Symposium review: Re-evaluation of National Research Council energy estimates in calf starters*

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ABSTRACT

Provision of nutrients in appropriate amounts to meet nutrient requirements for growth, production, and reproduction is the basis for modern animal nutrition. Ration formulation systems predict nutrient requirements based on numerous inputs and then predict nutrient supply based on predicted intake and nutrient content of feeds. Energy systems are used to predict energy supply based on gross caloric content of feeds followed by adjustments for digestion and metabolism of ingested energy. Many models of energy supply use static coefficients of digestibility based on nutrient composition of feed. Other models partition digestion dynamically between ruminal and postruminal digestion but use static estimates of intestinal digestibility to predict energy supplied to the animal. In young calves, both ruminal fermentation and intestinal digestion are underdeveloped; therefore, existing models of energy supply might overestimate the energy available before complete gastrointestinal maturation. In a series of experiments, we reported that total-tract digestion of nutrients changes with advancing age and nutrient intake. Total-tract digestion was measured in calves from 3 to 16 wk of age when fed different amounts and types of milk replacers. Calves were also fed different types of calf starter for ad libitum consumption. Total-tract digestibility of protein, fat, neutral detergent fiber, and nonfiber carbohydrate (NFC) was used to calculate the metabolizable energy (ME) in starter. We used nonlinear regression to estimate the contribution of protein and fat from starter and milk replacer before weaning. Early in life, calculated ME of starter was low and increased with increasing intake of NFC. Cumulative intake of NFC was more highly correlated with changing ME values than other indices, including

age, intake of milk replacer, or intake of other nutrients in starter. When calves consumed at least of 15 kg of NFC, ME calculated from digestibility measurements was similar to the ME calculated using National Research Council equations and indicated maturation of gastrointestinal digestion. Our data suggest that intake of NFC is critical to gastrointestinal maturation and the calf's ability to extract energy from calf starter.

Key words: calf, energy, rumen, digestibility

INTRODUCTION

Accurate prediction of nutrient supply and nutrient requirements is essential to modern ration formulations and animal production. Accurate and precise models allow provision of nutrients to meet requirements for maintenance, production, and reproduction without supplying excess nutrients that contribute to inefficiency or environmental damage. Most nutrient models predict supply of ME and MP. In many models, flows of nutrients are predicted from endogenous, microbial, and undegraded dietary sources and assume that rumen fermentation influences digestion. Nutrient requirements are usually predicted using factorial calculation of requirements for maintenance (adjusted for environmental and management considerations), growth, pregnancy, and lactation. Only maintenance and growth predictions are used to predict nutrient requirements for calves, with requirements for pregnancy included for primiparous heifers. The publication of *Nutrient Requirements of Dairy Cattle* (7th revised edition) by the National Research Council in 2001 (NRC, 2001) significantly improved methods used to calculate both nutrient requirements and nutrient supply for young calves and heifers. Resulting models for predicting nutrient requirements and allowing formulation of rations are used worldwide.

ESTIMATING ME IN CALF FEEDS

For young calves and heifers, prediction of nutrient supply by NRC (2001) assumes fixed digestibility and metabolizability of energy and protein. For example,

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calculation of ME from milk replacer (**MR**) is assumed to be the caloric content of protein, fat, and lactose adjusted for digestibility and metabolizability:

$$\text{ME (Mcal/kg)} = [(0.057 \times \text{protein \%}) + (0.092 \times \text{fat \%}) + (0.0395 \times \text{lactose \%})] \times 97\% \times 96\%,$$

where 97% = digestibility of nutrients and 96% = metabolizability of digested nutrients. Effects of age and maturation of the intestine with advancing age (particularly in the first 3 wk of age) are unaccounted for, and the user is cautioned that nutrient availability could be overestimated in the first 2 to 3 wk of life (NRC, 2001). However, more recent data (Liang et al., 2016) suggest that even week-old calves are able to efficiently absorb nutrients from high-quality MR.

Metabolizable energy content of calf starters (**CS**) is calculated as the sum of the digestible fractions of NFC, NDF, CP, and fat as described in the 2001 Dairy NRC (NRC, 2001) for adult cattle and corrected for metabolizability of digested energy. Equations were based on data from Weiss et al. (1992) that estimated truly digestible fraction (CP, fat, NDF, and NFC) based on chemical composition of feeds and digestibility estimates from adult cattle. Thus, the prediction of digestible energy (**DE**) is relatively straightforward and can be calculated independent of animal inputs. Then, ME is calculated and adjusted for reduced digestion due to intakes above maintenance. Other models, such as the Cornell Net Carbohydrate and Protein System, also use digestibility estimates to predict DE and ME (Fox et al., 2004; Tylutki et al., 2008) in feeds. For young calves, digestion of neither liquid nor starter feeds is corrected for changing digestibility caused by age, intake, or development of the gastrointestinal tract in these models. Further, changing metabolizability of DE is not factored into models of ME in young calves (Schrama et al., 1992; Arieli et al., 1995).

DIGESTION OF SOLID FEED

Rumen Development and Digestion

Many researchers have evaluated the effect of various compounds on development of epithelial tissue in relation to size and number of papillae and their ability to absorb and metabolize VFA (Flatt et al., 1958; Sander et al., 1959; Tamate et al., 1962). Results of these studies indicate that the primary stimulus to development of the epithelium is VFA, particularly propionate and butyrate (Sander et al., 1959). Milk, hay, and grain added to the rumen are fermented by resident bacteria and contribute VFA for epithelial development.

Plastic sponges and inert particles—both added to the rumen to provide scratch—did not promote epithelial development. Therefore, rumen development (defined as the metabolism by rumen epithelium) is primarily controlled by chemical, not physical, means and is critical to successful weaning. Development of microbial fermentation changes flow of nutrients from the stomach. Before weaning, nutrients are derived primarily from milk protein, butter fat (in whole milk) or animal or vegetable fats (in MR), and lactose. After weaning, nutrients are provided by VFA used in or absorbed from the rumen and microbial protein that increases in flow with increasing dry feed intake (Leibholz, 1975; Quigley et al., 1985).

In young calves, digestibility of dry feeds (concentrates and forages) depends on development of ruminal fermentation and intestinal digestion. This is particularly true of carbohydrates in dry feeds, which are not normal constituents of milk or MR, and, thus, metabolic adaptations are required for proper digestion (Huber, 1969; Baldwin et al., 2004; Guilloteau et al., 2009). On the other hand, milk contains significant amounts of fat and protein; thus, enzyme systems for protein and fat digestion in milk develop early in life (Huber et al., 1961; Huber, 1969; Baldwin et al., 2004; Guilloteau et al., 2009).

Studies have shown that fiber digestion is limited in neonatal calves (Chapman et al., 2016; Hill et al., 2016a, b). Further, pancreatic α -amylase production is low at birth (Siddons, 1968) but increases with age (Huber et al., 1961; Morrill et al., 1970) along with total pancreatic secretion (McCormick and Stewart, 1967), thereby affecting small intestinal digestion of starch (Morrill et al., 1970). Thus, it seems logical to assume that DE and ME available from feed should be dynamic and not static early in life. Because CS typically contain >60% carbohydrates, the dynamic nature of carbohydrate digestibility can significantly affect ME available in CS. Rumen development should have a major effect on the calf's ability to obtain energy from CS.

Gastrointestinal development can also change the site of digestion. Leibholz (1975) monitored digestion of nutrients in calves fed whole milk or MR to weaning at 35 d of age. After weaning, calves were offered a pelleted feed consisting of 58% barley, 20% soybean meal, 15% wheat straw, and 3% molasses, plus vitamins and minerals. The diet contained 15% protein and 13% ADF; we estimated that the diet contained 50% NFC and 2.7 Mcal of ME/kg (NRC, 2001). By 6 wk of age (1 wk postweaning), ADF digestibility was 57% and did not change markedly thereafter. However, the site of ADF digestion changed dramatically with time after weaning as most ADF was digested in the hindgut during the first 4 wk of the trial. The proportion of ADF

digested in the hindgut declined from 63% at 1 wk postweaning to 0.3% by 8 wk after weaning, suggesting that more ADF was fermented in the rumen as the rumen developed with increasing postweaning feed intake.

Several authors have also reported that rumen development changes the nature of protein reaching the intestine, with the proportion of microbial protein reaching the intestine increasing with increasing dry feed intake and weaning (Leibholz, 1975; Quigley et al., 1985). Others (Leibholz, 1978; Lallès et al., 1993) reported that >90% of postweaning starch digestion occurs in the rumen, with only limited amounts occurring in the large intestine. Calves were weaned at 9 to 10 wk of age in the study by Lallès et al. (1993). More recent data (Gilbert et al., 2015) reported that a significant amount of starch entering the small intestine is fermented in veal calves.

Effects of Age and Intake on Total-Tract Digestibility

Differences in growth rate postweaning in calves fed differently preweaning could be due to differences in gastrointestinal development and digestion. Several recent studies indicate that digestion of nutrients from dry feeds varies when calves are fed varying amounts of liquid preweaning.

Terré et al. (2007) fed Holstein bull calves MR at levels typical of conventional feeding (CF; 4 L/d with weaning at 35 d of the study) or an enhanced feeding (EF) program wherein amount of MR was increased to 7 L/d and then reduced to weaning at 35 d. Total starter intake on the CF and EF programs before weaning was 23.8 and 12.6 kg, respectively. Digestion of NDF (derived primarily from wheat middlings, soybean hulls, and wheat distillers grains) was lower in EF calves compared with CF calves (20.3 vs. 34.7%). Because disappearance of NDF is due primarily to ruminal fermentation, it is likely that reduced NDF digestion was due to inadequate or incomplete rumen fermentation in EF calves. Reduced NDF digestibility occurred in EF calves, possibly because of lower rumen pH (5.73 vs. 5.99 for CF calves). Ruminal pH less than approximately 6.0 is associated with impaired ruminal fiber fermentation (Shriver et al., 1986; Allen, 1997) due to pH sensitivity of cellulolytic bacteria in the rumen (Hoover, 1986; Russell and Wilson, 1996). In the study by Terré et al. (2007), the authors attributed higher ruminal pH in CF calves to lower ruminal activity due to lower starter intake and a lack of substrate available for fermentation.

Hill et al. (2010) fed calves (2–3 d of age at start of study) 1 of 4 MR programs: 0.44 kg of DM of a 21% CP, 21% fat MR powder fed daily for 42 d (treatment A); 0.66 kg of DM of a 27% CP, 17% fat MR powder

fed daily for 42 d (treatment B); 0.66 kg of DM of a 27% CP, 17% fat MR powder fed daily for 28 d (treatment C); and up to 1.09 kg of DM of a 29% CP, 21% fat MR fed daily for 49 d (treatment D). Digestibility estimates were made on d 53 to 56. Digestion of DM and OM was lower when calves were fed treatment D. During the digestibility period (d 53–56), DMI was 2.2, 2.3, 2.5, and 1.9 kg/d for treatments A, B, C, and D, respectively. The trend ($P < 0.08$) for lower starter DMI coupled with significantly lower digestion of DM resulted in calves on treatment D consuming only about 71% of the digestible DM of calves on other treatments.

Araujo et al. (2014) fed 66 Holstein calves (12 d of age at start of the trial) either 4 or 6 L/d of MR to 42 d and then 2 or 3 L/d to weaning at 42 d and CS containing 4.1 or 11.2% fat. Apparent digestion of nutrients was measured on d 49 to 55 of the study. Digestion of CP and fat was lower when calves were fed high-fat CS; however, there was no effect of MR feeding level on digestion of DM, CP, or fat.

Most of these data suggest that calves fed large amounts of milk preweaning may have difficulty digesting nutrients from dry feed immediately postweaning. These findings have numerous implications. For example, calves fed elevated MR programs may gain more BW preweaning but gain more slowly postweaning (e.g., Bach et al., 2013). Further, digestion of CS containing greater amounts of fibrous by-products can be difficult if calves are fed large amounts of liquid preweaning. Also, it may be necessary to use increasingly complex liquid reduction strategies to ensure that CS intake (and digestibility) is adequate before weaning. For example, de Passillé et al. (2011) reported that calves fed 12 L of milk/d from an autofeeder until 89 d maintained greater dry feed intake and weight gains at weaning compared with calves fed 12 L of milk/d and weaned at 47 d. Sweeney et al. (2010) also suggested that a 10-d weaning period was superior to abrupt weaning or a weaning period of 4 or 22 d. Dennis et al. (2018a) reported that feeding calves up to 1.1 kg of MR powder/d and weaning gradually from 35 to 53 d resulted in greater NDF and ADF digestion at 84 d compared with calves fed similar amount of MR powder and weaned abruptly at 53 d. However, calves fed 0.66 kg of MR/d to weaning at 42 d had greater postweaning BW gain and nutrient digestion at 84 d. Hill et al. (2012b) concluded that calves fed >0.88 kg of MR powder/d required at least 14 d of weaning transition to maintain BW gain and intake during the postweaning period. Others have also recommended an extended (>10 d) transition period (Khan et al., 2007a; Steele et al., 2017) or delayed age at weaning (Eckert et al., 2015) for calves fed more than approximately 700 to 800 g of milk or MR solids daily. On the other hand,

stepwise weaning strategies were ineffective in improving performance when small differences in feeding rates (e.g., 5.5 vs. 7 L/d to weaning at 60 d) were evaluated (Daneshvar et al., 2017).

Effect of CS Form on Total-Tract Digestibility

Calf starters are often manufactured as pelleted or texturized (pellet plus whole or processed grains such as corn, barley, and oats) feeds, or ingredients can be blended and the mixture offered as a meal without further processing. Effects of ration form on rumen development, intake, and performance have been evaluated; in many cases, however, ingredients varied among treatments so that effect of form was confounded with ingredient and nutrient content.

Porter et al. (2007) fed calves pelleted or textured CS containing the same ingredients and measured apparent total-tract digestibility (TTD) at 7 to 8 wk of age. Calves were weaned at 27 to 29 d of age. The TTD of DM, fat, nitrogen-free extract, and NDF was greater when calves were fed textured CS compared with pelleted CS. Conversely, Nejad et al. (2012) found no difference in TTD of DM, CP, ADF, or NDF when calves were fed pelleted or textured CS, whereas TTD of nutrients was consistently lower when calves were fed a meal CS. Calves were weaned at 41 to 52 d of age, and TTD was measured for the first 5 d postweaning. More recent data from Pazoki et al. (2017) also showed little difference in TTD between diets of similar ingredient composition that were pelleted or textured. However, TTD of DM, OM, and CP in calves fed a meal diet without forage were consistently lower than pelleted or textured CS. Differences between results of these 2 experiments could be attributed to different intakes, ages at weaning, TTD measurements, and diets fed. Increasing total ration particle size has been shown to increase TTD when CS was mixed with 10% forage that was ground to 3 to 4 mm versus 2 mm (Montoro et al., 2013). Further, ground diets might promote low rumen pH, reduced numbers of cellulolytic bacteria, and, potentially, malformation of rumen papillae (McGavin and Morrill, 1976; Beharka et al., 1998). Whole grains in textured feeds may be more effective in supporting rumen health and animal performance compared with highly processed grains (Terré et al., 2015).

Moeini et al. (2017) fed calves diets containing 23% corn and 25% barley with soybean meal (34%) and other ingredients in ground, pelleted, or textured (steam flaked) forms. A fourth treatment included ground diet plus 10% chopped alfalfa hay. Calves were fed whole milk (4 L/d to 42 d; 2 L/d to 49 d) and starter plus water for ad libitum consumption to 70 d. In this study, calves fed diets containing 10% forage had

greater starter intake, final BW, and ADG compared with calves fed pelleted starter. Textured and forage-containing diets had greater feed efficiency. Finally, calves fed added forage had improved indices of rumen and intestinal development, suggesting that sufficient particle size (via provision of 10% forage or textured starter) was important to gastrointestinal development. On the other hand, Bach et al. (2007) reported that calves fed a texturized starter (20% cracked corn, 15% whole oats) consumed more starter compared with calves that were offered the same formula but in pellets only. Calves fed the pellets were more efficient in utilizing nutrients, so ending BW (64 d of the study) was not different (82.7 and 83.6 kg of BW for calves fed pellets and textured CS, respectively). Collectively, these data suggest that the availability of energy from CS is dependent on type of carbohydrate, form of the starter (meal, texturized, or pelleted) and carbohydrate, age of the calf, and intake of liquid preweaning.

Current nutrient models to predict nutrient supply of calves and heifers (e.g., 2001 Dairy NRC) ignore effects of previous nutrition and extent of rumen development. The ME content of CS is a static calculation based on expected digestibility of nutrient fractions (NDF, NFC, CP, and fat). No provision is made for differing nutrient digestibilities with advancing age or intake. Conversely, models for lactating cows use dynamic calculations of energy based on rates of ruminal digestion of each fraction (NFC, NDF, CP, and fat) and rate of passage (Higgs et al., 2015; Van Amburgh et al., 2015). Intestinal digestibility coefficients are then applied to the ruminally undegraded fractions to estimate total nutrient supply.

Effect of Carbohydrate Source on TTD

The 2001 Dairy NRC calculates energy in feeds using a factorial approach with expected digestibilities of CP, fat, NDF, and NFC. However, the NFC fraction is actually made up of several different types of carbohydrates that can have different digestibilities in young calves. Further, the manner in which digestion changes might differ among carbohydrate types, further confounding accurate prediction of energy content of dry feeds with advancing age and gastrointestinal development.

Khan et al. (2007b, 2008) reported differences in animal performance and rumen development in calves fed pelleted CS containing 25% starch and based on wheat, oats, barley, and corn. However, total-tract digestion, measured at 77 to 84 d of age, did not differ among treatments (Khan et al., 2008). Suárez et al. (2006a, b) fed young veal calves CS containing NDF, pectin, starch, or combinations thereof. Differences in diet composition resulted in differences in intake and

growth (Suárez et al., 2006a) as well as rumen size and morphological development at 8 and 12 wk of age (Suárez et al., 2006b). Plasma acetate and BHB were higher in calves fed pectin-containing diets at 8 wk of age but not 12 wk of age.

Dennis et al. (2018b) fed young CS containing 0, 15, or 20% beet pulp to increase pectin concentration from 3 to 7% of ration DM. Starch concentrations in the pelleted rations declined from 44 to 26% of ration DM with increasing beet pulp. Digestion of DM, OM, CP, and starch (measured at 77–84 d) declined with increasing beet pulp, whereas digestion of NDF and ADF increased. Conversely, Laarman et al. (2012) reported minimal effects on animal performance or rumen parameters when beet pulp (10%) replaced corn (10%) in textured CS fed to 11 wk of age. In this study, calves fed CS containing more distillers grains had greater incidence and severity of SARA when measured after weaning (Laarman et al., 2012). Inclusion of 10% beet pulp to replace 10% barley in pelleted starters fed to calves to 70 d tended to increase preweaning rumen pH and growth but had no effect on TTD of DM, CP, or NDF measured during the week prior and 1 wk after weaning at 50 d (Maktabi et al., 2016).

Simple sugars such as glucose or lactose increase butyrate production in the rumen without a significant effect on rumen pH (Chamberlain et al., 1993). However, Saegusa et al. (2017) fed texturized CS containing 0, 5, or 10% lactose and reported no effect on ruminal butyrate concentrations, though increasing lactose increased

molar proportion of acetate and minimum ruminal pH. Others have reported that replacing starch with sugars (e.g., molasses or glucose) increased growth (Atai and Harshbarger, 1965), increased plasma BHB (Inabu et al., 2017), or altered rumen fermentation (Oltamari et al., 2016). Differences in metabolism of carbohydrates categorized as NFC (NRC, 2001) and their effects on changing rates and extent of gastrointestinal development suggest that further refinement of equations to predict energy in dry feeds for calves is required.

EVALUATION OF ME IN CS

Changing digestibility with advancing age, intake of dry feed, and feeding program indicates a need to adjust estimates of ME available from CS based on an index of changing digestive maturity. Recent studies from our laboratory (Table 1) documented changing apparent TTD of nutrients with advancing age and feeding program from 0 to 16 wk of age. In each of these studies, the amount and type of MR offered preweaning varied by treatment. Also, form and composition of CS varied by treatment and experiment. Least squares means of apparent TTD of CP, fat, NDF, and starch from experiments in Table 1 were plotted in Figure 1.

Apparent TTD of total CP generally reflected intake of CP from MR versus CS. Calves fed greater amounts of MR had greater TTD of CP to 8 wk of age; thereafter, CP digestion did not vary markedly from approximately 80%. Decline in CP digestion to 8 wk of age

Table 1. Studies evaluating effects of calf starter carbohydrate source and milk replacer feeding program on total-tract digestibility in young calves

Reference	Starters ¹	Milk replacer ²	Age (no. of observations) ³
Quigley et al., 2018a	High starch (T)	0.66 kg/d	5, 8 wk (20)
	Low starch (P)	Up to 1.1 kg/d	
Dennis et al., 2018a	High starch (T)	0.66 kg/d	5, 7 wk (20)
		Up to 1.1 kg/d	9, 11, 13 wk (12)
Dennis et al., 2018b	0–15% Beet pulp (P)	0.66 kg/d	12 wk (12)
Chapman et al., 2017	High starch (T)	0.45 kg/d	6 wk (24)
		0.67 kg/d	
		0.89 kg/d	
Hill et al., 2016c	High starch (T)	0.66 kg/d	11, 16 wk (12)
		Up to 1.1 kg/d for 23 d	
		Up to 1.1 kg/d for 37 d	
Hill et al., 2016b	High starch (T)	0.66 kg/d	3, 6, 8 wk (20)
		Up to 1.31 kg/d	
Hill et al., 2016a	High starch (T)	0.66 kg/d	10 wk (12)
	Low starch (P)		10 wk (12)
	Soy hulls, middlings, corn (P)		
Chapman et al., 2016	High starch (T)	0.44 kg/d	8 wk (15)
		0.66 kg/d	
		Up to 0.87 kg/d	

¹Calf starters were pelleted (P) or texturized (T) and contained >35% starch (high) or <30% starch (low).

²Amount of milk replacer powder fed to each calf daily. Milk replacers contained 24 to 26% CP, 17 to 19% fat, all milk protein, lard as fat source. Weaning ages varied from 42 to 56 d of the trial.

³Age (weeks) at which digestibility measurements were made and number of observations per measurement period.

Figure 1. Least squares treatment means of apparent total-tract digestibility of CP (a), fat (b), NDF (c), and starch (d) in calves fed approximately 0.66 kg/d (Mod) or >0.9 kg/d (High) of milk replacer powder to weaning at 42 to 49 d of age. Means (n = 39) are from studies outlined in Table 1.

could reflect lower digestibility of CP in CS compared with MR. Similarly, TTD of fat (Figure 1b) declined with advancing age and changing intake of CS and MR. It is likely that declining TTD of fat was due to less digestible fat in CS replacing highly digestible fat in MR. It is unclear whether increasing contribution of microbial protein (and microbial lipid) influenced TTD of fat.

Apparent TTD of NDF (Figure 1c) increased from very low levels at 3 wk of age to >60% in measurements at 16 wk of age. Least squares means were generally higher at similar ages when calves were fed moderate amounts of MR (~0.66 kg of MR powder/d) compared with calves fed >0.9 kg/d. Significant variability in least squares means with advancing age suggests that factors other than MR intake contributed to changing NDF digestion of CS.

Starch digestion in experiments from our laboratory (Figure 1d) show a clear increase from 3 wk to 7 wk, when TTD of starch was >97%. Thereafter, the disap-

pearance of starch in the digestive tract was essentially complete.

Quigley et al. (2019a, b) conducted an analysis of 3 studies (Hill et al., 2016b; Dennis et al., 2018a; Quigley et al., 2018) using individual digestibility measurements (n = 207). Multiple modeling approaches were used (Quigley et al., 2019a), including linear mixed models, exponential models, and broken-line regression models. The model that was consistently most predictive of changing nutrient digestibility in CS was the linear mixed model, calculated using procedures outlined in St. Pierre (2001). Quigley et al. (2019a, b) estimated ME in CS by measuring apparent TTD of CP, fat, NDF, and starch. Before weaning, the authors used nonlinear regression procedures to partition the contribution of CP and fat from MR and CS. Also, NFC digestion was estimated by assuming that sugar TTD = 96% and TTD of starch plus pectins was equal to starch digestibility. The authors calculated DE using the equation (NRC, 2001)

$$\text{DE (Mcal/kg)} = \text{dNFCcs} \times 4.2 + \text{dNDFcs} \times 4.2 \\ + \text{dCPcs} \times 5.6 + \text{dFATcs} \times 9.4,$$

where dNFCcs = TTD of NFC from CS; dNDFcs = TTD of NDF from CS; dCPcs = TTD of CP from CS; and dFATcs = TTD of fat from CS. Then, ME was calculated as follows:

$$\text{ME (Mcal/kg)} = (1.01 \times \text{DE} - 0.45) \\ + [0.0046 \times (\text{ether extract} - 3)].$$

Calculated ME in CS increased with increasing age and CS intake. However, the authors (Quigley et al., 2019a, b) reported that cumulative intake of NFC from CS was more highly correlated with changing TTD of most nutrients and calculated ME than other measures. Cumulative intake was defined as consumption of a nutrient from the beginning of the trial (d 0) until the end of the digestibility measurement period. Age of calf, intake of MR, and daily intake of nutrients were not as highly correlated with changing digestion or calculated ME (Quigley et al., 2019b). This is an interesting observation, as rumen development is promoted by availability of fermentable carbohydrate, which is consistent with consumption of NFC from CS. However, the fact that cumulative rather than daily intake of NFC was more related to changing TTD suggests that effects of carbohydrate fermentation in the rumen are cumulative. Thus, managing calves to promote early and consistent consumption of CS might be advantageous. Further,

proper weaning strategy to promote consistent increases in CS intake before weaning is critical to postweaning growth. Calves weaned abruptly from high amounts of MR often have eaten little CS before weaning. Rapid increases in CS intake following weaning in these calves do not allow for proper nutrient utilization as rumen development was insufficient to allow the calf to extract sufficient ME from the CS as predicted by the NRC (Dennis et al., 2018a; Quigley et al., 2018). Quigley et al. (2019b) calculated that 15 kg of cumulative NFC was needed for sufficient digestive maturation to allow the calf to obtain ME from CS. Ratio of ME in CS (MEcs; calculated using TTD measures) divided by ME calculated using NRC (2001) equations (MENrc) was calculated to determine the point at which ME predictions were equivalent to ME predicted using NRC equations. When calves consumed ≥ 15 kg of cumulative NFC, the MEcs:MENrc ratio was 1.0 (Figure 2). Calves were ≥ 51 d of age when they consumed at least 15 kg of NFC in each of the 3 studies in the database. Also, the MEcs:MENrc ratio was constant and approximately 1.0 when calves consumed ≥ 15 kg of NFC, suggesting that the NRC equations were satisfactory after rumen function was mature.

Before consumption of about 15 kg of NFC, the ME provided by the diet was overestimated using the NRC model of nutrient supply. It may be possible to use the MEcs:MENrc ratio to adjust existing estimates of ME for incomplete rumen development, thereby allowing more accurate estimate of actual nutrient supply and energy available for growth.

Figure 2. Ratio of calculated ME (Mcal/kg) using total-tract digestibility measurements divided by ME (Mcal/kg) using NRC equations (NRC, 2001) from 3 trials ($n = 207$). Calves were fed a pelleted (PEL) or texturized (TEX) calf starter to 8 wk of age and then the same starter plus grass hay in a 95:5 ratio (TMR). From Quigley et al. (2019b).

Feeding large amounts of milk or MR will delay initiation of starter intake and amount of CS NFC consumed by the calf. Formulation of CS has a profound effect on cumulative NFC intake and preparation for weaning. It is less clear whether the type of NFC (e.g., sugar, starch, pectins) will differentially influence the rate of rumen development and preparation for weaning. Sugar added to CS alters rumen VFA concentrations in young calves and might support higher rumen pH concentrations (Saegusa et al., 2017) and increase plasma BHB (Beiranvand et al., 2014b; Inabu et al., 2017), suggesting improved butyrate absorption from the rumen. However, animal performance in these studies has generally not been affected by inclusion of sugar in the ration. High concentrations of starch that are rapidly fermented in the rumen (e.g., pelleted or ground starters) might result in lower rumen pH, changes in ruminal digestion, and lower animal performance (Pezhveh et al., 2014) compared with CS containing whole grains. Thus, selection of type of carbohydrate, form, and processing of carbohydrate likely all contribute to degree of rumen development and preparation for weaning. Hill et al. (2012a) concluded that high-starch textured diets supported greater intake and growth than CS in meal form. Fiber from fibrous concentrates and roughages reduced calf performance and should be introduced slowly to calves less than 4 mo of age.

Formulas containing greater amounts of NDF will contribute less NFC and thus delay the time at which calves are prepared for weaning. Also, inclusion of forage in the diet reduces NFC intake, as most forages (e.g., hay) contribute little NFC. However, the importance of rumen health (Beiranvand et al., 2014a), proper rumen fermentation, and DMI are not included in the calculations by Quigley et al. (2019b). Further research is needed to determine the role that ration particle size and rumen pH play in promoting DM (and thus NFC) intake and preparedness for weaning.

SUMMARY

The 2001 Dairy NRC represented an important improvement in our understanding of nutrient requirements for young calves and heifers. However, static estimates of ME in CS based on chemical composition of ration ingredients do not reflect changing nutrient digestion with advancing gastrointestinal maturation. Early in life, contribution of ME in CS could be overestimated, as the calf is unable to effectively digest nutrients (especially carbohydrates) to extract ME from CS. Dynamic models are needed to better predict the changing TTD with gastrointestinal development. Further refinement of methods to estimate nutrient supply of young calves will improve our ability to calculate

growth under a wide range of feeding and management conditions.

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