General Sessions

Moderators: Camilla Hill, Renee Dewell

Forages, Fiber and the Rumen

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Take Home Messages

- The goal of formulating diets for carbohydrates is to provide low fill, highly fermentable diets that result in consistent ruminal fermentation over time.
- Forage fiber content of diets limit feed intake of high producing cows.
- Rapidly fermented starch sources can decrease feed intake and efficiency of microbial protein production.
- Forages with highly digestible NDF with a high ruminal turnover rate are most valuable for high producing cows.
- Consideration of carbohydrate digestion characteristics when formulating diets is important to maximize energy intake and microbial protein production.

Introduction

One of the most challenging aspects of diet formulation for lactating cows is balancing for carbohydrates. Adequate effective fiber must be provided to stimulate chewing and secretion of salivary buffers. However, effective fiber is more filling than other nutritional components of the diet and the filling effect of the diet often limits energy intake of high producing cows. Therefore, diets for high producing cows should be balanced to provide adequate effective fiber with the least filling effect. A balance must also be attained for ruminal carbohydrate fermentation. Carbohydrate fermentation in the rumen is desirable to provide fuels for microbial growth and production of microbial protein, yet the fermentability of the diet must be limited to prevent excessive production of fermentation acids. Inadequate effective fiber or excessive fermentability of the diet can decrease ruminal pH, feed intake, diet digestibility and microbial protein production. This is a major problem on many dairy farms that results in poor health, and reduces milk yield and farm profitability. On the other hand, diets with excessive effective fiber that are more filling and diets that are poorly fermentable can also result in lower milk yield and profitability because of reduced energy intake and microbial yield. Both situations can be thought of as lost opportunity for maximization of farm profits. Understanding the complex factors that interact to determine energy intake and microbial protein production in the rumen can pay off generously by allowing increased milk yield and reduced diet costs. The goal of formulating diets for carbohydrates is to provide low fill, highly fermentable diets that result in consistent ruminal fermentation over time. This paper addresses how to attain this goal by discussing how carbohydrates affect feed intake, ruminal pH and microbial protein production.

Dietary Carbohydrates

The main carbohydrates in diets for dairy cattle are those in the neutral-detergent fiber (NDF) fraction (cellulose and hemicellulose) and starch. The starch content of dairy cattle diets is inversely related to the NDF content and concentrations of both are typically in the range of ~ 25 to 35% of dietary DM for lactating cows. Other common carbohydrates include pectin and sugars, both with concentrations that are typically less than ~5% of dietary DM. The highly digestible carbohydrates including starch, sugars, and pectin are often referred to collectively as non-fiber carbohydrates (NFC). Because NFC is obtained by subtracting the measured fractions NDF, crude protein, fat and ash from 100%, it is subject to many errors. It is also a misnomer because it doesn't include all non-fiber carbohydrates (the protein fraction is overestimated when non-protein nitrogen is present) and because it includes soluble fiber (pectin, gums). In addition, when fermented feeds are included in the diet, NFC includes fermentation products such as lactic acid, acetic acid and ethanol.

Long fiber particles (effective fiber, mostly from forage) are needed in the diet to maximize production at least three different ways:

- 1) Stimulation of chewing which results in the secretion of salivary buffers
- 2) Formation of a rumen mat that entraps small particles, increasing their ruminal digestibility
- 3) Providing a consistent source of fuels to the microbes in the rumen which functions to provide a steady supply of fuels to the liver and mammary gland over time

Some sources of fiber are very effective at stimulating chewing and mat formation in the rumen (long and coarsely chopped forages) while others are not (most high fiber byproducts). Also, sources of fiber vary greatly in NDF digestibility and retention time in the rumen. All three of these functions mentioned above are important to maximize milk yield, and the most valuable sources of fiber are those that are effective at stimulating chewing and formation of the rumen mat, and highly digestible with a rapid rumen turnover (less filling).

Starch is an inexpensive source of energy that can be fermented by microbes in the rumen to produce microbial protein and volatile fatty acids (VFA) used as fuels by the cow. Starch that passes from the rumen can be also digested in the small intestine or fermented in the large intestine, also providing fuel, but not microbial protein, to the cow. A large fraction of the fuels produced (propionate, lactate) are used by the liver to produce glucose, which the mammary gland needs to produce lactose, the major determinant of milk yield; 100 lb of milk contains nearly 5 lb of lactose. Ruminal digestibility of starch can range from less than 40% to greater than 90%, depending on the type of grain (barley, corn, sorghum), conservation method (dry, high moisture), and processing (ground, rolled, steam flaked). Alteration of rate and site of starch digestion is important for optimal diet formulation as discussed below.

Pectin is normally found in low concentrations in most feeds consumed by dairy cows (< 2-3%), but several feeds contain higher concentrations, such as citrus pulp (~15%), beet pulp (~15-20%) and alfalfa (3-10%). Pectin is of interest because it is highly fermentable and whole tract digestibility is high, but it can help moderate fermentation in the rumen. This is because, unlike fermentation of starch, rate of fermentation of pectin slows as ruminal pH decreases. This might help attenuate the rapid decline in ruminal pH following a meal and keep ruminal pH within a narrower desirable range. Sugars are highly fermentable and completely digested. Like pectin, the sugar content of most feeds is low, but there are exceptions such as fresh forages, molasses, whey, citrus pulp and candy waste. Concentrations and characteristics (physical and fermentation) of these different types of carbohydrate vary greatly in diets of lactating cows and this variation can have dramatic effects on feed intake, ruminal pH, digestibility and microbial protein production. One of the greatest opportunities to increase milk yield and profitability is to understand how dietary carbohydrates can be manipulated to maximize energy intake and microbial yield.

Regulation of Intake

Feed intake is a function of meal size and meal frequency. The brain receives many different signals that affect satiety and hunger. A British researcher, Dr. Mike Forbes, recently proposed that animals eat the amount of a particular diet that minimizes the total discomfort produced by signals from various receptors in the body to the brain. Distension in the rumen causes discomfort and can reduce feed intake, but high producing animals might tolerate a greater degree of discomfort from physical fill to offset discomfort from hunger. Manipulating diets to increase meal size and increase frequency of meals can lead to greater feed intake. An understanding of the basic mechanisms regulating intake is invaluable for diet formulation to maximize milk yield. Although regulation of feed intake is very complex, two primary mechanisms regulating DMI that are related to dietary carbohydrates are:

- Filling effect of diets
- Ruminal fermentability of diets

Ruminal fill can limit intake of high producing cows and other cows fed high forage diets. Tension receptors in the rumen wall signal brain satiety centers when the rumen is stretched. The rumen doesn't have to be full for ruminal fill to limit intake. Diets with a greater filling effect limit meal size but hunger occurs sooner and the number of meals consumed per day might partially or completely compensate for the decreased meal size. When a group of cows is offered a diet, feed intake of the highest producing cows are most limited by ruminal fill and these cows present the greatest opportunity to increase energy intake by manipulation of dietary carbohydrates. When the filling effect of the diet is decreased, problems can occur with slug feeding because low-fill diets can be consumed rapidly. This is a common problem when cows compete for feed bunk space in overcrowded facilities and requires diets that are either more filling or less fermentable to prevent ruminal acidosis.

Rapid fermentation of ingested feed during a meal produces VFA that can cause satiety. Although acetate is produced in the greatest quantity, propionate has a greater effect on limiting intake. When dietary NDF is held constant, increasing the fermentability of the diet by substituting a rapidly fermentable starch source, such as rolled barley, for a starch source with more moderate rate of fermentation, such as corn meal, will likely reduce meal size, and possibly decrease daily DMI. The degree to which fermentation acids limit DMI depends upon many factors, some of which are currently being investigated.

Filling Effect of Diets

The filling effect of a diet is determined primarily by the initial bulk density of feeds as well as their filling effect over time in the rumen. The overall filling effect is determined by:

- Forage NDF content
- Forage particle size
- Forage type (legumes, perennial grasses, annual grasses)
- NDF digestibility (within a forage family)

Forage NDF is less dense initially, digests more slowly and is retained in the rumen longer than other diet components. Feed intake of high producing cows is often dramatically reduced by increasing the forage NDF concentration of the diet. Several studies in the literature reported a decrease in DMI of ~ 5 to 9 lb/d when diet NDF content was increased from 25 to 35% by substituting forages for concentrates. Although most studies reported a significant decrease in DMI as forage NDF increased, the DMI response was variable, depending upon the degree to which intake was limited by ruminal fill. Higher producing cows are limited by fill to the greatest extent, and the filling effect of forage fiber varies depending upon particle size and fermentation characteristics.

Experiments that have evaluated effects of forage particle size have generally shown small effects on DMI. However, one experiment showed little effect of particle size of alfalfa silage when fed in high grain diets, but a large reduction in DMI for the diet containing longer alfalfa silage when fed in a high forage diet. Feed intake might have only been limited by ruminal fill in the high forage diet, which could explain the interaction observed.

Increasing diet NDF content by substituting nonforage fiber sources (NFFS) for concentrate feeds has shown little effect on DMI in studies reported in the literature. NFFS include byproduct feeds with significant concentrations of NDF such as soyhulls, beet pulp, cottonseeds, corn gluten feed and distiller's grains. Fiber in NFFS is probably much less filling than forage NDF because it is less filling both initially (smaller particle size) and over time in the rumen because it digests and passes from the rumen more quickly.

Forage NDF has a much longer ruminal retention time than other major dietary components. Retention time in the rumen is longer because of longer initial particle size, and greater buoyancy in the rumen over time, which differs greatly across forages. As forages mature, the NDF fraction generally becomes more lig-nified. Lignin is a component of plant cell walls that helps stiffen the plant and prevent lodging. It is also essentially indigestible by ruminal microbes and limits fermentation of cellulose and hemicellulose. Within a forage type, the degree to which NDF is lignified is re-lated to the filling effects of the NDF. Fiber that is less lignified clears from the rumen faster, allowing more particle size, and greater buoyancy in the rumen over lignified clears from the rumen faster, allowing more space for the next meal. However, ruminal retention time of NDF from perennial grasses is generally longer than for legume NDF in spite of being less lignified. Because of this, it is more filling and should not be included in high concentrations in diets of cows for which feed intake is limited by ruminal fill, unless it is of exceptionally high quality. Corn is an annual grass, and corn silage NDF digests and passes from the rumen quickly and can be an excellent source of FNDF for high producing cows.

The extent of lignification of NDF is a useful way to estimate the filling effects of forage NDF. To calculate lignification of NDF, divide the lignin content as a percent of DM by the NDF content as a percent of DM and multiply by 100. Data from the upper midwestern US indicates that the lignin content of alfalfa NDF ranges from ~11 to 20%, and the lignin content of corn silage NDF ranges from ~ 3 to 9% when measured as acid-detergent sulfuric acid lignin. Forages with low lignified NDF are especially valuable and should be targeted to the highest producing cows to allow them to consume more feed and attain higher milk yield. This is true even if the forage has low protein content or high NDF content, both of which can be compensated for by diet formulation. Forages with greater lignification of NDF should be targeted to animals whose DMI is not limited by ruminal fill, such as cows in late lactation, dry cows (except those close to calving) and heifers.

Besides forage maturity, the extent to which NDF is lignified is also greatly affected by growing conditions such as light, heat and water stress. Lignification of NDF is not related to NDF or protein content for either alfalfa or corn silage. Because alfalfa is priced in some markets based upon NDF or protein content or RFV, and not on the lignification of NDF, this presents an opportunity to purchase a valuable diet ingredient (effective, digestible NDF) inexpensively.

Ruminal Fermentability of Diets

The fermentability of diets depends on digestion and passage characteristics of individual feed ingredients and interactions among them. Starch is generally fermented faster than NDF, but passes from the rumen more quickly. Although NFC is often used as a proxy for the fermentability of diets, it is poorly related to fermentability because fermentability of both starch and NDF vary greatly by source.

Factors affecting ruminal fermentability of fiber include extent of lignification, rate of fermentation and ruminal retention time. As discussed above, rate of fermentation is dependent on intrinsic characteristics of the feed and on ruminal pH over time. Rate of passage is related to particle size and fermentation characteristics that affect buoyancy in the rumen over time. Retention time of forage NDF ranges from 24 to over 40 hours for lactating cows, depending on the amount of feed intake, diet characteristics and source of NDF.

Ruminal fermentation of starch is affected by particle size, gelatinization of starch and amount and solubility of endosperm proteins. Dry rolling and grinding decrease particle size of grains, which increases surface area of the grain available to microbes and therefore, rate of fermentation. Steam rolling or flaking increases surface area and also gelatinize starch, which increase accessibility by microbes and rate of fermentation. Endosperm proteins surround starch granules and inhibit accessibility to starch by ruminal microbes. Different grain types such as wheat, barley, corn and sorghum have major differences in amount and solubility of endosperm proteins that dramatically affect rate of fermentation. Wheat and barley have low concentrations and greater solubility of endosperm proteins, resulting in greater rates of fermentation than corn or sorghum. There is also great variation in amount and solubility of endosperm proteins among corn hybrids. Some hybrids have floury endosperm with soluble proteins and are more readily digested, and others have more vitreous endosperm with insoluble proteins and are more resistant to digestion. High moisture fermentation results in proteolysis and an increase in the solubility of endosperm proteins, increasing rate of starch digestion.

As previously discussed, ruminal starch fermentation ranges from less than 40% to greater than 90%, depending upon source. Ruminal fermentability depends upon rate of digestion and rate of passage from the rumen, which depend upon intrinsic characteristics of individual feeds, other diet components, and on characteristics of the animals fed. For instance, rate of starch digestion for a particular feed depends on the population of starch digesting microbes in the rumen. Rate of starch fermentation can increase dramatically when the fermentable starch content of the diet is increased. Rate of passage is affected by the size and density of particles, but also by the filtering effects of the rumen mat and by level of intake. The major limitation to fermentation rate of sugars is accessibility by rumen microbes. Although sugars from whey or molasses are fermented very quickly and completely, sugars in fresh forages are less accessible and probably fermented more slowly, but completely, because of the long retention time of forage particles in the rumen.

Fermentation of organic matter (OM) in the rumen results in the production of fermentation acids. The primary acids produced are acetic, propionic and butyric, but other acids are produced as well. Lactic acid is also produced, but its rate of utilization by microbes is usually sufficient to keep concentrations low. If a diet suddenly becomes more fermentable, lactic acid concentrations can increase and ruminal pH can drop rapidly because lactic acid is a much stronger acid than the VFA. This happens when abrupt changes occur in the diet, such as when a much more fermentable starch source is substituted for one that is less fermentable, or when heavy rains result in more moisture and less forage DM and NDF added when total mixed rations (TMRs) are mixed. When cows have clinical ruminal acidosis it is because of elevated lactic acid concentrations. Increasing consistency in all aspects of feeding programs, paying particular attention to mixing and to variation in forage DM and NDF content, will help prevent lactic acidosis. Lactic acid is not usually a factor in sub-clinical acidosis that results in lower energy intake and poor microbial efficiency. This happens when production of VFA exceeds the buffering capacity of the rumen contents, resulting in a decline in ruminal pH.

The optimal ruminal pH to maximize milk yield and efficiency of milk production is unknown. It probably varies for different cows and feeding conditions. However, we do know that fiber digestion decreases as pH is reduced from \sim pH 6 to pH 5.5 and below. This is because growth of fiber-digesting microbes becomes inhibited as pH declines. We also know that once populations of fiber digesting microbes are reduced, it can take many days to restore their numbers. On the other hand, the starch-digesting microbes have shorter doubling times and their populations can increase quickly. The implication of slower fiber digestion in the rumen is that fiber becomes more filling and feed intake might decrease. Fermentation acids are also absorbed from the rumen more quickly as pH declines and this might result in smaller meal size. While this might benefit cows "on the edge" of ruminal acidosis, it might result in lower DMI for others. The average ruminal pH throughout a day is much less meaningful than the fraction of time ruminal pH is below a threshold value such as pH 5.7. Therefore feeding management decisions should be made to minimize variation not only from day-to-day, but also within a day. Factors affecting variation in ruminal pH throughout a day include those that affect the number and size of meals discussed above, and the fermentability of diets.

sources such as molasses, whey and citrus pulp. Adjust site of starch digestion by altering the ruminal degradability of starch. This is easily done by substituting starch sources, with lower ruminal degradability, for those with higher ruminal degradability. It is important to use starch sources with high whole tract digestibility to maximize energy intake. Finely ground dry corn is generally less fermentable than barley, lowdensity steam-flaked corn, or ground high moisture corn and can be used to manipulate site of starch digestion because it has high whole tract digestibility. Coarsely rolled corn or sorghum is less desirable because whole tract digestibility is lower for these starch sources. Substitution of a less fermentable starch source, such as dry ground corn for high moisture corn, can increase DMI when it is limited by propionate production and increase microbial efficiency.

- Concentrations of very rapidly degraded carbohydrates (sugars and starch sources such as wheat and barley) should be limited in the diet. Rapid fermentation of carbohydrates can reduce efficiency of microbial protein production and limit meal size. Adequate ruminally degraded protein should be provided to maximize microbial efficiency.
- Avoid rolling corn silage too finely. Adjust the rollers so that the cobs and most of the grain is in the middle sieve of the Penn State Particle Size Separator. Rolling corn silage too finely can result in excessive ruminal starch fermentation.
- Diet fermentability can also be adjusted by substituting NFFS such as beet pulp or soyhulls for starch in the diet. This might be a reasonable alternative to altering site of starch digestion depending upon the relative prices of the NFFS to starch sources. Rate of fermentation of NDF from NFFS is generally slower than that of starch and sugars and less propionate is produced. Also, rate of fermentation of NDF from NFFS will decline as pH decreases. This has the benefit of limiting the decline in ruminal pH following meals, but it might reduce digestibility of the NFFS. Because effectiveness of NFFS are generally very low and because they are generally highly fermented, they are not filling like forage NDF and have little effect on DMI when substituted for grains. Addition of NFFS can result in large reductions in optimal FNDF of diets. While this is desirable to minimize the filling effect of diets, it might not maximize energy intake because of possible rapid passage from the rumen, which results in decreased digestibility.

- Avoid feeding starch sources that are poorly fermented such as dry corn silage, or coarsely rolled corn or sorghum to high producing cows. Diets that are poorly fermented decrease microbial yield and fuels for the production of glucose and milk lactose. In addition, decreased production of fermentation acids results in greater DMI until it is limited by ruminal fill. This often results in increased passage rate from the rumen, decreasing digestibility and feed efficiency.
- Another alternative for limiting diet fermentability is to increase the diet FNDF content. However, unless the FNDF digests and passes from the rumen quickly, this approach will increase the filling effect of the diet and reduce DMI when limited by ruminal fill (see next).
- Feeding forages with highly fermentable NDF with high ruminal NDF turnover will require higher FNDF in the diet, but will allow greater energy intake and provide a more consistent source of energy to the cow throughout the day. Forages with high ruminal NDF turnover include alfalfa with low lignification of NDF (<16% for midwestern data), corn silage with low lignification of NDF (< 6% for midwestern data). Brown midrib corn silage has been shown to have high rates of clearance from the rumen that allows higher DMI when fill limitations exist. In one recent experiment, response in milk yield to brown midrib corn silage was much higher for high producing cows, presumably with DMI limited by ruminal fill, than for lower producing cows.
- NDF content of forages influences the fermentability and the optimal FNDF concentration of the diet. Forages such as grasses or mature alfalfa with high NDF contents require much more grain or NFFS to formulate diets optimally. Because supplements are generally more fermentable than forages, FNDF concentrations must be higher but this might lower DMI. However, immature alfalfa or corn silage with low NDF contents (< 36%) requires very high forage in the diet. Because forages have lower energy density than most grains and NFFS, energy density of the diet is lower for diets containing high concentrations of low NDF forages. Unless the forage has high NDF digestibility, energy intake might be restricted, limiting milk yield.
- Variation in DM and (or) NDF of forages will cause great variation in ration FNDF and fermentability. Cows consuming low FNDF diets are not able to deal with this variation. If ration FNDF content decreases and

fermentability increases, ruminal acidosis might occur. However, if forage NDF or DM content increases and is undetected and uncorrected, energy intake will be somewhat reduced and this is not a great problem to animal health. Therefore, when variation is expected, higher diet FNDF levels must be fed to lower the risk of acidosis.

- All efforts should be made to reduce variation when forages are harvested (or purchased) and stored. Identify individual lots of forage and have them tested. Variation in forage DM and quality is often a problem for silage. Bunker silos have less daily variation than uprights or bags because the silo is filled in layers that tend to be mixed when removed from the silo. In contrast, abrupt shifts in DM and NDF can occur when removing silage from upright silos or silage bags. Silage DM concentration should be tested routinely. Frequency of testing depends upon the amount of variation and the type of silo. Silage DM in upright silos should be tested twice weekly and when changes are noticed, while silage in bunker silos can be tested less frequently. Mixing loads of silage from wet and dry parts of the bunker face when removed from the silo can help reduce variation, particularly after a substantial rainfall.
- Restrict the concentration of individual ingredients with variable quality or DM. Variation in ingredients that comprise a large fraction of the diet can have a great effect on FNDF and fermentation characteristics of the entire diet. Variation in forages or other feeds can be accommodated if they have relatively little effect on the total diet.
- Sorting can cause variation in diets consumed throughout the day. If sorting is a problem, it can be reduced by more uniform chopping of forages, processing corn silage, avoiding dry rations and feeding more than one time per day.
- Feeding TMRs will allow lower FNDF concentrations. TMRs have a great advantage because rapidly fermented carbohydrates are consumed along with effective fiber that limits size of meals and the decline in pH following meals. Concentrates can be fed separately, but they should be fed four or more times per day and rapidly degraded starch sources should be limited.
- Provide adequate particle length in diets. Reduction in particle length starts when forages are chopped. Further reduction occurs when corn silage is processed and when forages are ensiled in bags by augers during filling. Particle size is also reduced when diets are mixed

in many TMR mixers. A constant mixing time should used that is sufficient to adequately mix TMRs while avoiding excessive particle length reduction. Finally, particles are reduced still further when eaten by the cow. Effective fiber is needed to form a rumen mat to selectively retain small particles in the rumen and to stimulate rumination. While there is little to be gained in effectiveness of NDF by having particle length beyond a certain point, particle size in TMRs consumed by cows is sometimes inadequate. The Penn State Particle Size Separator, available from NASCO, is useful to monitor changes in particle size from mechanical treatment and to ensure adequate particle length in TMRs. Less than 40% of the TMR should be recovered in the bottom box following sieving to provide adequate particle length. When more than 10-15% of the TMR is recovered on the top sieve, the TMR will be more subject to sorting. This leaves over 45% on the middle sieve, which provides most of the effective NDF in the diet. Diets containing silages that are chopped too finely can benefit by including 2-3 lb of longchopped hay in the diet to improve the effectiveness of NDF.

- Addition of buffers to the diet can increase the buffering capacity of rumen fluid and help attenuate the reduction in pH following a meal. However, they will not have a great effect on optimal FNDF concentration in the diet.
- Diets with added fat require somewhat less FNDF because fat is not fermented in the rumen to acids. Although fat can be included in diets to increase energy intake beyond what can be attained by diet formulation for carbohydrates, some fat sources have been shown to reduce DMI and might not improve energy intake. In addition, highly fermentable diets containing added fat with polyunsaturated fatty acids might be more prone to reduction in milk fat by production of trans fatty acids in the rumen.
- Grouping cows by milk yield will help increase energy intake because diets can be more closely formulated to meet their needs. High producing cows should be fed low fill diets to maximize energy intake. However, lower producing cows can be offered diets with higher FNDF content which provides the benefit of more consistent supply of fuels throughout the day. A more consistent supply of nutrients might help partition more fuels to milk and help prevent excessive body condition. Wide variation in DMI and milk yield of cows within groups makes it difficult to

optimize FNDF concentration for all cows in the group.

Conclusions

The different factors discussed above are important to formulate diets to maximize energy intake and microbial protein production. The complex interactions among these factors prevent accurate prediction of optimal FNDF concentration for cows or groups of cows. Diets should be formulated by evaluating cow response to dietary changes and adjusting the diet based on this response. Lower FNDF contents will generally allow higher energy intake and higher milk yield. Exceptions are when FNDF is highly fermentable, which will allow higher FNDF contents and higher energy intakes, and when passage rates of NFFS in low FNDF diets are excessive and digestibility is reduced. Diets with low optimal FNDF content will have starch sources that have moderate ruminal fermentation, forage particles that are sufficiently long, moderate to low forage NDF content, be fed as a TMR and have little daily variation. Diets with high optimal FNDF contents will limit energy intake of high producing cows. They will generally have rapidly fermented starch sources, finely chopped forages, no NFFS, limited feed bunk space, infrequent grain feeding and high daily variation. The information presented here can be used to develop a strategy to maximize energy intake and microbial protein production and should be refined with experience.

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