

Mind Over Models

Michael S. Allen¹

Department of Animal Science
Michigan State University

Summary

Our collective knowledge from research and experience related to diet formulation vastly exceeds our ability to apply it in quantitative relationships necessary for diet formulation models. However, this knowledge can be readily applied when formulating diets to increase health and production of dairy cows. In addition, availability of accurate data and incorrect structure limits usefulness of rumen models for diet formulation. Nutritionists often spend an inordinate amount of time and resources considering inputs required by complex models that do not improve diet formulation. This time and money can be better used to improve feeding management and evaluate response of cows to diet changes in cooperation with the management team on the farm.

Introduction

Nutrition models are used to predict requirements and supply of energy and nutrients based on animal characteristics, diet composition, and environmental parameters. These models have empirical components for which prediction equations are developed based upon relationships without regard to mechanisms, as well as more mechanistic components that help us explore and better understand the complex biology of the system. Diet formulation for ruminant animals is greatly complicated by pregastric fermentation of feeds. The rumen is a complex biological system

that affects the type and temporal pattern of fuels from carbohydrates, fatty acid (FA) profile, and the amount and profile of absorbed amino acids (AA), all of which can affect energy intake and partitioning and therefore milk yield and efficiency of nutrient utilization. Because the effects of ruminal fermentation on nutrient supply to the animal and subsequent animal performance are so great, rumen models have been developed and incorporated into some diet formulation programs. While mechanistic modeling of the rumen is worthwhile to better understand the biology and to identify research needs, complex mechanistic models are not useful for routine diet formulation. Great advances in our understanding of the biology of ruminants have been made over the last 20+ years that can be used to better formulate diets. However, advances in mechanistic models for diet formulation have lagged behind; models have become more complex (e.g. addition of AA and FA), but the basic flaws in structure and inaccurate inputs limit their usefulness for diet formulation. Further, the focus of rumen models used in diet formulation programs has been limited to the prediction of digestibility and absorbed protein. Energy intake and partitioning are the “holy grail” of diet formulation, and are greatly affected by diet, but these effects are completely ignored by diet formulation programs. Prediction of milk yield and energy balance is poor for all models using *a priori* information. Model “evaluations” for milk yield response might look surprisingly good, but the results of the diet response on actual measured dry matter intake (DMI) and body condition score

¹Contact at: 2265G Anthony Hall, East Lansing, MI 48824-1225, (517) 432-1386, FAX: (517) 432-0147, Email: allenm@msu.edu

(BCS) changes are often used as model inputs. This is misleading because they are among the most important factors affecting milk yield! It is useful to examine the limitations of our current diet formulation and feeding systems to gain perspective on what is important. The goal of this paper is to assess the status of diet formulation models for dairy cows to provide a reality check as well as to explore alternative diet formulation strategies.

Diet Variation

One of the greatest limitations to diet formulation is the variation of nutrients in rations supplied to cows. This has been captured well in the adage “There are 3 rations: the one that is formulated, the one that is mixed, and the one that is consumed”. There are many sources of variation that affect the concentration of nutrients supplied in rations delivered to the feed bunk. Variation in forages as well as concentrates can be great and depends upon many factors but that discussion is beyond the scope of this paper. It is very important to sample frequently to understand this variation and reduce it to increase consistency of rations provided to cows. Variation also occurs from inaccurate measurement of dry matter (DM) for each ingredient added to the mixer, physical changes during mixing, incomplete mixing, and sorting (longitudinally and laterally) by the mixer during feed delivery to the feed bunk. These sources of variation require careful review on every farm and are highly affected by type of storage structure, type and condition of mixing equipment, and management. While variation can never be eliminated, it can be greatly reduced; success of diet formulation depends on it!

Animal Variation

The number of groups of lactating cows varies from one to several among farms, and characteristics of cows within groups vary based on a variety of factors, including stage of lactation, parity, milk yield, reproductive status, and body

condition. To formulate a diet for cows within the group, a “representative” cow is selected with specific milk yield, milk components, body weight (BW), BCS, day in milk, etc. However, even when there are several different groups of cows on a farm, there is great variation in nutrients required by cows within the group based upon DMI, milk yield, growth, repletion of body energy reserves, etc. Cows within a group vary greatly in their response to the diet formulated for the “representative” cow in regard to DMI, digestibility, and nutrient partitioning, and this variation is discussed below.

Variation in digestibility among cows

It is widely recognized that diet selection by cows varies and that the diet consumed differs among cows offered the same ration. Potential for selection is enhanced for dry rations, rations with longer fibrous particles, and when cows are housed and fed in groups, and efforts are often made to reduce diet selection so that cows consume similar diets. Differences in selection among cows can affect diet composition and digestibility. However, there is also great variation in digestibility of DM among cows consuming the same diet, even when opportunity to select is minimized. Dry matter digestibility ranged from 51 to 72% for 29 cows in tie-stalls offered the same diet (Figure 1; Voelker et al., 2002). The variation in DM digestibility was primarily because of variation in digestibility of NDF (CV = 26.5%), rather than starch (CV = 5.7%), and was not related to DMI ($P = 0.48$), despite a range among cows of 37 to 69 lb/day. The large range in digestibility of NDF was likely because of differences in ruminal pH. In a recent experiment, mean ruminal pH measured every 15 hours for 5 days (mean of 8 samples per cow) ranged from 5.7 to 6.5 for 14 cows housed in tie-stalls and offered the same alfalfa-based ration (Figure 2; Kammes and Allen, Michigan State University, unpublished). Ruminal pH was not related to DMI ($P = 0.81$), which ranged from 45 to 67 lb/day. In another experiment, mean ruminal pH (measured

continuously for 4 days) ranged from 5.7 to 6.6 for cows fed diets containing high-moisture corn or dry ground corn in 21 or 32% starch diets, but treatment effects accounted for less than 25% of this range; mean ruminal pH ranged only from 6.12 to 6.32 across treatments, despite a very large range in ruminal starch digestibility among treatments of 46 to 71% (Figure 3; Oba and Allen, 2003). Rate of digestion of potentially digestible NDF was linearly related to ruminal pH and ranged from less than 1%/h to more than 4%/h. Although ruminal pH is affected by diet, individual differences among cows [e.g. feeding behavior, rate of absorption of volatile fatty acids (VFA) from differences in rumen motility and surface area, buffering by digesta mass, and saliva] likely have a much greater effect. Therefore, there is great variation on digestibility of NDF among cows consuming the same diet that has considerable effect on diet energy concentration.

Diets affect energy intake and partitioning

Dry mater intake is most commonly predicted from milk yield, BW, and days postpartum and these prediction equations do not consider the effects of diet and its interaction with the physiological state of the cow. The effects of diet on energy intake and partitioning are the most important but overlooked elements of diet formulation. There is a great deal of research and knowledge in this area that can be applied during diet formulation, but the relationships are qualitative, not quantitative, and not in a form that can be included within our traditional modeling framework. Our traditional procedures for diet formulation are generally adequate for nutrients that are provided in excess, such as minerals and vitamins, with reasonably high levels of tolerance, but they are a limitation when it comes to balancing for energy because diet composition affects energy intake and nutrient partitioning independent of energy concentration. Feed intake is affected by many dietary factors, including forage NDF concentration and digestion characteristics, ruminal starch

fermentation, unsaturated FA, etc. (Allen, 2000). Each of these are highly variable and can affect DMI by 10 to 15% or more, but they aren't considered by models to predict DMI because of the complex interactions among them, production level, physiological state, and environment. However, we can use the knowledge that we have acquired, even if we don't have enough data to capture them in mathematical equations required by models. A few examples are described below:

Example #1. Slow fiber digestion and passage from the rumen can increase ruminal distention and decrease feed intake, but we are unable to predict the relationship between digestion characteristics of NDF and DMI because it differs with level of milk production, the NDF concentration of the diet, and other factors. We know that enhanced NDF digestibility within a forage family decreases gut fill and has greater potential effect on DMI as milk yield increases (Allen, 2000). We also know that NDF from cool-season grasses, although more digestible than NDF from legumes, is generally more filling and is a greater benefit when DMI is not limited by rumen distention (Voelker Linton and Allen, 2007). Just because we can't quantify the response from digestion characteristics of fiber doesn't mean that we can use the information that we have learned.

Example #2. As lactation proceeds and milk yield declines, feed intake is increasingly dominated by metabolic signals. Highly fermentable diets often decrease feed intake in mid to late lactation, likely from stimulation of hepatic oxidation by propionate (Allen et al., 2009). Reducing ruminal fermentability of starch by substituting dry corn for high moisture corn often increases energy intake and partitioning to milk for these cows. Response in energy intake and partitioning to ruminal fermentability of starch cannot be predicted by models because of modulation of the response by other factors, including the physiological state of the cows (Bradford and Allen, 2007) and the starch concentration of the diet.

Example #3. Certain conjugated linoleic acid (CLA) isomers (e.g. trans-10, cis-12 C18:2) decrease expression of genes related to milk fat synthesis in the mammary gland (Harvatine et al., 2009a) and have the opposite effect on expression of genes in adipose tissue (Harvatine et al., 2009b). Therefore, they can have a large effect on energy partitioning and milk yield. These CLA isomers are produced when normal biohydrogenation pathways in the rumen are altered and risk factors include high concentration of polyunsaturated fat in the diet, high diet fermentability, low milk yield, inadequate effective fiber, and rumen modifiers. Although production response to the diet cannot be predicted, these factors affect production and must be considered when formulating diets.

Composition and digestion characteristics of the diet can have large effects on energy intake and partitioning and milk yield. Models cannot predict accurately the effect of diet on feed intake and milk yield because of numerous interactions involved. However, these effects can be used in diet formulation by evaluation of cow response (see below).

Rumen Models

There is no doubt that the rumen is very complex, and rumen models cannot be simple. In fact, the rumen is so complex and there is so much that we don't understand about the biology, that it seems overwhelming to attempt to model it. However, "The problem of biology is not to stand aghast at the complexity but to conquer it" (Sydney Brenner, Nobel Prize in Physiology or Medicine, 2002; Brenner, 2004) and "models provide a logical and systematic way to examine a complex system" (Joandet and Cartwright, 1975). The rumen isn't a black box, but it is very dark and can be illuminated by modeling. Rumen models have made valuable contributions by integrating research results and identifying gaps in research, and development of rumen models for research and teaching purposes

will continue to advance our knowledge. However, mechanistic rumen models add needless complexity to diet formulation and likely do not increase accuracy as discussed below.

Ruminal digestibility of a feed is a function of the rate at which the fraction is digested and passed from the rumen. Digestibility increases as digestion rate increases or as passage rate decreases (i.e. retention time in the rumen increases). Both digestion rate and passage rate can vary widely, even as much as one order of magnitude among fractions (such as fiber and starch) within a single feed ingredient. Because the various fractions are digested and utilized at different rates and through different mechanisms, digestibility and digestion rate are measured for feed fractions rather than entire feeds. While partitioning of feeds into more homogeneous, chemically or biologically-defined fractions is a logical approach to modeling the rumen, data for rates of digestion and passage of feed fractions are largely inaccurate or non-existent. Rates of digestion of individual fractions measured using *in vitro* or *in situ* techniques are readily available in the literature and can be measured for individual feeds by commercial laboratories, but the data are not useful for models to predict ruminal digestibility. This is because *in vitro* and *in situ* techniques measure relative, not absolute, rates of digestion and because data for passage rates of individual feed fractions are lacking. Prediction of ruminal digestibility requires absolute values for both rate of digestion and rate of passage of each feed fraction.

Passage rates are incorrect!

Nearly all passage data available in the literature have been measured by analysis of fecal excretion curves of external markers applied to intact forages and concentrates and pulse dosed to the rumen. Although these data might be useful to evaluate relative differences among treatments within experiments (even this is doubtful – see below), they

are not useful to predict digestibility of fractions within feeds across a wide range of conditions. Fecal excretion curves of marked feeds dosed to the rumen are very difficult to interpret. Although 2 or more significant pools and rates can be determined, it is not clear which rate represents passage from the rumen or even that assignment of the resulting mathematically-defined pools to specific biological pools is valid. In many current models (e.g., CNCPS 6.1, CPM, NRC 2001, and Spartan 3), ruminal fermentation or protein degradation are predicted using degradation rates of individual fractions and passage rates of entire feeds derived from experiments using external markers. This is problematic because differences in fraction solubility, particle size, specific gravity, and buoyancy result in different passage rates for the various fractions within a feed, and external markers cannot be used to measure passage rates of fractions within feeds. The use of the same overall passage rate for all fractions within feeds will overestimate ruminal digestibility of soluble fractions and small particles that have faster rates of passage and will underestimate ruminal digestibility of large particles that have much slower rates of passage.

Problems with passage markers limit their usefulness, even as a measure of passage rate of entire feeds (Firkins et al., 1998). Markers overestimate passage rates of feeds because they bind preferentially to small feed particles due to their increased surface area (Erdman and Smith, 1985), increase density of feeds to which they are attached directly (Ehle et al., 1984), or by inhibiting fermentation and production of gases within particles, decreasing buoyancy (Allen, 1996). Most importantly, rare-earth markers migrate extensively from the labeled feeds (Teeter et al. 1984; Combs et al., 1992) and precipitate as phosphates in the rumen (Van Soest et al., 1988), or bind to microbial cells and salivary mucins (Allen, 1982). The small size and increased weight and density of these particles and precipitates cause the markers to escape the rumen quickly. Therefore, labeled feeds

not only overestimate passage rate but also fail to represent the actual passage rate of the feed ingredient with which they are originally dosed.

Although accurate passage rates of feed fractions are not widely available for use in models, these rates can be measured using the pool-and-flux method (Robinson et al., 1987). This method calculates passage rate by dividing duodenal flux of an individual digesta fraction by its ruminal pool size. Data using this method are rare compared to data using external markers because the method requires surgically prepared animals (ruminal and duodenal cannulas) and is expensive and labor intensive. However, it is the only method capable of accurately measuring passage rates of individual feed fractions. Mean passage rates of dry and wet forages were 4.5 and 5.2 %/h for rare earth markers (Seo et al., 2006; Table 1), which are twice as high as the mean passage rate of potentially digestible NDF (2.4%/h) from 315 records in 11 experiments using the pool and flux method in our laboratory (Voelker-Linton, 2006). In contrast, mean passage rate reported for concentrates using rare earth markers (6.7%/h) is less than one-half the mean passage rate of starch in our studies (15.3%/h). Similar passage rates for forages and concentrates when rare earth markers were used is likely because the markers migrate from the feeds soon after entering the rumen!

Rate of passage of individual feed fractions are not constant and are greatly affected by other dietary factors (Table 2). Passage rates of fiber fractions were affected by forage type (brown midrib vs. conventional corn silage, Oba and Allen, 2000; orchardgrass vs. alfalfa silage, Voelker Linton and Allen, 2008), NDF concentration of the diet (29 vs. 38%, Oba and Allen, 2000), forage to concentrate ratio (45 vs. 61%, Voelker Linton and Allen, 2007), conservation method of corn grain (high-moisture corn vs. dry ground corn, Oba and Allen, 2003), and substitution of beet pulp for high moisture corn (Voelker and Allen, 2003). In

addition, passage rate of starch was greatly affected by corn grain endosperm type (Ying and Allen, 2005; Allen et al., 2008). The reduction in passage rate of indigestible and potentially digestible NDF with greater diet NDF concentration (Table 2) is likely because of selective retention of small particles by the rumen mat comprised of larger particles. The critical particle size for passage from the rumen of lactating cows is that which passes through a screen with a 2.4 mm aperture size, but over half of the NDF in the rumen is in particles below this size because of selective retention (Voelker Linton and Allen, 2007), and the rate of breakdown of large particles was much greater for NDF from alfalfa compared to grass (5.7 vs. 3.1%/h, $P < 0.0001$; Kammes and Allen, 2011). Most rumen models used for diet formulation do not include selective retention; in contrast to reality, all particles, regardless of size and density, in these models have equal probability of escape!

Inaccurate passage rates of nutrient fractions determined for entire feeds from fecal excretion curves of markers that migrate, as well as inaccurate representation of passage in models, are major sources of error for rumen models, rendering them useless for diet formulation. Passage rates of individual feed fractions are highly dependent upon their digestion characteristics, particle size, density, and associative effects of the diet. Lack of absolute rates and numerous interactions limit our ability to predict ruminal digestibility, and there are no solutions to this problem on the horizon.

Digestion rate of feed fractions are also incorrect!

Measurement of digestion rate of feed fractions *in vitro* and *in situ* can provide relevant information regarding relative differences among feeds. However, as mentioned above, absolute, not relative, values are required by models to predict ruminal digestibility. The primary factors limiting accurate determinations of digestion rate *in vitro*

or *in situ* are: 1) the inability to mimic the increase in surface area and breakdown of particle size by rumination and 2) variation in enzyme activity and ratio of enzyme to substrate. Grinding feeds is necessary to obtain uniform samples for analysis in the laboratory, but grinding increases surface area accessible to microbes, increasing rate of digestion compared to intact feeds *in vivo*. On the other hand, not grinding at all will underestimate rate of digestion because feeds are crushed and ground by chewing over time, before they pass from the rumen. This is an unsolvable problem because simulation of the effects of chewing over time of incubation *in vitro* or *in situ* is infeasible.

In vitro digestibility of NDF is fairly consistent across determinations over time; coefficient of variation (CV) of a standard sample across runs of less than 3% is possible in a well-buffered system. This indicates that enzyme activity of rumen fluid is either consistent or, more likely, in excess for digestion of NDF. However, as discussed above, rate of digestion of potentially digestible NDF is highly affected by ruminal pH, which is not accurately predicted by current models. In contrast, variation in enzyme activity of rumen fluid and the ratio of enzyme to substrate has profound effects on rate of digestion of starch. We have observed dramatic differences for *in vitro* starch digestibility (IVSD-7h) measured for the same sample from one run to the next. The CV across runs was high (~25%) despite mixing rumen fluid from several cows fed a consistent diet and sampling at the same time every day relative to feeding. It is most likely that the enzyme activity of the rumen fluid is highly variable from one run to the next because the within-run CV was low (~2%). This prompted us to evaluate the effect of rumen fluid sampled before and after feeding on IVSD-7h which was 33% greater after feeding compared to before feeding (41.2 vs. 30.9%, $P < 0.01$; Fickett and Allen, 2002). Furthermore, enzyme activity related to starch fermentation is increased with higher starch diets; we reported that the fractional rate of starch

digestion determined *in vivo* with the pool and flux method was greater for diets with higher starch concentration and lower NDF from forage (Oba and Allen, 2003) or beet pulp (Voelker and Allen, 2003). Therefore, at least for starch, digestion is a second-order process dependent upon both substrate and enzyme activity. This is a problem for utilization of current data with most existing models in which digestion is modeled as a first-order process. It results in great variation among studies reported in the literature (either *in vitro* or *in situ*), the results of which were highly influenced by the diets fed to the animals used as the source of rumen fluid.

The difficulty of predicting protein flow from the rumen

Protein flow to the duodenum is affected by true protein consumed, as well as that degraded and synthesized by microbes in the rumen. Degradation of feed proteins is dependent on rate of degradation and rate of passage, the accuracy of which is subject to all of the issues discussed above. While dietary nitrogen can be classified into fractions that have more homogeneous rates of degradation, variation in microbial populations can dramatically affect enzyme activity and degradation rates. Therefore, laboratory measurements are relative, not absolute, and useful only to compare feeds under the same conditions. Passage rates of nitrogenous fractions are largely unknown and application of passage rates of entire feeds determined with rare earth markers to determine ruminal degradation and passage of true protein from feeds is an exercise in futility.

Determination of protein synthesis by ruminal microbes and flow of microbial protein from the rumen is even more challenging. Microbial protein production in the rumen is dependent upon substrate supply (primarily carbohydrates), but prediction of carbohydrate fermentation in the rumen suffers from problems related to data availability

and model structure as discussed above. In addition, yield of microbial protein from organic matter consumed is highly variable because of energy spilling by microbes and because microbial composition varies with growth rate and cannot be predicted accurately by models. Furthermore, passage of microbial protein is dependent upon the competition between cell death from lysis or predation and passage, which are unknown. Although one of the primary reasons for the development of rumen models was to predict absorbed protein, increased accuracy of prediction is highly doubtful.

Ockham's Razor

Because the remainder of this paper pertains to the philosophy of diet formulation, it is appropriate to draw from the wisdom of philosophers. Ockham's razor is a principle that was used by the 14th century philosopher William of Ockham who stated "Plurality should not be posited without necessity". This has been interpreted as suggesting that we should tend towards simpler theories unless simplicity can be traded for increased explanatory power. Einstein apparently agreed when he stated "It can scarcely be denied that the supreme goal of all theory is to make the irreducible basic elements as simple and as few as possible without having to surrender the adequate representation of a single datum of experience" (Einstein, 1934). This is often paraphrased as "Everything should be made as simple as possible, but not simpler." Formulation of diets for ruminants is greatly complicated by pregastric fermentation in the rumen, and rumen models give the false impression of increased accuracy of nutrient supply to the animal because of their complexity. However, the rumen is much more complex than current mechanistic models represent, and there is no proof that the non-validated rumen models used in diet formulation programs increase accuracy of nutrients supplied to the animal; mechanistic models are less accurate than empirical models because of their increased

complexity and numerous inputs (France et al., 2000). Current models are either structurally incorrect (i.e. using passage rates of entire feeds to calculate digestibility of fractions, assumption of first order digestion), and/or models are so detailed that we have no data to parameterize them. The wisdom of Ockham and Einstein must be applied here; use of complicated models for routine diet formulation is illogical because the added complexity does not increase accuracy considering the great variation in nutrient composition of rations delivered to the feed bunk from day-to-day, diet selection by cows, and effects of diet on feed intake, digestion and partitioning that are not considered or poorly predicted by these models. We should reflect on how we approach diet formulation and how we use our resources of time and money. We will be better served with a simplified approach to diet formulation, concentrating on what we can measure rather than using what is predicted poorly. “Can’t see the forest for the trees” is an adage that pertains to the use of complex models; when one is so immersed in the detail, the “big picture” becomes blurred.

Prepare for Success

Production response has little to do with the program used for diet formulation but is highly dependent upon the experience and knowledge of the nutritionist, the management team on the farm, and their interaction. The primary factors allowing increased production response to diet formulation are:

- Facilities and personnel that minimize stress,
- Low variation in nutrient concentration of feed ingredients,
- High quality feeds and water,
- Group cows by their physiological and metabolic responses to diets, and
- Forage selection and allocation.

Nutritionists have a unique perspective and knowledge base and can play an important role as

an integral member of the management team on farms. The nutritionist and designated member(s) of the management team on the farm should routinely inspect all feeds for quality, including moisture, fermentation quality for silages, particle size of forages, presence of molds, etc. Management of silage, feed bunks and water troughs, the TMR mixing process, and access to feed and water should be evaluated routinely. Grouping strategies have a huge effect on milk yield, management of body condition, and feed efficiency, and options should be considered carefully. The nutritionist should be involved in the selection process for forage types and genetics. Forages and grains should be tested for *in vitro* digestibility of NDF and/or starch to aid in diet formulation and ingredient allocation. These factors are much more important than programs used for diet formulation, which should not be unnecessarily complicated.

“You need to take a step before you can tell if you’re going in the right direction”
(Anonymous).

Diet formulation should be an iterative process that includes cows in the loop; evaluation of cow response will provide feedback to optimize diets. Cow responses include DMI; yields of milk, fat, and protein; milk urea nitrogen (MUN), body condition; manure consistency; ketones; urine pH; etc. Group feeding complicates interpretation of responses for DMI and milk yield. Mean milk yield for the group masks effects of diets because large changes in milk yield of individual cows within the group might occur with no change in milk yield for the group overall. For instance, high moisture corn grain compared to dry ground corn had opposite effects on milk yield for cows depending on milk yield, with no change for the group overall; high moisture corn increased milk yield for cows producing over ~90 to 100 lbs/day but decreased milk yield for cows producing less than that amount (Bradford and Allen, 2004). Individual milk meters provide timely feedback regarding response of

individuals within the group and are an important tool for diet formulation and grouping. The same is true for individual DMI response, but this is not feasible economically for group-housed cows. While that limits the usefulness of DMI determination for the group, it is still a very useful measurement, particularly in combination with milk yield as a measure of production efficiency and to provide important clues for the effects of the diet change.

Process Control

Methods should be instituted to understand and reduce variation of feed ingredients. Process control is a management science that should be applied to our diet formulation system. Dry matter concentration of silages and wet feeds should be determined at least twice per week, and all feeds should be analyzed routinely for concentrations of DM, NDF, and CP (starch should be included for all feeds containing grains). Frequency of analysis should be every 2 weeks, and results should be plotted over time. Once variation is determined, frequency can be decreased for feeds that are less variable but should be maintained for more variable feeds. This will give information on when diets must be adjusted for real changes in nutrient concentrations of ingredients, rather than day-to-day fluctuations. Although more frequent sampling will increase cost, eliminating unnecessary characterization required by complex models will offset the cost. Variation in rations delivered to the feed bunk should be assessed periodically by “TMR audits”, which can reveal problems related to mixing and delivery of rations.

A More Effective Approach

An alternative approach to diet formulation allows more time and money to be focused on the factors that have greater importance. The key factors to consider when formulating diets are related to: 1) the filling effect of the diet over time in the rumen, 2) diet fermentability, 3) quantity and

quality of absorbed protein, and 4) amount and type of fat.

The filling effect of diets is related to forage NDF concentration, forage particle size (only when finely chopped or with high NDF diets), and the digestion characteristics of forage NDF (Allen, 2000). Because feed intake limits DMI as milk yield increases, diets for high-producing cows should be formulated for lower forage NDF concentration. However forage NDF is also positively related to ruminal pH because it stimulates rumination and secretion of salivary buffers, it stimulates rumen motility and mixing and absorption of fermentation acids, and it increases retention of digesta in the rumen, increasing direct buffering of fermentation acids produced. Therefore, the optimal concentration of forage NDF in the diet must be balanced between its effects on DMI and ruminal pH. Because rumen models cannot accurately predict either effect and response to forage NDF concentration varies greatly by cow and NDF digestion characteristics, optimal forage NDF concentration for a given group of cows and source of forage can only be determined by careful evaluation of cow responses (e.g. DMI, milk yield, and feed efficiency).

Diet fermentability is largely affected by the concentration and fermentability of starch and can affect DMI, nutrient partitioning, microbial protein production, and total-tract digestibility. The physiological state of animals determines the effects of starch fermentability on DMI (Bradford and Allen, 2007) and production response (Bradford and Allen, 2004), and this is not considered by models but must be determined by animal response. Access to grains that differ in ruminal starch fermentability, but have high whole tract digestibility (e.g. high moisture corn and ground dry corn), allows evaluation of optimal ruminal starch digestibility without other confounding effects, such as forage or non-forage NDF, while diet starch concentration can be reduced by substitution of a non-forage fiber

source, such as beet pulp, soyhulls, or corn gluten feed, for grains.

Absorbed protein is affected by the amount and ruminal degradation of CP consumed and production and passage of microbial protein from the rumen. Although prediction of absorbed protein has been the primary emphasis of some rumen models, their improvement in accuracy is doubtful for the reasons discussed above. Diets should be formulated for CP and rumen undegraded and degraded protein, considering characteristics of the protein sources included. Once production response to forage NDF and fermentability are determined and diets are adjusted, response to protein concentration, ruminal protein degradation, and AA profile can be determined by substituting ingredients and evaluating response for milk and milk components. Response to protein concentration can be evaluated by substitution of soybean meal for dry ground corn, rumen degradation can be evaluated by substitution of heat or chemically treated soybean meal for solvent extracted soybean meal, and AA profile can be evaluated by addition of rumen-protected methionine or lysine or substitution of protein sources varying in AA profile.

Fat is often added to diets to increase energy density or to improve reproduction. However, source of fat must be carefully considered because fat can negatively affect energy intake and cause milk fat depression, increasing energy partitioned to body condition. Effects of fat on energy intake and partitioning are greater for unsaturated fat sources, although medium chain FA also can have negative effects. Because ruminal outflow of CLA isomers that cause milk fat depression and partitioning of energy to body condition cannot be predicted by rumen models, supplementation of unsaturated fat sources must be carefully considered by evaluating cow response.

While diet formulation can be simplified, evaluation of cow response requires more attention

by nutritionists and coordination with the management teams on farms. The extent to which nutritionists and the management team interact will vary from farm-to-farm, but this is an important determinant of the success of the nutrition program.

Conclusions

Many dairy nutritionists are implementing some or most of what is presented in this paper to the extent possible. However, increased emphasis on minutiae required by overly complex models dilutes their effectiveness in other important areas. The information presented in this paper can help nutritionists decide how to balance their efforts. Energy intake and partitioning are affected by diet and should be the primary consideration when formulating diets; unfortunately, they often get less attention than they deserve. Reducing variation of rations delivered to the cow and evaluation of cow response are integral to successful diet formulation and require greater involvement of nutritionists in the nutritional management on the farm.

“All models are wrong, but some are useful” (Box, 1979). Some of the information presented in this paper will likely raise a few eyebrows, or incur even stronger reactions by some, especially in regard to the questionable accuracy of the increasingly complex models that were originally developed as research models but found their way into the field. Most models can be used successfully to formulate diets as long as you know what the model can and can’t do and what to trust and not to trust. Understanding the model used is imperative, but complex models are very difficult to understand, even among academics that have the time and resources to study them. The simplest model that adequately describes the system should be used; if a more complex model does not increase accuracy, it should not be used for routine diet formulation. One of the most important functions of diet formulation programs is to act as accounting systems to provide a baseline, keep track of what has been

tried, and help think about what to try next. It is my hope that this paper will start a dialog about the accuracy of models among nutritionists that has festered among those in the academic community for more than 2 decades, and to focus on what is important in the diet formulation process, separating the wheat from the chaff.

References

- Allen, M.S. 1982. Investigation into the use of rare earth elements as gastrointestinal markers. M.S. Thesis. Department of Animal Science, Cornell University.
- Allen, M.S. 1996. Physical constraints on voluntary intake of forages by ruminants. *J. Anim. Sci.* 74:3063-3075.
- Allen, M.S. 2000. Effects of diet on short-term regulation of feed intake by lactating dairy cattle. *J. Dairy Sci.* 83:1598-1624.
- Allen, M.S., B.J. Bradford, and M. Oba. 2009. BOARD-INVITED REVIEW: The hepatic oxidation theory of the control of feed intake and its application to ruminants. *J. Anim. Sci.* 87: 3317-3334.
- Allen, M.S., R.A. Longuski, and Y. Ying. 2008. Endosperm type of dry ground corn grain affects ruminal and total tract digestion of starch in lactating dairy cows. *J. Dairy Sci.* 91(E Suppl):529. (Abstr.)
- Box, G.E.P. 1979. *Robustness in statistics.* Academic Press, London, p. 201.
- Bradford, B.J., and M.S. Allen. 2004. Milk fat responses to a change in diet fermentability vary by production level in dairy cattle. *J. Dairy Sci.* 87: 3800-3807.
- Bradford, B.J., and M.S. Allen. 2007. Depression in feed intake by a highly fermentable diet is related to plasma insulin concentration and insulin response to glucose infusion. *J. Dairy Sci.* 90:3838-3845.
- Brenner, S. 2004. Interview, *Discover Magazine*, Vol. 25 No. 04, April issue.
- Combs, D.K., R.D. Shaver, and L.D. Satter. 1992. Retention of rare earths by hay particles following incubation in fresh or autoclaved rumen fluid. *J. Dairy Sci.* 75:132-139.
- Ehle, F.R., F. Bas, B. Barno, R. Martin, and F. Leone. 1984. Particulate rumen turnover rate as influenced by density of passage marker. *J. Dairy Sci.* 67:2910-2913.
- Einstein, A. 1934. On the methods of theoretical physics. In: *Philosophy of Science*, 1:163-169.
- Erdman, R.A., and L.W. Smith. 1985. Ytterbium binding among particle size fractions of forage cell walls. *J. Dairy Sci.* 68:3071-3075.
- Fickett, F.M., and M.S. Allen. 2002. Ruminal fluid effects on in vitro digestion kinetics of starch. *J. Dairy Sci.* 85(Suppl. 1):181. (Abstr.)
- Firkins, J.L., M.S. Allen, B.S. Oldick, and N.R. St. Pierre, 1998. Modeling ruminal digestibility of carbohydrates and microbial protein flow to the duodenum. *J. Dairy Sci.* 81:3350-3369.
- France, J., M.K. Theodorou, R.S. Lowman, and D.E. Beever. 2000. Feed evaluation for animal production. In: Theodorou, M.K., France, J. (Eds.), *Feeding Systems and Feed Evaluation Models.* CABI Publishing, New York, pp. 1-9.
- Harvatine, K. J., Y. R. Boisclair, and D. E. Bauman. 2009a. Recent advances in the regulation of milk fat synthesis. *Animal* 3:40-54.

- Harvatine, K.J., J.W. Perfield, and D.E. Bauman 2009b. Expression of enzymes and key regulators of lipid synthesis is upregulated in adipose tissue during CLA-induced milk fat depression in dairy cows. *J. Nutr.* 139:849-854.
- Joandet, G.E., and T.C. Cartwright. 1975. Modeling beef production systems. *J. Anim. Sci.* 41:1238-1246.
- Kammes, K.L., and M.S. Allen. 2011. Rates of particle size reduction and passage are faster for legume compared to C3 grass resulting in lower rumen fill and less effective fiber. *J. Dairy Sci.* 94(Suppl. 1):submitted.
- Oba, M., and M.S. Allen. 2000. Effects of brown midrib 3 mutation in corn silage on productivity of dairy cows fed two concentrations of dietary neutral detergent fiber: 3. Digestibility and microbial efficiency. *J. Dairy Sci.* 83:1350-1358.
- Oba, M., and M.S. Allen. 2003. Effects of corn grain conservation method on ruminal digestion kinetics for lactating dairy cows at two dietary starch concentrations. *J. Dairy Sci.* 86:184-194.
- Robinson, P.J., S. Tamminga, and A.M. Van Vuuren. 1987. Influence of declining level of feed intake and varying proportion of starch in the concentrate on rumen ingesta quantity, composition and kinetics of ingesta turnover in dairy cows. *Livest. Prod. Sci.* 17:37-62.
- Seo, S., L.O. Tedeschi, C.G. Schwab, B.D. Garthwaite, and D.G. Fox. 2006. Evaluation of the passage rate equations in the 2001 dairy NRC model. *J. Dairy Sci.* 89:2327-2342.
- Teeter, R.G., F.N. Owens, and T.L. Mader. 1984. Ytterbium chloride as a marker for particulate matter in the rumen. *J. Animal Sci.* 58:464-473.
- Van Soest, P.J., C.J. Sniffen, and M.S. Allen. 1988. Rumen dynamics. In: *Aspects of Digestive Physiology in Ruminants*. A. Dobson, ed., Cornell University Press, Ithaca, NY.
- Voelker, J.A., and M.S. Allen. 2003. Pelleted beet pulp substituted for high-moisture corn: 2. Effects on digestion and ruminal digestion kinetics in lactating dairy cows. *J. Dairy Sci.* 86:3553-3561.
- Voelker, J. A., G.M. Burato, and M.S. Allen. 2002. Effects of pretrial milk yield on responses of feed intake, digestion, and production to dietary forage concentration. *J. Dairy Sci.* 85:2650-2661
- Voelker Linton, J.A. 2006. Effects of dietary forage characteristics on digesta passage rate in dairy cows. Ph.D. Dissertation, Department of Animal Science, Michigan State University.
- Voelker Linton, J.A., and M.S. Allen. 2007. Nutrient demand affects ruminal digestion responses to a change in dietary forage concentration. *J. Dairy Sci.* 90:4770-4779.
- Voelker Linton, J.A., and M.S. Allen. 2008. Nutrient demand interacts with forage family to affect intake and digestion responses in dairy cows. *J. Dairy Sci.* 91:2694-2701.
- Ying, Y., and M.S. Allen. 2005. Effects of corn grain endosperm type and conservation method on site of digestion, ruminal digestion kinetics and microbial nitrogen production in lactating cows. *J. Dairy Sci.* 88(Suppl.1):393. (Abstr.)

Table 1. Rate of passage of feeds determined by excretion pattern of rare earth markers in feces or of nutrient fractions by the pool and flux method.

	Mean	Range
Rare earth markers ¹		
Dry forage	4.5%/h	3.4 – 5.7%/h
Wet forage	5.2%/h	3.9 – 6.3%/h
Concentrate	6.7%/h	3.6 – 9.2%/h
Pool and flux ²		
iNDF	3.2%/h	1.2 – 5.3%/h
pdNDF	2.4%/h	0.2 – 4.3%/h
Starch	15.3%/h	3.4 – 33.9%/h

¹Seo et al., 2006.

²Voelker Linton, 2006; 315 records from 11 experiments conducted in our laboratory at MSU; iNDF = indigestible neutral detergent fiber and pdNDF = potentially digestible NDF.

Table 2. Effects of dietary treatment on rate of passage (kp) of feed fractions determined by dividing duodenal flux (g/h) by rumen pool size (g).¹

Experiment	Fraction	Treatment	kp, %/h	P value
Oba and Allen, 2000	iNDF	bm3 corn silage	3.64	<0.0001
		control corn silage	3.20	
	pdNDF	29% diet NDF	3.49	<0.0001
		38% diet NDF	2.43	
	starch	bm3 corn silage	12.9	0.02
		control corn silage	10.6	
starch	29% diet NDF	14.45	<0.0001	
	38% diet NDF	9.00		
Oba and Allen, 2003	iNDF	high-moisture corn	3.35	0.03
		dry ground corn	3.65	
	starch	high-moisture corn	15.4	0.07
		dry ground corn	19.7	
Voelker and Allen, 2003	starch	high-moisture corn	15.9	0.01
		24% beet pulp	23.5	
Voelker Linton and Allen, 2007	pdNDF	45% forage	1.57	0.06
		61% forage	1.04	
Voelker Linton and Allen, 2008	iNDF	orchardgrass silage	2.4	0.06
		alfalfa silage	2.9	
Ying and Allen, 2005	starch	high-moisture corn	7.1	<0.0001
		dry ground corn	16.3	
	starch	vitreous endosperm	16.0	<0.001
		floury endosperm	7.5	
Allen et al., 2008	starch	vitreous endosperm	25.7	<0.001
		floury endosperm	16.0	

¹iNDF = indigestible NDF, pdNDF = potentially digestible NDF, and bm3 = brown midrib.

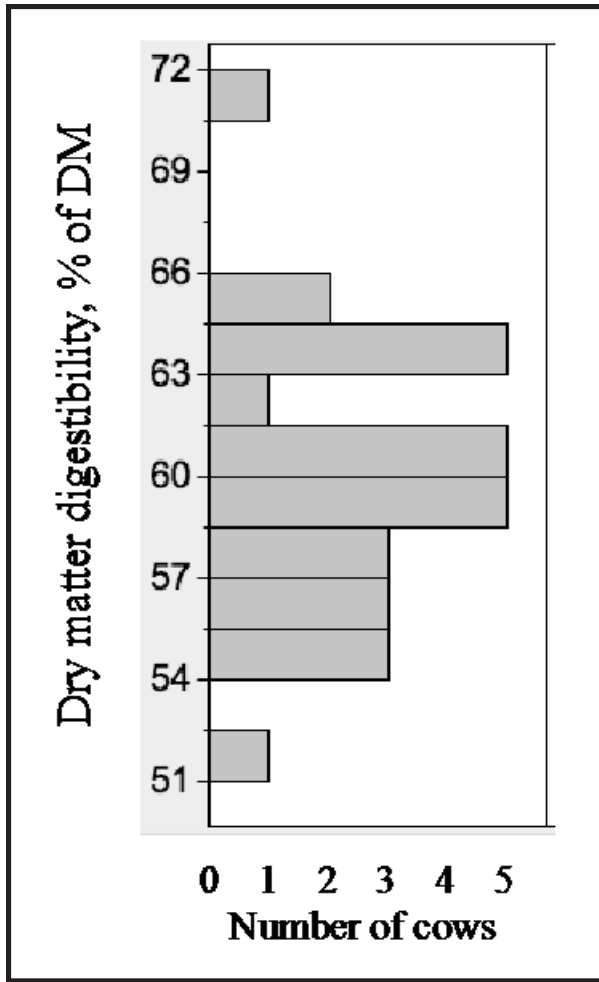


Figure 1. Distribution of dry matter digestibility determined for 29 cows consuming the same diet. The DMI of individual cows ranged from 37 to 69 lb/day and was not related to DM digestibility ($P = 0.48$; Voelker et al., 2002).

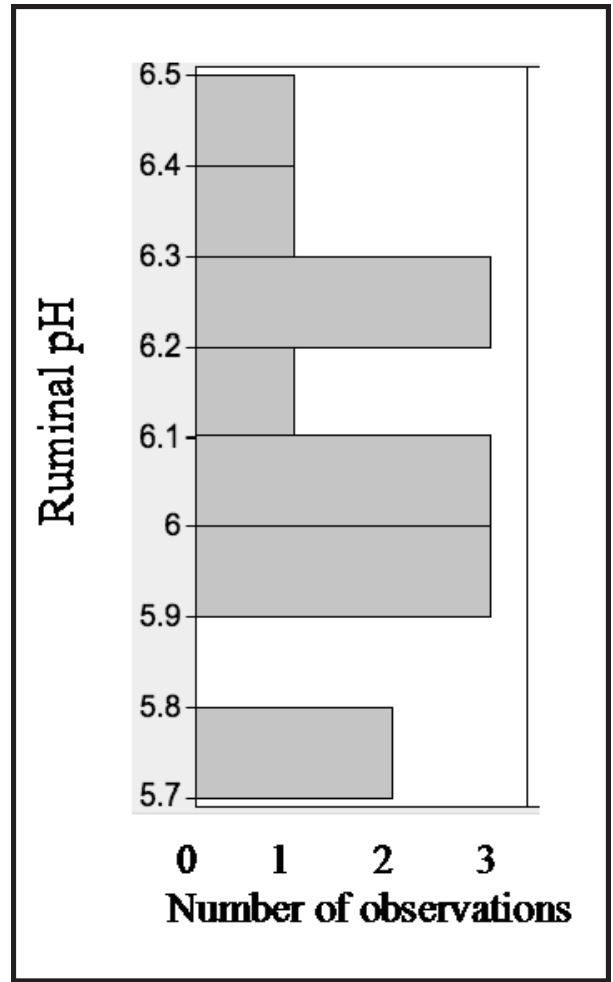


Figure 2. Distribution of mean ruminal pH (measured every 15 hours for 5 days, $n=8$) for 14 cows consuming the same alfalfa silage-based diet. Dry matter intake ranged from 45 to 67 lb/day and was not related to ruminal pH ($P = 0.81$) (Kammes and Allen, Michigan State University, unpublished data).

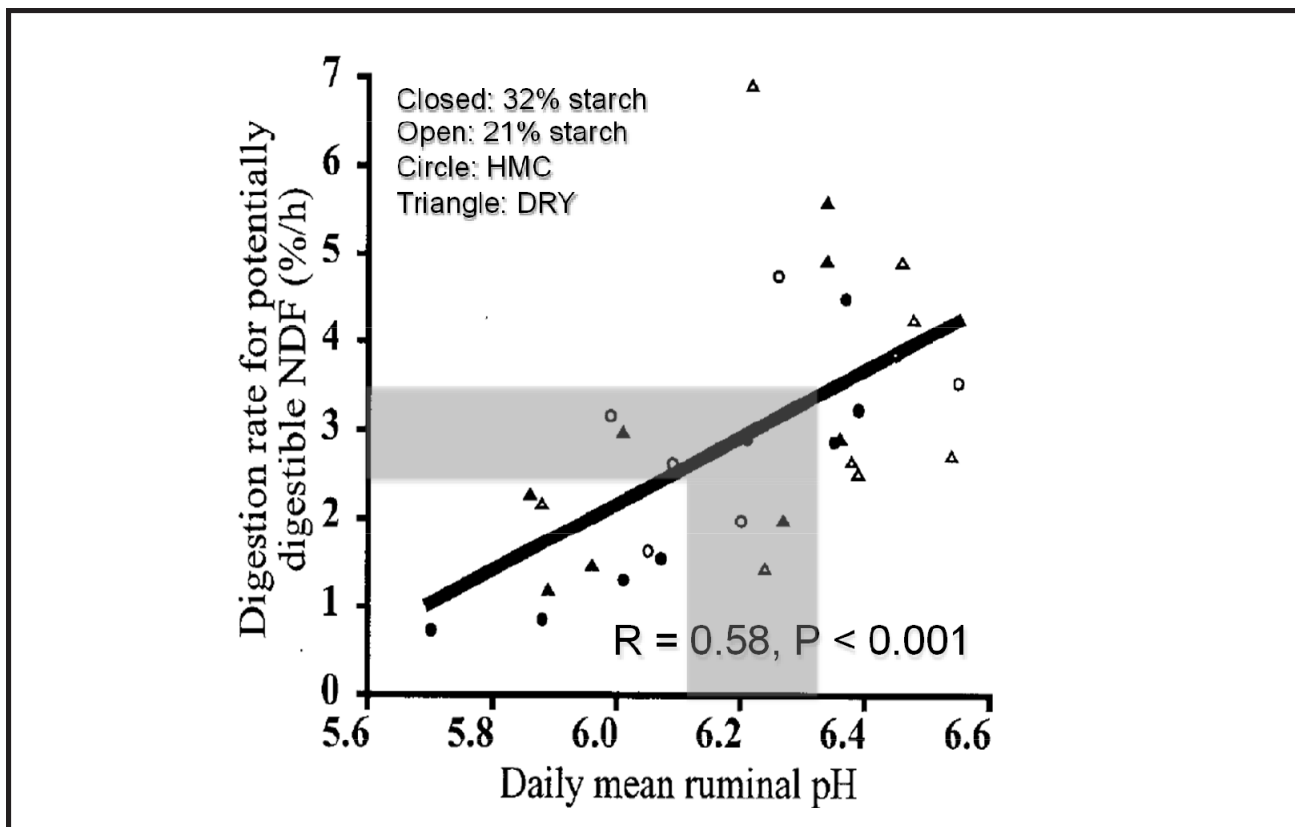


Figure 3. Relationship between mean ruminal pH and digestion rate of potentially digestible NDF for 8 cows consuming 4 treatment diets varying in concentration and ruminal fermentability of starch (Oba and Allen, 2003) (HMC = high moisture corn and DRY = dry ground corn). The shaded area represents the range in ruminal pH and digestion rate represented by the treatment means.