (Crustacea), and deposit-feeding polychaetes (Annelida) with simple tubular guts.

**Continuous-flow, stirred-tank reactors.** The design of the continuous-flow, stirred tank reactor (CSTR) incorporates both constant flow of material through the reactor and complete mixing within it. At steady state, the composition of material is both uniform throughout the reactor and invariant over time. Input of reactant  $A$  is a function of input rate ( $F_{A0}$ ) and output of  $A$  is thus a function of input rate and the fraction of  $A$  that is not converted to products ( $1 - X_A$ ). The amount of  $A$  that disappears by reaction is a function of reaction rate ( $-r_A$ ) and reactor volume ( $V$ ). The mass balance equations become

$$F_{A0}(X_A) = (-r_A)V$$

or

$$\tau = \frac{V}{v_0} = C_{A0} \frac{X_A}{-r_A}$$

To maximize their energy or nutrient production rates, animals with CSTR guts should, like animals with PFR guts, process food to minimize the throughput time required for any given conversion ( $-r_A$ ,  $C_{A0}$  specified). Again, gut volume and throughput rate are the important operating variables.

We know of no animal that has a gut that can be modeled entirely as a CSTR. There are many animals, however, in which a portion of the gut operates as a CSTR, and the entire gut can be modeled as a series of reactors—a common arrangement in chemical process design. A ruminant gut, for example, can be represented simply as a CSTR followed in series by a PFR.

### Applying reactor theory and models to digestion

Principles of chemical reactor design can be used to analyze the kinematics of digestion, and the three ideal reactors can serve, singly or in series, as models for animal guts. Reactor-specific mass balance equations can then be used, without any initial modifications, to predict the performance of gut reactor models with respect to digestive reactions.

Numerous empirical models have been developed to describe rates of digesta throughput and gut evacuation (e.g., Brandt and Thacker 1958, Grovum and Williams 1977, Mills et al. 1984). Rate descriptions resulting from such empirical models hold only for the specific conditions prevailing when the data were collected. They cannot predict, as reactor models can, changes that should occur in digesta throughput rates with changes in, for example, food concentration or ingestion rate.

Among empirical approaches, the compartmental method of kinetic analysis (e.g., Brandt and Thacker 1958, Hughes and Matis 1984) has become popular, and a two-compartment model is somewhat successful in describing cumulative fecal output in large herbivores. Previous interpreta-

tions of observed defecation patterns traced with, for example, soluble markers, dyed or radioisotopically labeled plant material, or metal oxides suggest that the ruminant digestive system functions as a sequential, irreversible, two-compartment flow process with complete mixing in each compartment (Figure 1a) and exponential loss of material from each compartment (Ellis et al. 1979; Figures 1b,c,d). This model comes close to our model from chemical reactor theory, but important differences exist.

We propose that the ruminant gut be modeled as two reactors in series, a continuous-flow, stirred-tank reactor (the rumen) followed by a plug-flow reactor (the remainder of the gut; Figure 2a), a model that exactly accounts for observed tracer residence-time distributions. The residence time distribution for a CSTR-PFR series is an exponential function resulting from CSTR mixing characteristics. If a tracer were introduced at the beginning of the reactor series (ingestion) and its output from the reactor series (defecation) were monitored, the results would match the exponential output curve observed for ruminants (Figure 2b). The CSTR-PFR series model also explains the residence-time distributions observed when tracers are introduced at different points along the ruminant's gut, whereas the compartmental model does not. The residence-time distribution for a single, ideal CSTR is an exponential function (Figure 2c), but a step function for a single, ideal PFR (Figure 2d).

Balch (1950) fed stained hay to cows and also injected stained hay into the abomasum of fistulated individuals. The observed residence-time distributions for these tracers confirm our hypothesis that the rumen operates as a CSTR (stained particles were present close to the reticulo-omasum orifice from the beginning of the meal) and that the rest of the gut approximates a PFR (tracer excretion from the abomasum occurred over a very short time period, indicating that mixing in posterior gut segments is slight). With this better empirical fit and predictive ability, the CSTR-PFR model offers excellent prospects for improved understanding of ruminant digestive systems.

Guts can be modeled variously as batch reactors, plug-flow reactors, and CSTR-PFR reactor series, but one basic set of operating variables exists. Given an expression for the rate of digestive reactions—the appropriate choice of which depends on gut chemistry—the extent to which ingested food is digested and converted to usable products depends on the concentration of a limiting, or otherwise important, component of the material ingested; volume of material ingested and/or volume of the gut; and holding or throughput time of material in the gut.

The importance of quantifying each operating variable in these reactor models to determine an animal's production rate of energy and nutrients from food materials under diverse conditions seems obvious after the equations are written, but the entire set of variables has rarely been measured. For example, values for digestibility ( $X_{Af}$ ) of specific diets or for energy or nutrient assimilation are frequently presented without reference to the concentrations of important food components, throughput rates, or throughput times. Not only do operating variables remain unquantified, but those variables considered are often quantified with inappropriate measurements. For example, it is not valid to measure gut passage, or "clearance," time under starvation ( $v_0 = 0$ ) for animals that normally feed continuously if these measures are intended to apply to normal conditions.

Having identified the operating variables for digestion, we can also more closely examine our initial predictions relating digestive strategies and diet breadth. Flexibility in digestive strategies can now be more specifically described as the ability of an animal to vary gut volume or the food's throughput rate or time as the composition of its diet changes. Although appropriate data are extremely limited, some evidence suggests that certain animals can accommodate a variety of diets because they can vary  $V$ ,  $v_0$ , or  $\tau$  in response to a change in concentration of a food component. The most striking examples are presented by gallinaceous birds, such as grouse, quail, or ptarmigan, whose intestinal length (a component of  $V$ ) varies seasonally

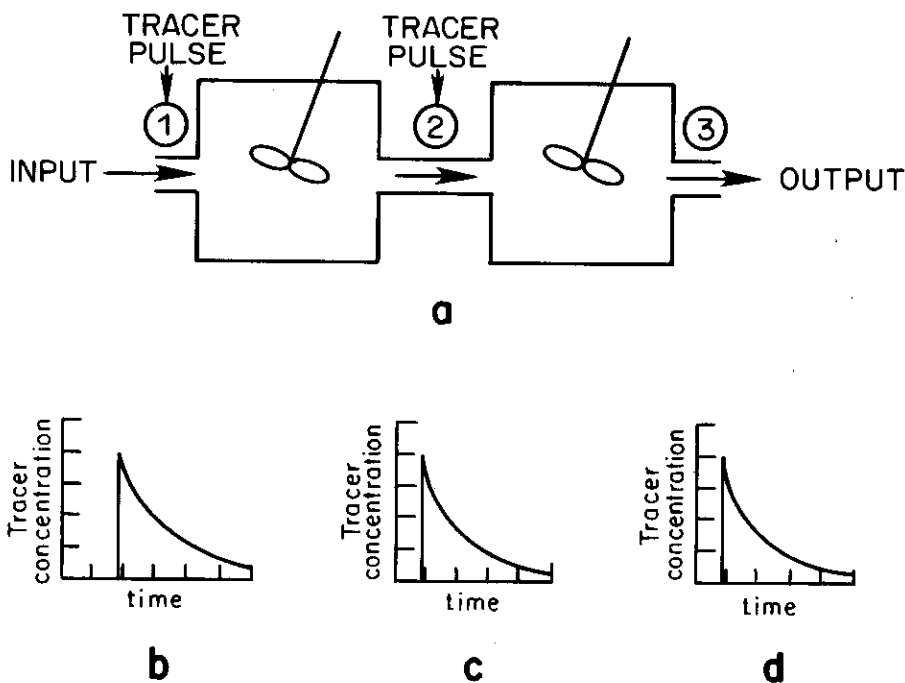


Figure 1.a. Empirical compartmental model for a ruminant gut. b. Tracer residence-time distributions resulting when tracer is introduced at 1, measured at 3. c. Tracer introduced at 1, measured at 2. d. Tracer introduced at 2, measured at 3.

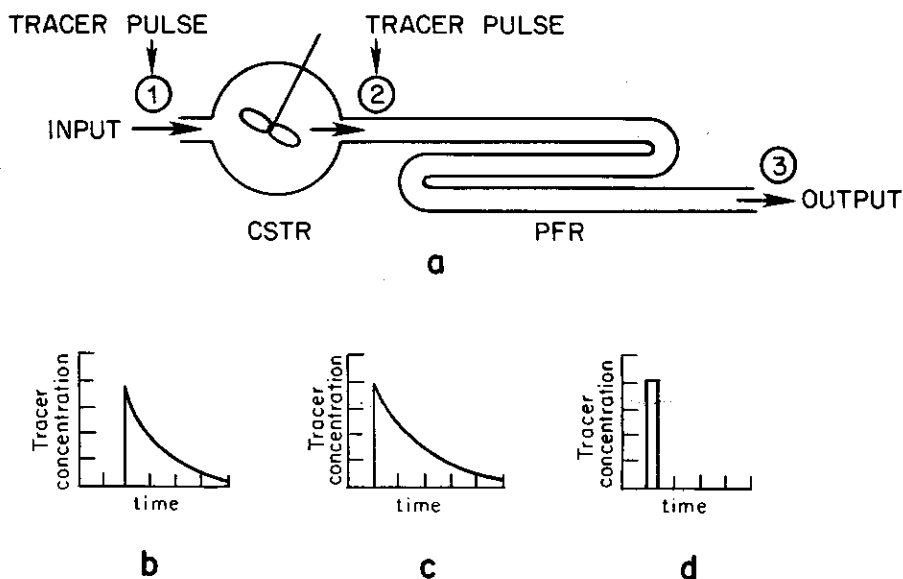


Figure 2.a. Theoretical reactor model for a ruminant gut. b. Tracer residence-time distributions that result when tracer is introduced at 1, measured at 2. c. Tracer introduced at 1, measured at 3. d. Tracer introduced at 2, measured at 3.

with changes in diet. Birds eating poorer diets have longer intestines (Leopold 1953, Moss 1974). Laboratory studies have shown that starlings (Al-Joborae 1980) and Japanese quail (Savory and Gentle 1976) with longer

guts can process more food per day than conspecifics with shorter guts while maintaining the same digestive efficiency ( $X_{Af}$ ).

Other evidence suggests that animals unable to alter their digestive

strategies must consume fairly constant diets. In a comparative study of food choice and digestive strategies in howler (*Alouatta palliata*) and spider monkeys (*Ateles geoffroyi*), Milton (1981) found that howlers, with their larger hindguts and longer throughput times can ferment plant material more efficiently than spider monkeys and thus maximize energy and nutrient gains on a diet consisting primarily of leaves. Spider monkeys, with smaller hindguts and shorter throughput times, can process more food per unit time and thus specialize on a diet of fruit too low in protein to support howlers. Milton concluded that each species is committed, by physiological and morphological adaptations, to a particular digestive strategy and diet.

On evolutionary scales, ruminants (foregut fermentation, CSTR-PFR gut) outcompete horses (hindgut fermentation, PFR-CSTR gut) when food is scarce because ruminants can extract greater amounts of energy (greater  $X_{Af}$ ) from limited amounts of food. When food of high nutrient concentration is abundant, horses outcompete ruminants because horses can obtain energy faster by processing

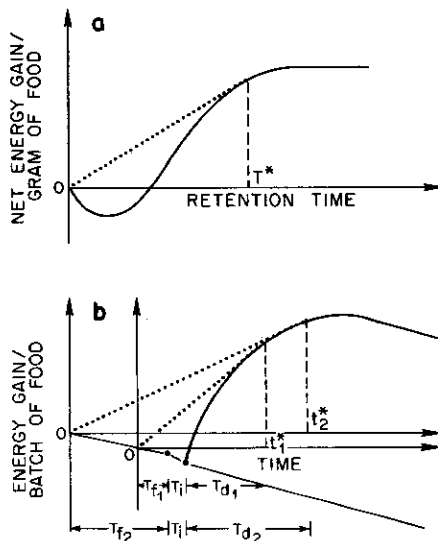


Figure 3a. Digestive performance curve proposed by Sibly (1981). Optimal digestion time ( $T^*$ ) maximizes net rate of gain of energy per gram of ingested food. b. Digestive performance curve for a batch process given as gain or loss per batch of any limiting dietary component. Increasing time spent foraging ( $T_{f1} \rightarrow T_{f2}$ ) increases optimal batch holding time ( $t^*_1 \rightarrow t^*_2$ ).

large amounts of food more quickly than ruminants can. Neither can adopt the digestive strategy of the other (Janis 1976).

The digestive strategies open to an animal in turn place constraints on its foraging strategies; any consideration of optimal strategies for maximizing energy gains should therefore include the role of digestion as well as foraging. Sibly (1981) recognized this need, arguing on intuitive grounds what the form of a digestive performance curve must be (plotted as retention time versus net energy gain per gram of ingested food). His digestion curve (Figure 3a) bears a remarkable resemblance to the profit curve for a batch reactor derived by Aris (1965), but again, some important differences exist that demonstrate the value of reactor theory.

The steps in batch operation of an industrial reactor or animal gut can be arranged in series and repeated in each complete operation cycle. For any animal batch-processing food, these steps are (1) foraging time,  $T_f$ ; (2) ingestion time,  $T_i$ ; and (3) digestion time,  $T_d$ . In some cases, a fourth step—time spent in activities other than foraging, ingestion, and digestion—might be included. The time invested in one step results in a gain or loss of some limiting dietary component (e.g., energy), which is independent of gains or losses in every other step (except that digestive gains and losses are concurrent). Optimal holding time,  $t^*$ , of a batch of food material is the time that maximizes net rate of gain of the important component.

From this reactor analysis of digestion, two things become apparent that are not obvious from Sibly's argument. First, optimal holding time increases with increasing  $T_f$ , or foraging time between meals (Figure 3b) as, analogously, optimal foraging time in a prey patch increases with increasing travel time between patches (e.g., Figure 1 in Cowie 1977). Second, gain from digestion reaches a plateau, but the costs of maintaining and operating a gut never cease. There must, therefore, be a holding time beyond which net loss occurs.

In contrast to both Sibly's model and our batch-processing model, gains and losses must all be considered simultaneously for an animal

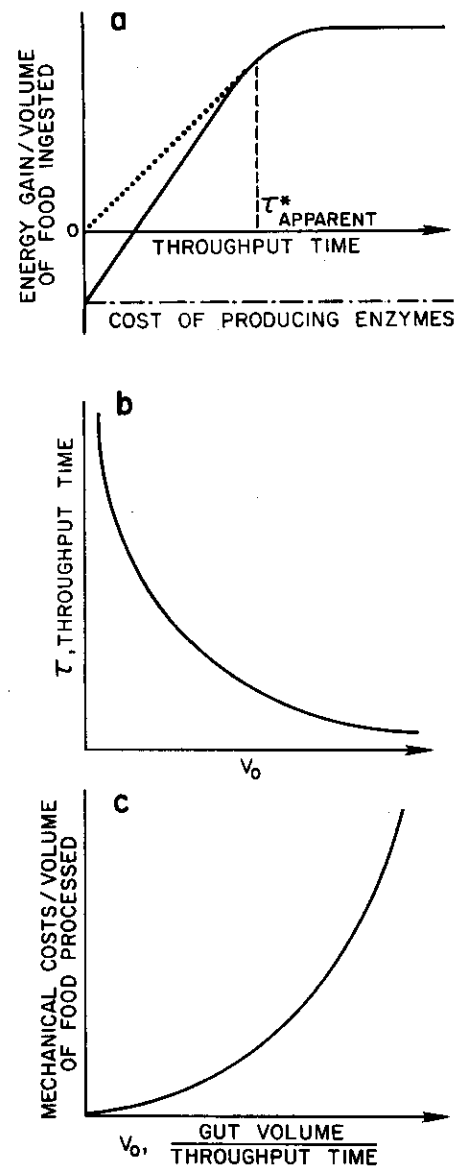


Figure 4. Digestive performance of a continuous-flow gut at steady state. In this example, energy is the limiting component. a. The throughput time ( $\tau$ ), which appears to maximize the net rate of gain of chemical energy per volume of food ingested, is given by  $\tau^*$ . However, to find net rate of gain and the true optimum for an individual, the throughput rate  $v_0$  (b) and the mechanical energetic costs associated with that throughput rate (c) must also be considered. These costs are in addition to basic metabolic costs (not figured), which include the cost of maintaining a gut of volume  $V$ .

that feeds continuously. Some aspects of the steady-state performance of continuous-flow guts can be represented graphically (Figure 4), but a graphical solution for optimal mean

gut residence time is convoluted at best. Net digestive gain (Figure 4a) is a function of throughput time, the cost of producing enzymes, and digestive reaction kinetics. For the sake of simplicity, the latter two components are assumed to be invariant with time, but even so, this optimization exercise is more complex than it may seem initially. Throughput time is some function of throughput rate (Figure 4b), which must also be considered to determine net gain to an individual. Moreover, as throughput rate increases, the mechanical costs of moving material through the gut increase (Figure 4c; Taghon 1981). Consequently, since the relevant interdependencies are explicitly included, specific and quantitative predictions are best made using the equations for ideal reactor performance rather than a graphical approach.

Applying chemical reactor theory to characterize digestive strategies offers a powerful framework within which different tactics can be analyzed and compared. It also generates both focus and incentive for new studies in digestive anatomy, histology, and enzymology as well as feeding ecology.

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