PREDICTING INTAKE AND DIGESTIBILITY USING MATHEMATICAL MODELS OF RUMINAL FUNCTION ¹

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ABSTRACT
Intake and digestibility of feeds by ruminants are influenced by characteristics of the feed, animal and feeding situation. Integration of these characteristics in mathematical models is critical to future progress in forage evaluation and optimal formulation of diets for ruminants. The physiological and physical theories of intake regulation can be described by simple mathematical equations. These equations indicate that intake is a linear function of animal characteristics, such as body weight and production level, and a reciprocal function of feed characteristics, such as fill effect and energy content. Theoretical equations were developed to predict intake when the neutral detergent fiber and energy content of the diet and the energy requirements of the animal are known. The theoretical model also can be used to predict the maximum intake that will maintain a given level of animal production by solving the physiological and physical intake equations at their intersection. Psychogenic intake regulation, which is related to the animal's behavioral response to factors not related to physiological or physical characteristics, can be described mathematically as a multiplier. Digestibility can be predicted by summing the contents of ideal nutritive entities in feeds, which have true digestibilities near 100%, subtracting their associated endogenous losses and adding the variable digestible fiber content. Steady-state models indicate fractional rates of digestion and passage can be used to define ideal nutritive entities and predict digestibility over a range of kinetic characteristics. The steady-state solutions are particularly useful in understanding and predicting the depression in digestibility associated with changes in rates of passage at high levels of feed intake.

(Key Words: Bulk, Digestibility, Feed Formulation, Capacity, Transit Time, Ruminant Feeding.)

Introduction
Intake and digestibility of feeds by ruminants is dependent upon the interaction of the diet, animal and feeding environment. Historically, feed evaluation has been used to predict the intake potential and digestibility of a feed from its chemical composition alone. Although research should continue in developing new laboratory methods, more rapid progress may be made by developing systems that use current analytical information in integrated models. It should be recognized that no matter how complete the analytical method, feed analysis describes only one component of the system that results in intake and digestion of feed by the animal.

In order to design crucial experiments and discriminate among alternative hypotheses, theories must be described in ways that can be tested quantitatively (Platt, 1964). The objectives of this review are: 1) to provide mathematical descriptions for the physical and physiological theories of intake regulation, 2) to describe a quantitative procedure for testing the model of intake regulation using neutral detergent fiber (NDF), 3) to present the basis for the ideal nutritive entity theory for describing digestibility and 4) to illustrate how kinetic characteristics of the feed and animal can be incorporated into these static models of intake and digestibility regulation.

Models for Predicting Intake
Dry matter intake is the most important variable affecting animal performance (Waldo and Jorgensen, 1981). Intake regulation is a function of both short-term and long-term mechanisms. Short-term regulation of intake refers to within-day events that affect the frequency, size and pattern of meals. Research in this area has focused on specific chemical, endocrine and nervous stimuli that trigger hunger or satiety signals (Baile and Forbes, 1974; Baile and McLaughlin, 1987). Long-term regulation of intake refers to average daily...

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intakes over periods of time during which animal nutrient requirements for maintenance and production are stable (Baumgardt, 1970). Although research on short-term mechanisms of meal regulation provide valuable insight into the specific processes and signals involved in intake regulation, this information has not been used to predict daily intake. First, the processes and signals have not been related to specific animal and dietary characteristics that can be measured and used to predict intake. Second, use of specific chemical, hormonal or nervous stimuli to predict intake require complex, dynamic models that have not been developed.

Simplified dynamic models that predict daily intake by summing meal events (Forbes, 1977) or by iterating solutions to arrive at steady-state (Mertens and Ely, 1979) can be used to describe current information about intake regulation and explain interactions among mechanisms. However, dynamic models have limited usefulness as predictive systems because they cannot be easily solved backward to obtain the diet and animal characteristics that match a desired level of intake. Static, or steady-state, models that are based on the concepts of long-term intake regulation offer the potential for developing useful mathematical models for predicting intake. The work of Conrad et al. (1964) and Baumgardt (1970) indicate that long-term regulation of intake is dependent on both dietary and animal characteristics. When high fiber, low energy diets are fed, intake is limited by the physical capacity of the animal and becomes a function primarily of dietary characteristics (Conrad et al., 1964; Montgomery and Baumgardt, 1965b; Baile and Pfander, 1967; Osbourn et al., 1974). When low fiber, high energy diets are fed, intake is controlled by the physiological energy demand of the animal, and is primarily a function of animal characteristics (Conrad et al., 1964; Montgomery and Baumgardt, 1965a; Baile and Pfander, 1967). To be complete, a third mechanism of intake regulation must be developed and superimposed on the physical and physiological theories. The psychogenic mechanism represents the animal's behavioral and metabolic intake responses to stimuli that are not related to physical capacity or energy demand (figure 1).

**Empirical Equations.** The most common approach for predicting intake is to derive empirical equations by statistically selecting and fitting variables to intakes observed in a measured population. Cause and effect is

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**Figure 1.** Conceptual diagram of intake regulation based on psychogenic (1), physiological (2) and physical (3) theories of intake regulation. Solid lines are nutrient flows while dashed lines are information or stimuli flows. The symbol X indicates a nutrient flow regulation point.
implied, but not established by these models. In the simplest form, intake regulation is treated like a black box about which little is known. Feed and animal attributes are used as input variables, which are related to intake using statistical approaches. Sometimes theories of intake regulation are used to select input (independent) variables to improve their general applicability. However, the regression coefficients are a function of the specific data set used to derive the equation and they predict well only when the situation to be predicted is similar to the original data set, i.e., both predicted and original data sets belong to the same population. It is a statistical limitation that the farther the unknown situation is from the mean conditions of the original population, the less accurately it will be predicted.

Most empirical systems for predicting intake are based on animal (Curran et al., 1970; Monteiro, 1972; McCullough, 1973; NRC, 1978) or feed characteristics (Van Soest, 1965; Osbourn et al., 1974; Rohweder et al., 1981). Typically, these equations work well only on one end of the physical limitation/physiological demand continuum describing intake regulation. For example, equations based on the body size and production level of the animal may predict well when high energy diets are fed and intake is regulated by physiological demand, but will predict poorly when low energy, high fiber diets are fed. Similarly, equations based on fiber content of the diet may be accurate when high fiber diets are fed, but will predict poorly when low fiber diets are fed. Multiple regression models have been developed in an attempt to include both dietary and animal characteristics in a single equation to predict intake. Brown et al. (1977) used a large data set to select and fit variables most significantly related to intake. Their equation includes terms related to animal size and production, stage of lactation, crude fiber content of the diet and season of the year. Conrad et al. (1964) and Conrad (1971) predicted intake using two intersecting equations. One equation was empirically fitted to animal characteristics while the other was related to the indigestibility of the diet and the fecal output of the cow. Conceptual Equations. To predict intake in ruminants over the full range of animal requirements and dietary characteristics, it is important that theoretical concepts be used to develop the equations. Since average daily intake prediction is typically the goal, theories relating to long-term intake regulation are the most appropriate starting points for deriving prediction equations. Furthermore, static or steady-state equations can be realistic starting points for model development because the intake estimate that is needed should relate to daily intakes when animals are adapted to the diet and in an equilibrium state.

Mertens (1973, 1985a) has derived simple mathematical models that describe intake regulation. In its most simple form, the regulation of intake by physiological energy demand indicates that the animal eats to meet its energy requirement. At steady-state, i.e., no change in energy requirement or energy content of the diet, the physiological theory of intake regulation can be described mathematically by stating that daily intake \( I \) multiplied by the energy content of the diet \( E \) equals the animal's daily energy requirement \( R \):

\[ I \times E = R. \]  \[1\]

This equation can be rearranged to determine the expected intake \( I_e \) when the energy content of the diet and energy requirement of the animal are known:

\[ I_e = \frac{R}{E}. \]  \[2\]

Equation [2] is subject to the biological, but not mathematical, restriction that it is valid only when the energy content \( E \) of the diet is adequate to cause physiological feedback stimuli to regulate intake. It predicts unacceptable high intakes when the energy content of the diet is low.

Similarly, at steady-state, the physical limitation theory of intake regulation states that the animal eats to the limits of its fill capacity. Mathematically, this theory can be described by stating that daily intake \( I \) times the fill effect \( F \) of the diet equals a constant daily fill capacity \( C \):

\[ I \times F = C. \]  \[3\]

Rearranging this equation to determine expected intake \( I_e \) obtains:

\[ I_e = \frac{C}{F}. \]  \[4\]

Equation [4] is subject to the biological restriction that it is valid only when the fill effect of the diet is high. Diets with low fill
effects will result in unrealistically high estimates of intake.

Both equations [2] and [4] predict intake that is not influenced by behavioral or metabolic responses of the animal to stimuli that are not related to energy demand or fill capacity. To predict actual intake, the expected intakes of equations [2] and [4] must be adjusted for the animal's response to external stimuli, such as stress, social interactions, feed pH, feed flavors, disease, etc. However, environmental factors, such as cold temperatures, that influence production or maintenance requirements of the animal are not psychogenic responses because they alter intake via physiological energy demand. The psychogenic mechanism proposed by Mertens (1985a) can be described mathematically as a multiplier, where actual daily intake \( I \) is equal to the expected intake \( I_e \) from equation [2] or [4] multiplied by the psychogenic multiplier \( M \):

\[
I = I_e \times M. \quad [5]
\]

In general, it is envisioned that the psychogenic multiplier will be less than or equal to 1.0. It is possible for external factors to reduce intake below that expected based on physiological or physical intake control mechanisms; however, it is difficult to encourage animals to eat more than expected in relation to their energy demand or fill limitation. For example, when feeds are moldy, intake may be reduced below that predicted by physiological or physical mechanisms. Equation [5] provides a method for quantifying the psychogenic multiplier. The expected intake \( I_e \) can be measured on a group of animals when no psychogenic influence occurs and intake is regulated by either physical or physiological mechanisms. A second group of animals, having the same energy requirements \( R \) or fill capacity \( C \), are fed diets similar in energy content \( E \) or fill effect \( F \) with the psychogenic factor in effect to determine the actual intake \( I \). The psychogenic multiplier can be determined as: \( M = I/I_e \).

The psychogenic concept is more difficult to use in field situations where the only intake available is actual intake \( I \) measured under all known and unknown psychogenic influences. However, \( I_e \) could be calculated using equations [2] and [4], assuming that representative values for \( E, F, C \) and \( R \) could be estimated for the field situation. Comparison of actual intake with the expected intake that was calculated would provide an estimate of the total psychogenic influence on the farm for use in discovering and correcting factors inhibiting intake or adjusting intakes for a specific feeding situation. It must be recognized that the energy requirement \( R \) used to calculate expected intake in the field situation should not be based on actual production of the animals. In these cases, \( R \) should be calculated from estimated requirements for animals of similar potential in feeding situations with no psychogenic influences. The actual production of the animals in field situations cannot be used to calculate \( R \) because energetic equilibrium will eventually balance production output with intake input and expected intake will equal actual intake, suggesting no psychogenic effect.

In research relating intake to diet and animal characteristics, every attempt is made to minimize psychogenic factors so they do not influence the measurement of main effects. Since the goal in most feeding situations is to provide psycho-neutral environments, it will be assumed for the rest of the discussion that the psychogenic multiplier has a value of one, and that expected intake predicted by equations [2] and [4] will be the actual intake that was observed: \( I = I_e = R/E = C/F \).

Equations [2] and [4] indicate that intake is a direct linear function of animal characteristics \( R \) and \( C \) but a reciprocal function of dietary characteristics \( E \) and \( F \). The relation-
ship between intake and dietary characteristics is shown in figure 2. These equations explain why linear terms for body weight, milk production and weight gain often are observed in empirical equations, while logarithmic or quadratic transformations are selected for dietary characteristics (Brown et al., 1977; Rohweder et al., 1981). However, equations [2] and [4] suggest that reciprocal transformations of dietary characteristics are most appropriate for use as predictors of intake within the constraints of each intake mechanism. Figure 2 also illustrates that no transformation of either single dietary characteristic, whether related to fill units or energy content, can be used to fit accurately the discontinuous solid line representing the complete range in dietary characteristics. The physiological and physical intake regulation theories clearly indicate the inability of a single continuous equation to relate dietary characteristics to intake over the complete range of dietary compositions.

Predicting Intake Using Theoretical Models. Equations [2] and [4] express dietary and animal characteristics in general terms. To make these equations useful for predicting dry matter (DM) intake, the terms on the right-hand side of each equation must be expressed in units that are appropriate and can be readily determined. Energy content and energy requirement can be expressed in terms of total digestible nutrients (TDN), digestible energy (DE), metabolizable energy (ME) or net energy (NE) as long as both R and E are expressed in the same units. Net energy of lactation (NE₁) will be used to predict dairy cow intake in the remaining discussion. The dairy cow was chosen to evaluate the equations due to the wide range of intakes that are potentially feasible for this animal.

Of the chemical analyses presently available, NDF should be most highly related to the space-occupying, or fill effect, of the diet. Soluble constituents in feeds dissolve and contribute very little to the fill effect. However, fiber displaces volume in the rumen and NDF is the only fiber method routinely used that isolates all fibrous components (cellulose, hemicellulose and lignin). Neutral detergent fiber has been shown to be highly correlated with the volume or bulk density of feeds (Mertens, 1980, 185b). Thus, it is proposed that NDF can be used to represent dietary fill (F). Daily fill capacity (C) must be expressed in units of NDF to achieve internal consistency in equation [4]. If intake is expressed as kilograms per day, then the daily NDF capacity must be expressed in units of kilograms NDF per day. Mertens (1985a) summarized data from several experiments and estimated that daily NDF intake was 1.2 ± .1% of body weight per day (% BW/d) in diets that produced maximum daily 4% fat-corrected milk yields. The small variation in NDF intake among optimal diets suggests that it can be used in models to predict intake when long or coarsely chopped forages are fed with ground corn and soybean meal mixtures to lactating cows after peak milk production. For diets of predetermined composition, NDF intakes of 1.2% BW/d will provide the most accurate prediction of intake. However, when formulating optimum diets, it is important that the diet does not limit intake or production. Reducing NDF intake by one standard deviation results in diets with more concentrate and less forage than required by the average cow and ensures that intake does not limit production for 85 to 90% of the cows in a given production group. A NDF intake of 1.1% BW/d was selected to provide a conservative estimate of intake in the calculations to be presented.

Theoretical equations [2] and [4] must be redefined in terms of the new definitions for energy and fill effect. Equation [2] is converted to equation [6] where intake (I in kg DM/d) is a function of the NE₁ requirement (NER in Mcal NEᵢ/d) divided by the NE₁ content (NEᵢ in Mcal/kg DM) of the diet:

\[
I = \frac{NER}{NEᵢ}. \quad [6]
\]

The NER can be determined using NRC (1978):

\[
NER = 0.08(BW^{0.75}) + 0.74(FCM) - 4.92(LOSS) + 5.2(GAIN), \quad [7]
\]

where BW is body weight (kg), FCM = daily 4% fat-corrected milk (kg). LOSS is daily body weight loss (kg) and GAIN is daily body weight gain (kg). The NEᵢ of the total diet can be obtained by summing the proportion of the diet that is forage (A) times the NEᵢ content of the forage (FNE) and the proportion of the diet that is concentrate (1 - A) multiplied by the NEᵢ content of the concentrate (CNE). In the examples to be presented CNE was set equal to 1.90 Mcal/kg DM.
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\[
\text{NE} = (1 - A) \left( C\text{NE} \right) + A \left( F\text{NE} \right).
\]

The FNE of forages can be estimated by the equations \( F\text{NE} = 2.323 - 0.0216 \left( \%\text{NDF} \right) \) and \( F\text{NE} = 2.863 - 0.0262 \left( \%\text{NDF} \right) \) for legumes and grasses, respectively (Mertens, 1983, 1985a). Using NDF content of forages to predict FNE allows both the fill units and energy content of the diet to be assessed by a single laboratory method. The \( \text{NE}_1 \) for concentrates and forages assume intakes that are three times maintenance requirements (NRC, 1978). The effect of level of intake on \( \text{NE}_1 \) could be incorporated into the solution of the model by using iterative procedures.

Equation \[4\] can be converted to equation \[9\] by expressing the physical limitation theory of intake in terms of NDF. Intake (I in kg DM/d) equals the NDF intake capacity (NDFIC in kg NDF/d) divided by the NDF content of the total diet expressed as a fraction (NDF in kg NDF/kg DM):

\[
I = \frac{\text{NDFIC}}{\text{NDF}}. \tag{9}
\]

Since daily NDF intake capacity was estimated to be 1.1% of body weight (kg),

\[
\text{NDFIC} = 0.111 \text{ (BW)}. \tag{10}
\]

The NDF content of the total diet is determined by summing the proportion of forage in the diet (A) multiplied by its NDF content (FNDF in kg NDF/kg DM) and the proportion of the diet that is concentrate \((1 - A)\) multiplied by its NDF content (CNDF in kg NDF/kg DM). In the examples presented, the NDF content of concentrates is kept constant at .12 kg NDF/kg DM:

\[
\text{NDF} = (1 - A) \left( \text{CNDF} \right) + A \left( \text{FNDF} \right). \tag{11}
\]

If the NER of the animal and the NE and NDF content of the total diet are known, expected intake can be determined in a two-step process. First, equations \[6\] and \[9\] are solved to obtain expected intake based on the physiological and physical theories of intake, respectively. Second, the smaller of the two estimates is selected as the estimate of intake and the corresponding theory represents the mechanism limiting intake in that specific situation. For example, a 600-kg cow producing 20 kg FCM daily is offered a diet containing 35% NDF and 1.55 Mcal \( \text{NE}_1 \) /kg DM. Expected intakes would be:

\[
I = \frac{\text{NER}/\text{NE} = (24.5 \text{ Mcal/d})}{(1.55 \text{ Mcal/kg DM})} = 15.8 \text{ kg DM/d}
\]

or

\[
I = \frac{\text{NDFIC}/\text{NDF} = (6.6 \text{ kg NDF/d})}{(.35 \text{ kg NDF/kg DM})} = 18.9 \text{ kg DM/d}.
\]

This cow would be expected to consume 15.8 kg DM/d and achieve the target milk production. However, if the same diet was to be fed to a 600-kg cow with a production potential of 40 kg FCM daily, the expected intakes would be:

\[
I = \frac{\text{NER}/\text{NE} = (39.3 \text{ Mcal/d})}{(1.55 \text{ Mcal/kg DM})} = 25.4 \text{ kg DM/d}
\]

or

\[
I = \frac{\text{NDFIC}/\text{NDF} = (6.6 \text{ kg NDF/d})}{(.35 \text{ kg NDF/kg DM})} = 18.9 \text{ kg DM/d}.
\]

The expected intake would be 18.9 kg DM/d and, since the physiological energy demand would not be met, the target milk production level would not be achieved. The maximum milk production to be expected from this diet could be calculated from the daily \( \text{NE}_1 \) in 18.9 kg DM/d.

Equations \[6\] and \[9\] are difficult to use in formulating diets because the NDF and NE content of the diets are not known until intake is established and diet composition is determined. Assuming NER and NDFIC can be established, there are still three unknowns (NE, NDF and I), but only two equations. Mathematically, this problem cannot be solved for a unique answer. However, there are unique solutions at the points where the two equations intersect (figure 3). Because energy content and fill effect are inversely related, the two reciprocal equations will always intersect at a point that predicts maximum dry matter intake for a given level of production (NER). To maintain the given level of milk production at lower intakes (lines b to c on figure 3) the NDF content of the diet must be decreased. However, if the NDF content is higher than allowed for maximum intake (lines a to b on figure 3), intake will be limited by the fill effect of fiber and target production levels will not be achieved. Maximum intake (Im) is determined at the
intersection of equations [6] and [9]. Im is established when

\[ \text{NER/NE} = \frac{\text{NDFIC}}{\text{NDF}}. \]  

To calculate maximum intake and the NE and NDF content of the diet needed to obtain maximum intake, a three-step process is needed. First, equation [12] is rearranged to calculate the forage to concentrate ratio at the intersection of equations [6] and [9] by substituting equation [8] for NE and equation [11] for NDF and solving for the proportion of the diet that is forage A:

\[ A = \frac{\text{NDFIC} (\text{CNE}) - \text{NER} (\text{CNDF})}{\text{NDFIC} (\text{CNE} - \text{FNE}) + \text{NER} (\text{FNDF} - \text{CNDF})}. \]

Second, the NDF or NE content of the diet is determined using equation [11] or [8], respectively. Third, maximum intake is calculated using equation [6] or [9]. For example, if an average legume containing 50% NDF and an average corn-soybean meal concentrate containing 12% NDF and 1.90 Mcal NE/kg DM were used to formulate the diet for the 600-kg cow producing 30 kg FCM milk daily, the result would be:

\[ \text{FNE} = 2.323 - .0216 (50) = 1.243, \]

\[ A = \frac{[6.6 (1.90) - 31.9 (1.12)]/[6.6 (1.90 - 1.243) + 31.9 (.50 - .12)]}{[12.54 - 3.828]/[4.336 + 12.122] = .529} \]

\[ = 52.9\% \text{ forage in the diet}, \]

\[ \text{NDF} = (1 - .62) (.12) + .62 (.50) = .321 \text{ kg/kg DM} \]

\[ = 32.1\% \text{ NDF in the total diet}, \]

\[ \text{Im} = 6.6 /.321 = 20.5 \text{ kg DM/d}. \]

For the cow in the second example given earlier, producing 40 kg FCM/d, the maximum intake would be 24.1 kg from a diet containing 40.6% forage and 27.4% NDF. Maximum intakes calculated in these examples are conservative estimates because the value used for NDFIC was 1.1% BW/d.

**Limitations of the Theoretical Model.** Application of theoretical models to diet formulation for dairy cows allows the prediction of diet characteristics needed to meet target production levels (Mertens, 1985b). Preliminary investigations also indicate that the use of theoretical equations with NDF and TDN could be used to characterize diets for beef cows and heifers, feedlot steers, ewes and growing lambs. Although the physiological and physical theories of intake regulation are extensively documented and commonly accepted, the application of these theories in mathematical models is based on assumptions that require additional research and refinement. These assumptions are: 1) NDF can be used to represent adequately the fill effect, 2) the daily fill capacity is a relatively constant value and 3) static implementation of the theories adequately represents the dynamic nature of the intake regulation system.

At present, the model defined by equations [6] through [13] assumes that all NDF sources influence intake and energy value similarly. Although it is evident that NDF characteristics vary among fiber sources, NDF is useful in solving the theoretical equations because it measures the greatest difference among feed constituents. Neutral detergent fiber distinguishes between the slowly-digesting, space-occupying character of fiber and the rapidly-digesting, dissolved nature of neutral detergent solubles (NDS). Neutral detergent fiber provides an accurate method of formulating diets based on theoretical models because there is more difference between NDF and NDS within feeds than among NDF of different feeds. Nonetheless, it is reasonable to expect that the theoretical model of intake prediction can be improved by incorporating more quantitative information.
about the unique characteristics of NDF, such as lignin content, structural carbohydrate composition, digestion kinetics, fragility to particle size reduction and particle size distribution when ingested.

The importance of rates of digestion, passage and particle size reduction (Waldo et al., 1972; Mertens and Ely, 1979) suggests that kinetic characteristics should be included in the static theoretical model formulated in equations [6] and [9] to solve for intake under a variety of steady-state conditions. Both the theoretical R and C, and their practical approximations (NER and NDFIC), are fluxes with units of amount per unit time. This implies that they can be described in terms of kinetic pools and fractional disappearance rates because in dynamic systems:

\[ \text{flux (wt/time)} = \frac{\text{pool (wt)}}{\text{time}} \times \text{fractional rate (per time)} \]  

Thus, NDFIC can be expressed in terms of the weight of the ruminal pool of fiber multiplied by the total disappearance rate of fiber due to both digestion and passage. Whereas the initial formulation of the model using NDFIC made no assumption about the location of the fill capacity site, the kinetic refinement of the model assumes that the fill capacity limitation is located in the rumen (Campling and Balch, 1961). Mertens (1985c) has developed a model of intake that includes the rate of digestion, particle size reduction and passage. Not only can the rates be changed in this kinetic refinement of the theoretical intake model, but the pool size in the rumen can also be changed in accordance with the observations of Tulloh (1966). Furthermore, the density of different fiber fractions in the rumen could be measured and used to express the pool size of NDF in the rumen in terms of volume rather than weight.

The NER is also a flux that can be expressed in terms of the fractional rates at which energy is removed from the total metabolic energy pool in the animal. This would permit the inclusion of factors that alter the rate, efficiency, or partitioning of energy to alter the daily NER flux that is required to achieve a target level of milk production. This would allow the importance of the timing and composition of absorbed nutrients (Tyrrell et al., 1979), the effects of exogenous growth hormone (Bauman et al., 1985) and the normal homeoeretic cycle of body reserve utilization and deposition during lactation (Bauman and Currie, 1980) to be included in the theoretical models for predicting intake.

Models for Predicting Digestibility

As with intake, digestibility is a function of the feed, the animal and the feeding situation. In the past, variation in digestibility related to the animal and feeding situation were minimized by determining digestibility using mature animals that were restricted to intake levels near maintenance. By minimizing animal variation, the relationship between feed characteristics and digestibility can be elucidated more easily. Lucas and Smart (1959) and Lucas (1962) proposed a theoretical framework useful in identifying feed constituents that have ideal digestion characteristics. They theorized that, if feeds could be described by ideal nutritive entities which were defined as chemical fractions that were completely digestible or totally indigestible, the total dry matter digestibility of feeds could be easily calculated as the sum of the digestible ideal nutritive entities. Lucas and Smart (1959) provided a statistical method for identifying ideal nutritive entities. The digestible nutrient content of feeds is regressed on their total nutrient content. If the regression coefficient, or slope, is zero or one, the intercept is zero or negative, and the standard error of regression is small, the nutrient has ideal nutritive properties. The regression coefficient has the units digestible content per total content and can be interpreted as the true digestion coefficient of the nutrient. The intercept represents the digestion of the nutrient when no nutrient is present in the feed. A negative intercept can be interpreted as the excretion of nutrient in the feces when no nutrient is consumed and represents the endogenous loss of the nutrient by the animal.

The ideal nutritive entity concept proposed by Lucas provides a partial explanation for the success in using fiber content to predict digestibility or TDN content empirically. The non-fiber component of feeds has relatively high, constant digestibility that can be accurately predicted by the intercept constant in regression equations using fiber. If fiber is the only independent variable, the intercept represents the true digestibility of the non-fiber component in the feed minus endogenous losses. Based on the
analyses of Van Soest (1965) and Aerts et al. (1978), the endogenous loss for dry matter ranges from 10 to 30%; therefore, the intercept of most digestibility equations using fiber as the independent variable should range from 70 to 90%.

Van Soest (1967) used the concept proposed by Lucas to develop the summative equation approach for predicting digestibility using detergent fibers. Neutral detergent fiber was used to separate feed into ideal and non-ideal nutritive entities. Of all the analyses currently in use, NDF most completely isolates the fibrous constituents that have non-ideal digestion characteristics. Neutral detergent solubles represents the largest ideal nutritive fraction that has been identified because it contains proteins, lipids, soluble sugars and starch, all of which are almost completely digested by ruminants at maintenance levels of intake (Osborn, 1978). Van Soest (1967) determined that NDS had a true digestibility of 98%, with an endogenous loss of 12.9%.

The concept proposed by Lucas is a static model that is valid when digestibility is measured in animals fed in controlled conditions with intake levels at maintenance. Mertens (1983) has shown that the concept can be refined to include dynamic parameters associated with rates of passage and digestion. The simple model of Waldo et al. (1972) was used to define the true digestibility coefficients, which are the regression coefficients in the Lucas' model, in terms of rate of digestion and passage. True digestibility (TD) equals the fractional rate of digestion (kd) divided by the total fractional rate of disappearance due to digestion and passage (kd + kp):

\[
TD = \frac{kd}{kd + kp}. \quad [15]
\]

The dynamic interpretation of digestibility provides an explanation for the successful use of the Lucas concept when digestibilities are measured under relatively constant conditions. If the level of intake is controlled, the rate of passage is relatively constant, thereby removing much of the variability in digestibility associated with the animal. Under these circumstances, true digestibility becomes a function primarily of the rate of digestion that is characteristic of the chemical and physical properties of the nutrient. When kd is relatively constant for a nutrient and exceeds kp by a factor of 10 or more, true digestibility is relatively constant and is near 100%.

Mertens (1983) also has shown that the steady-state solution of the dynamic model for digestion also can be used to explain the depression in digestibility that occurs when rate of passage increases due to increased levels of feed intake (figure 4). For each rate of digestion, true digestibility decreases asymptotically as rate of passage is increased. The steady-state kinetic model also illustrates that nutrients with rapid rate of digestion (those with ideal nutritive digestibilities near 100% in the Lucas model) are depressed very little as rate of passage is increased. However, those feed constituents with slow rates of digestion such as fiber and raw corn or sorghum starch obtain digestibilities that are dramatically depressed by small changes in rate of passage. This provides a rationale for the observation of Mertens (1983) that the discount factors for adjusting individual feed energy values reported by Van Soest et al. (1979, 1984) were related to the NDF content of the feed. Mertens reported that the percentage depression in digestibility per change in intake expressed as multiples of maintenance (% DEPR) was related to the NDF and TDN content of the feed:

\[
% \, \text{DEPR} = 0.033 + 0.132 \times (\% \, \text{NDF}) - 0.033 \times (\% \, \text{TDN}). \quad [16]
\]

The negative regression coefficient for TDN indicates that feeds with higher digestibilities and more rapid rates of digestion at a given
NDF content will have less depression in digestibility, which is in agreement with the kinetic model. However, equation [16], as well as the equations of others (Robertson et al., 1974; Tyrrell and Moe, 1975), assumes that the depression in digestibility is a linear function of intake. Figure 4 illustrates that depression in digestibility is not a linear function of rate of passage in the simple kinetic model. If intake is linearly related to rate of passage, the depression in digestibility with increased intake would be curvilinear.

Conclusions

More complete models are needed to integrate chemical information collected in the laboratory with animal and feeding situation characteristics to predict more accurately intake and digestibility. The models do not need to be sophisticated mathematically, but must be realistic in terms of their dependence on, and correspondence to, biological principles and theories. Simple static models have been developed, which can be used as initial attempts to describe intake and digestibility. These models can easily incorporate kinetic parameters assuming animals have attained steady-state levels of intake and digestibility. Not only do these models provide information of theoretical interest to scientists, but also they have practical utility in assessing feed value and formulating optimal diets. The steady-state kinetic models emphasize the importance of gaining quantitative information about the rate of digestion, passage, particle size reduction, nutrient partitioning and nutrient metabolism. This information would provide the basis for more efficient forage utilization by ruminants through more accurate determination of feed nutritive value and optimum diet characteristics.

**Literature Cited**


