Estimates of calf starter energy affected by consumption of nutrients. 2. Effect of changing digestion on energy content in calf starters

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ABSTRACT

Apparent total-tract digestibility data from 3 published studies with calves from 0 to 4 mo of age were used to evaluate National Research Council (NRC; 2001) estimates of digestible energy (DE) and metabolizable energy (ME) in calf starters (CS). Calves ($n = 83$) or pens of calves ($n = 24$) were used in model development. In each study, 48 Holstein bull calves (2–3 d of age at initiation of each study) were fed varying amounts of milk replacer with CS and water for ad libitum consumption. Calf starters varied in nutrient composition and physical form (pelleted, textured, or mixed with 5% grass hay and fed as a total mixed ration). Apparent total-tract digestibility was measured at various ages. Feed and feces were collected from 20 calves per trial during 5-d collection periods during the first 56 d of each trial. In 2 studies, calves were grouped in pens (4 calves/pen) for a second 56-d measurement period. Fecal collections were repeated occasionally during the second period. Total-tract digestibilities ($n = 207$) of neutral detergent fiber, nonfiber carbohydrates (NFC), crude protein (CP), and fat were used to calculate ME in CS using equations from the 2001 Dairy NRC. Contributions of digestible CP and fat from milk replacer before weaning were estimated using nonlinear regression and removed from estimates of fat and CP digestibility in CS. Digestion of most nutrients in CS and calculated DE and ME in CS were low early in life and increased with increasing cumulative NFC intake. The natural logarithm of cumulative NFC intake, measured from d 0 to the end of each digestibility period, accounted for more variation in CS nutrient digestibilities, DE and ME estimates compared with daily NFC intake or intake of other nutrients, intake of milk replacer, or age of calf. Calculated ME values in CS were similar to those predicted by NRC after calves consumed approximately 15 kg of cumulative NFC or 28 kg of cumulative dry matter intake (assuming 53%

NFC in CS). Current estimates of energy in CS fed to 4 mo of age may overestimate contribution of dry feed to overall energy metabolism in young calves.

Key words: calf, digestion, energy, modeling

INTRODUCTION

Young dairy calves undergo fundamental changes in the source of nutrients in the first months of life. Maturation of the gastrointestinal tract, including development of fermentative capacity of the reticulorumen, occurs as calves transition from a diet consisting solely of highly digestible colostrum and milk to a postweaning diet consisting primarily of cereal grains and forages (Baldwin et al., 2004; Blum, 2006; Guilloteau et al., 2009). Fermentation of carbohydrates early in life initiates rumen development, which accelerates the time at which calves are prepared for weaning (Warner et al., 1956; Sander et al., 1959).

Energy available from dry feed depends on the caloric content of digestible nutrients and metabolizability of digested energy (NRC, 2001). The extent to which young calves use nutrients from dry feed before and immediately after weaning is not well defined. Studies have reported that digestion of nutrients, but particularly of carbohydrates (including NDF and NFC) are low in very young calves (Terré et al., 2007; Hill et al., 2016b; Chapman et al., 2016; Quigley et al., 2018). The ability to use fibrous feed components depends on development of ruminal fermentation (Hibbs et al., 1956; Stobo et al., 1966), whereas utilization of nonfibrous components such as starch depends on ruminal fermentation as well as intestinal digestion (Harmon et al., 2004; Nozière et al., 2010).

Prediction of digestible energy (DE) and ME in dry feed in current models (NRC, 2001) assumes nutrient digestion in calves is similar to the capacity of mature cows. However, recent research (Terré et al., 2007; Hill et al., 2016b; Dennis et al., 2017, 2018; Quigley et al., 2018) suggests that digestibility of nutrients in calf starter (CS), but particularly of starch and NDF, is poorly developed in young calves and increases with increasing age and CS intake. Further, delayed CS in-

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take due to high levels of preweaning liquid intake may impair nutrient digestion from dry feed (Terré et al., 2007; Hill et al., 2010; Chapman et al., 2016).

Equations to calculate dietary energy in current models of nutrient requirements for calves (NRC, 2001) do not reflect changing digestibility in young calves and, therefore, may overestimate the contribution of CS and other dry feeds to total nutrient supply in the first 4 mo of life. Objective of this study was to evaluate methods to calculate energy values of dry feeds (NRC, 2001) fed to young calves during the first 4 mo of life utilizing estimates of total-tract nutrient digestion.

MATERIALS AND METHODS

Calves and Management

Apparent total-tract digestibility (**TTD**) of nutrients was measured during 3 experiments (Table 1) published previously (Hill et al., 2016b; Dennis et al., 2018; Quigley et al., 2018). In each experiment, 48 newborn Holstein bull calves were transported to the experimental facility and assigned to treatments at 2 to 3 d of age for 56 (trial 1) or 112 d (trials 2 and 3). Calves were housed in individual pens from 0 to 56 d (trial 1, 2a, 3a). In experiments 2 and 3, calves were randomized within treatment on d 57 and moved to group pens (4 calves/pen) for a second 56 d (trials 2b and 3b). Publication of trial 2 (Quigley et al., 2018) only included trial 2a; trial 2b used the same animals and treatments as in trial 2a. Calf was the experimental unit in trials 1, 2a, and 3a, and pen was the experimental unit in trials 2b and 3b. Experimental treatments and animal management are described elsewhere (Hill et al., 2016b; Dennis et

al., 2018; Quigley et al., 2018). In each experiment, a subset of 5 calves/treatment (trials 1, 2a, and 3a) or all pens (trials 2b and 3b) were used for digestibility measurements. Samples of feed and feces were collected daily and composited during each 5-d digestibility measurement period. Fecal samples ($n = 4/\text{pen}$) were collected from group pens and representatively sampled to produce one daily composite. Before weaning, chromic oxide (Hill et al., 2016b) was added to milk replacer (**MR**) and used as a digestion marker. After weaning, feed and fecal concentration of acid insoluble ash (Van Keulen and Young, 1977) was used to estimate digestibility. Each trial used 4 experimental treatments that included varying MR feeding programs, volumes of MR fed, and ages at weaning. Two treatments (Quigley et al., 2018) used high-fiber (NDF = 37% of DM) pelleted CS (**PEL**) from 0 to 56 d; all other treatments from 0 to 56 d used high-starch (starch = 37 to 43% of DM) texturized CS (**TEX**). No forage was fed from d 0 to 56. From 57 to 112, CS was mixed with moderate quality chopped grass hay in the ratio of 95:5 in trials 2b and 3b (TMR). Ingredient and nutrient contents of experimental feeds are in Table 2.

Daily intakes of MR and CS were measured by calf (trials 1, 2a, and 3a) or pen (trial 2b and 3b) and calculated as amount offered minus refusal after 24 h. Average daily dry feed intake during the digestion period and cumulative dry feed intake from the beginning of the trial (d 0) through the end of the digestion period were calculated. For trials 2b and 3b, daily dry feed intake was calculated as total intake per pen divided by number of calves per pen. Cumulative dry feed intake was calculated as sum of intake for d 0 to 56 for all calves in a pen during trials 2a and 3a plus total intake

Table 1. Description of experiments

Item	Trial				
	1	2a	2b	3a	3b
Days of study	0 to 56	0 to 56	57 to 112	0 to 56	57 to 112
Experimental units ¹	20	20	12	19	12
Treatments ²	4	4	4	4	4
A	MOD NT+		MRM PEL		MOD6
B	MOD NT−		MRH PEL		HIGH6
C	AGG NT+		MRM TEX		HIGH8
D	AGG NT−		MRH TEX		GRAD8
Digestion periods, wk	3, 6, 8	5, 8	11, 13, 16	5, 7, 8	11, 15
No. of observations	60	40	36	47 ³	24
Reference	Hill et al., 2016b	Quigley et al., 2018	Unpublished data	Dennis et al., 2018	

¹Experimental units were calf in trials 1, 2a, and 3a, and pen ($n = 4$ calves/pen) in trials 2b and 3b.

²Treatments: trial 1: MOD = 0.66 kg of milk replacer DM to weaning at 49 d; AGG = 0.66 kg of milk replacer DM up to 1.31 kg and weaned at 49 d; NT+ = inclusion of functional fatty acids in milk replacer; NT− = absence of functional fatty acids in milk replacer. Trial 2: MRM = 0.66 kg of milk replacer DM/d and weaned at 49 d; MRH = 0.85 up to 1.07 kg of milk replacer DM/d and weaned at 49 d; PEL = high fiber, pelleted calf starter; TEX = high starch, texturized calf starter. Trial 3: MOD6 = 0.66 kg of milk replacer DM/d and weaned at 42 d; HIGH6 = up to 1.09 kg of milk replacer DM/d and weaned at 42 d; HIGH8 = up to 1.09 kg of milk replacer DM/d and weaned at 53 d; GRAD8 = up to 1.09 kg of milk replacer DM/d and gradually weaned from d 35 to 53.

³Digestion data were collected for only 10 calves during wk 7.

of the pen from d 57 to the end of the digestion period. This value was then divided by number of animals in each pen to determine per animal averages.

Description of experiments and experimental units used in model development are in Table 1. Ingredient and nutrient content of diets are in Table 2. Milk replacers fed in trials 1, 2a, and 3a were all-milk protein source with lard as primary fat source. Crude protein concentrations were 27.7, 25.1, and 24.9% of DM for trials 1, 2a, and 3a, respectively, and crude fat concentrations were 18.2, 18.6, and 17.9%, respectively. High-starch (>37% of DM) TEX were used in trials 1 and 3 and in 2 of 4 treatments in trial 2. Hay used in TMR in trial 2b contained 10.3% CP and 67.5% NDF, whereas hay in trial 3b contained 6.9% CP and 63.5% NDF.

Model Development and Evaluation

Digestible nutrients in CS were calculated by multiplying the TTD of each nutrient by content of the nutrient in CS. Digestible NFC fraction in CS (**dNFCcs**)

was calculated as [sugar in CS (% of DM) $\times$ 96%] + [SSF (% of DM) $\times$ starch digestibility], where SSF = starch + soluble fiber, calculated as NFC – sugar. Digestibility of sugar was not measured and was assumed to be 96%.

Digestible energy (Mcal/kg of DM; **DEcs**) and ME (Mcal/kg of DM; **MEcs**) in CS were calculated using equations from NRC (2001):

$$\begin{aligned} \text{DEcs (Mcal/kg)} &= (\text{dNFCcs}/100) \times 4.2 \\ &+ (\text{dNDFcs}/100) \times 4.2 + (\text{dCPcs}/100) \times 5.6 \\ &+ (\text{dEEcs}/100) \times 9.4, \text{ and} \\ \text{MEcs (Mcal/kg)} &= (1.01 \times \text{DEcs} - 0.45) \\ &+ 0.0046 \times (\text{fat in CS} - 3), \end{aligned}$$

where dCPcs = digestible CP in CS; dEEcs = digestible ether extract in CS; and dNDFcs = digestible NDF in CS.

Table 2. Ingredient and nutrient composition of diets used in trials 1 to 3

Feed type	Trial 1	Trial 2a		Trial 2b		Trial 3a	Trial 3b
	Textured	Pellet	Textured	TMR1	TMR2	Textured	TMR
Ingredient, % as fed							
Corn, whole	37.0		37.0		35.2	37.0	35.2
Oats, oats	25.0		25.0		23.8	25.0	23.8
Soybean meal	23.1	18.0	23.9	17.1	22.7	23.1	21.9
Molasses	3.0	2.5	3.0	2.4	2.9	3.0	2.9
Soybean hulls		41.3		39.2			
Wheat middlings	7.7	30.0	5.6	28.5	5.3	7.7	7.3
Alfalfa meal			0.7		0.7		
Fat		2.0	0.3	1.9	0.3		
Additives ¹	4.2	6.2	4.5	5.9	4.3	4.2	4.0
Grass hay				5.0	5.0		5.0
Nutrient							
DM, %	88.40	87.70	86.30	88.46	87.70	87.50	87.77
Ash, % of DM	7.30	6.98	6.42	7.68	7.90	6.30	6.28
OM, % of DM	92.70	93.02	93.58	92.32	92.10	93.70	93.73
CP, % of DM	21.20	17.30	18.10	19.52	20.66	20.80	20.11
ADF, % of DM	5.90	21.30	4.57	26.99	9.04	6.70	8.48
NDF, % of DM	12.90	36.90	13.30	43.47	16.20	15.30	17.71
Sugar, % of DM	6.70	5.90	7.90	6.02	7.35	6.10	6.01
Starch, % of DM	43.00	9.90	41.30	9.95	38.16	37.30	35.47
Fat, % of DM	3.90	4.30	3.50	4.47	3.90	3.60	3.50
NFC, % of DM	55.79	36.19	58.54	27.18	52.43	54.73	54.12
Lignin, ² % of DM	2.00	2.38	1.97	2.64	2.26	2.21	2.39
NDFIP, ^{2,3} % of DM	1.09	2.41	1.06	2.86	1.64	1.40	1.70
ADFIP, ^{2,3} % of DM	0.32	0.64	0.33	0.68	0.40	0.36	0.40
TDN, ⁴ % of DM	80.4	73.7	80.6	71.1	79.3	80.6	78.9
DE, ⁴ Mcal/kg of DM	3.66	3.33	3.63	3.25	3.61	3.67	3.59
ME, ⁴ Mcal/kg of DM	3.25	2.92	3.22	2.84	3.21	3.26	3.18

¹Additives included Ca carbonate, vitamin premix, trace mineral premix, salt, monocalcium phosphate, premix containing decoquinat (Zoetis, Kalamazoo, MI), Mg oxide, premix containing ionophore, limestone, maltodextrin, premix containing diflubenzuron (Clarify, Central Life Sciences, Schaumburg, IL), and binder.

²Nutrient content was estimated using nutrient content of each ingredient.

³NDFIP = neutral detergent insoluble protein; ADFIP = acid detergent insoluble protein.

⁴Energy values at 1 $\times$ maintenance; calculated as in NRC (2001). DE = digestible energy.

Estimates of ME in CS at each digestibility period were also calculated using NRC (2001) equations (**ME_{nrc}**). Calculated ME_{nrc} was not corrected for depression of ME with intakes above maintenance. Ratio of ME_c to ME_{nrc} (**ME_{ratio}**) was calculated to estimate the time at which estimates of ME_c were similar to ME_{nrc}. An ME_{ratio} of 100% indicated that ME_c was equivalent to ME_{nrc}, suggesting that the ability of the calf to extract ME from CS approached that predicted by NRC (2001).

Before weaning, TTD of CP and fat was partitioned between MR and CS using Proc NLIN in SAS (version 8, SAS Institute Inc., Cary, NC). Models to estimate CP and ether extract (**EE**) digestibility from MR were

$$\text{CPD} = \text{dCP}_{\text{mr}} \times \text{mrCP} + \text{dCP}_{\text{cs}} \times \text{csCP}, \text{ and}$$

$$\text{EED} = \text{dEE}_{\text{mr}} \times \text{mrEE} + \text{dEE}_{\text{cs}} \times \text{csEE},$$

where CPD = TTD of CP; dCP_{mr} = digestibility of CP in MR; mrCP = percent of CP intake from MR; dCP_{cs} = digestibility of CP in CS; csCP = percent of CP in the diet from CS; EED = TTD of EE; dEE_{mr} = digestibility of EE in MR; mrEE = percent of EE intake from MR; dEE_{cs} = digestibility of EE in CS; csEE = percent of EE in the diet from CS. Coefficients for dCP_{mr} and dEE_{mr} were generated for trials 1, 2a, and 3a, averaged across trial, and 1 value (81.8% for dCP_{mr}; 96.8% for dEE_{mr}) was used to estimate digestible nutrient contributions from MR before weaning. We assumed no contribution of NDF or starch from MR. A sensitivity analysis was conducted for variations in dCP_{mr} and dEE_{mr} by individually adjusting values for dCP_{mr} and dEE_{mr} from 60 to 100% and calculating the average ME_c for all observations where MR was fed.

Chemical composition of feeds was determined as in Hill et al. (2016b), Dennis et al. (2018), and Quigley et al. (2018). However, lignin, neutral detergent insoluble protein, and acid detergent insoluble protein were not measured as part of any study. Therefore, these values were estimated based on ingredient composition of CS and tabular values in the NRC feed library (NRC, 2001). Nutrient content of TMR offered during trials 2b and 3b was calculated as 95% × nutrient in concentrate + 5% × nutrient in grass hay (Table 2).

Statistical Models

Several statistical models were evaluated and linear mixed models were selected to describe the data (Quigley et al., 2019). Briefly, cumulative NFC intake from CS (**ccsNFCI**) or natural logarithm of ccsNFCI (**lncc-**

sNFCI), CS form (PEL, TEX, or TMR), and form × NFC intake interaction were included as independent variables. Form of starter was included as a fixed effect in the model. Data were analyzed using Proc Mixed of SAS. Age (wk) and MR intake were also evaluated as independent variables. Trial was included in all models as a random effect. Models were reduced when random covariance or random slope were not significant (St-Pierre, 2001). Values in all figures were adjusted as outlined in St-Pierre (2001). Models were constructed for all data (n = 207), during d 0 to 56 (n = 147) and d 57 to 112 (n = 60).

Because ME_{ratio} was more highly related to natural logarithm of cumulative DMI compared with lnccsNFCI, we also evaluated the relationship between ME_{ratio} and cumulative DMI using a similar modeling approach (St-Pierre, 2001).

RESULTS

A total of 207 individual 5-d digestibility measurements were used in the data set, including 147 observations from 83 calves from 0 to 56 d and 60 observations from group pens during d 57 to 112. Least squares means of average CS intake during each 5-d digestibility period are shown in Table 3. Apparent TTD of DM, OM, CP, EE, NDF, ADF, and starch were measured at various ages; descriptive statistics are shown in Table 4. Individual treatment least squares means of TTD within study are available elsewhere (Hill et al., 2016b; Dennis et al., 2018; Quigley et al., 2018).

Natural logarithm of cumulative NFC intake was most highly related to dDM_c, dNFC_c, DE_c, and ME_c. The ME_{ratio} was most highly correlated with natural logarithm of cumulative DMI (Quigley et al., 2019).

Models containing multiple independent variables, including MR intake or age of calf, did not significantly improve explanation of dependent variables (data not shown). Therefore, lnccsNFCI was used as the sole independent variable in further model development. Model evaluation statistics using lnccsNFCI and CS form as independent variables are shown in Table 5. Graphic presentation of TTD of DM, CP, EE, NDF, and NFC are shown in Figure 1. Generally, CS form or interaction of form × lnccsNFCI interactions were significant for TTD measurements (Table 5). For DE_c, ME_c, and ME_{ratio}, we also evaluated effects of lnccsNFCI on all data (n = 207), as well as during d 0 to 56 (trials 1a, 2a, and 3a; n = 147) and during d 57 to 112 (trials 2b and 3b; n = 60). Relationship between calf starter DE_c and lnccsNFCI for all data are shown in Figure 2a and d 0 to 56 are in Figure 2b. Similar relationships

Table 3. Least squares means of calf starter intake in calves fed varying amounts of milk replacer and calf starter during each digestion period

Trial	Week	Treatment ¹				SE	P-value ²		
		A	B	C	D		Week	Trmt	W × T
Trial 1	3	0.18	0.08	0.25	0.08	0.121	0.001	0.17	0.50
	6	0.71	0.33	0.56	0.31	0.121			
	8	1.92	1.58	1.84	1.80	0.121			
Trial 2a	5	0.37	0.19	0.24	0.16	0.144	0.001	0.20	0.40
	8	2.08	1.60	2.02	1.72	0.144			
Trial 2b	11	2.93	2.57	2.56	2.78	0.168	0.001	0.05	0.10
	13	3.40	3.27	2.73	3.32	0.168			
	16	4.71	4.26	3.83	4.02	0.168			
Trial 3a	5	0.63	0.18	0.20	0.19	0.103	0.001	0.001	0.09
	7	1.91	1.34			0.103			
	8	2.78	2.17	1.92	1.97	0.103			
Trial 3b	11	2.98	2.81	3.01	2.98	0.236	0.001	0.71	0.51
	15	3.50	3.59	3.81	3.98	0.236			

¹Treatments: trial 1: A = 0.66 kg of milk replacer DM to weaning at 49 d (MOD) + inclusion of functional fatty acids in milk replacer (NT+); B = MOD + absence of functional fatty acids in milk replacer (NT-); C = 0.66 kg of milk replacer DM up to 1.31 kg and weaned at 49 d (AGG) + NT+; D = AGG + NT-; trial 2: A = 0.66 kg of milk replacer DM/d and weaned at 49 d (MRM) + high fiber, pelleted calf starter (PEL); B = MRM + high starch, texturized calf starter (TEX); C = 0.85 up to 1.07 kg of milk replacer DM/d and weaned at 49 d (MRH) + PEL; D = MRH + TEX; trial 3: A = 0.66 kg of milk replacer DM/d and weaned at 42 d; B = up to 1.09 kg of milk replacer DM/d and weaned at 42 d; C = up to 1.09 kg of milk replacer DM/d and weaned at 53 d; D = up to 1.09 kg of milk replacer DM/d and gradually weaned from d 35 to 53.

²Probability of a significant effect of week, treatment (Trmt), and week × treatment interaction (W × T).

for MEcs and MERatio are shown in Figures 3a and 3b, and 4a and 4b, respectively.

Effects of varying dCPmr and dEEmr on MEcs are shown in Table 6. As predicted digestibility of CP and EE in MR increased, predicted digestibility of CP and EE in CS decreased, thereby reducing prediction of energy values in CS.

The MERatio was more highly related to the natural logarithm of calf starter DMI (**lnccsDMI**) rather than lnccsNFCI. Therefore, we conducted a similar analysis using MERatio as a dependent variable and lnccsDMI as an independent variable.

DISCUSSION

Rumen development is critical to the calf's ability to use nutrients postweaning. Calves lack the ability to ferment ration components to VFA at birth; this capacity develops with fermentation of ingested carbohydrates to butyrate and propionate that induce changes in rumen papillae and initiate rumen development (Warner et al., 1956; Sander et al., 1959; Stobo et al., 1966). Thus, estimates of energy in CS in young calves should consider rumen development and changing digestion with advancing gastrointestinal maturity. Further, very young calves lack the ability to use starch (Morrill et al., 1970; Guilloteau et al., 1984). Starch utilization appears to be related more to age of the calf rather than intake of starch per se (Guilloteau et al., 2009), although production of amylase appears to be influenced by weaning (Zabielski et al., 1999). Because

many CS contain significant amounts of starch and NFC, changing NFC digestion should be important to prediction of DE and ME in feeds.

It is noteworthy that cumulative intake of NFC was most highly related to digestibility of most nutrients and to MEcs in our data. Digestion of NDF was highly related to both NDF and NFC intakes. Calf starters generally contain ≥60% carbohydrates; therefore, utilization of carbohydrates is essential to the animal's ability to derive energy from CS. Most of the CS used in these studies were texturized (pellet plus whole corn and whole oats), containing approximately 40% starch and 6 to 8% sugar. Thus, digestion of NFC would profoundly affect availability of energy from these feeds. Most of the variation in dNFCcs (Figure 1e) was explained by lnccsNFCI, particularly during the first 56 d of each study when calves were fed no forage (R^2 of regression of dNFCcs to lnccsNFCI = 0.85 and 0.71 for TEX and PEL diets, respectively; Figure 1e). On the other hand, digestibility of most nutrients did not change markedly when calves were fed TMR during d 57 to 112 (trials 2b and 3b), although Hill et al. (2016a) reported that digestion of DM and NDF increased by 10 and 30% between 11 and 16 wk. However, TTD of CP (Figure 1b) and particularly NDF (Figure 1d) increased from d 57 to 112, possibly due to continued maturation of the rumen and improved fiber digestion with increasing rumen size and intake of more fiber in the TMR.

Previously, we reported that digestion of NFC and NDF increased with increasing cumulative intake of

NFC and NDF, respectively (Quigley et al., 2018). These data were included in this analysis as trial 2a. This finding suggests that cumulative exposure to fermentable carbohydrate may be an important criterion for determining maturation of the gastrointestinal tract in general and the rumen in particular and is consistent with current theories regarding the importance of fermentable carbohydrate to initiate rumen development (Baldwin et al., 2004; Khan et al., 2016).

Calculated DEcs and MEcs increased with increasing NFC intake and varied by ration form (Table 5 and Figures 2 and 3). Apparently, much of the CS form effect was due to differences between TMR fed during the grower period (d 57 to 112) and either PEL or TEX

fed during the first 56 d of the trial. Effect of CS form during the first 56 d (PEL vs. TEX) was not significant in predicting MEcs (Figure 3b), suggesting that form of CS was less important than NFC content per se during the first 56 d. However, the number of observations of calves fed PEL diets ($n = 20$) was limited and additional data are required to determine whether form of CS may influence availability of ME from CS. During the period of d 57 to 112, TTD of NDF from the TMR increased from approximately 50 to 60% (Figure 1d), thereby increasing MEcs (Figure 3a) from CS.

The MERatio was calculated to determine the time at which MEcs met or exceeded MENrc. In this analysis, MERatio (Figure 4a) varied by ration form. The MERatio increased with increasing ccsNFCI when calves were fed PEL or TEX (Figure 4b) during the first 56 d. However, there was no apparent effect of TMR on MERatio during d 57 to 112. It should be noted that MENrc in our analysis was not adjusted for depression in digestibility with intakes above maintenance.

The MERatio reached approximately 100% when calves consumed at least 15 kg of NFC (Figure 4b). This suggests that MENrc overestimated the energy available in CS until gastrointestinal development matured, which may have occurred at approximately 15 kg of cumulative NFC intake. When calves were fed the TMR during d 57 to 112, MERatio was similar to 100%, suggesting that calf starter ME predicted using NRC (2001) equations accurately predict ME in TMR containing CS and 5% forage.

When calves consumed a TEX containing 55% NFC, 15 kg of NFC equated to 27 kg of total CS intake (DM basis), or approximately 30 kg of CS on an as-fed basis. In cases where calves are fed higher amounts of MR preweaning and cumulative NFC intake is delayed, reduced MERatio may contribute to observed reduction in postweaning BW gain (Chapman et al., 2016; Hill et al., 2016b). Average ages at which MERatio = 100% (i.e., intake of ccsNFCI ≥ 15 kg) varied by trial and treatment. Trial 1 ended at 56 d and only calves on treatment A consumed 15 kg of ccsNFCI before the end of the study (d 54). Other calves did not reach ccsNFCI = 15 kg by the end of the study. For trial 2, ages were 57, 63, 51, and 58 d for treatments A, B, C, and D, respectively. For trial 3, ages were 51, 57, 58, and 59 d, respectively.

A common recommendation is to wean calves when CS intake reaches a specific criterion such as consumption of at least 1 kg of CS/d for 1 or more days (Quigley, 1996; Greenwood et al., 1997). Our data suggest that both intake and digestibility are essential considerations in preparation for weaning. Our data suggest that cumulative intake may be a more appropriate cri-

Table 4. Mean apparent total-tract digestibility (%) in calves fed treatments in trials 1 to 3¹

Item	n	Mean	SE	Minimum	Maximum
Trial 1					
DM	60	81.6	0.81	68.6	90.8
OM	60	82.7	0.78	69.7	91.7
CP	60	74.2	1.03	54.3	89.4
Fat	60	90.0	0.96	62.6	98.9
ADF	60	10.3	1.10	0.7	43.4
NDF	60	16.8	1.40	1.5	54.0
Starch	60	74.6	2.54	38.2	99.8
Trial 2a					
DM	40	76.7	1.19	54.3	89.9
OM	40	77.4	1.16	57.0	90.4
CP	40	74.1	1.39	39.3	87.2
Fat	40	89.6	0.76	76.1	97.2
ADF	40	32.1	4.00	0.1	78.1
NDF	40	41.7	3.06	0.4	75.8
Starch	40	79.7	3.62	0.1	99.3
Trial 2b					
DM	36	78.9	0.89	66.4	88.2
OM	36	79.7	0.91	66.9	89.2
CP	36	81.8	0.69	73.3	89.9
Fat	36	86.6	0.61	77.8	92.3
ADF	36	55.0	2.64	12.3	75.2
NDF	36	57.4	2.84	10.6	76.6
Starch	36	96.8	0.32	92.3	100.0
Trial 3a					
DM	47	84.4	0.63	72.0	94.7
OM	47	85.1	0.61	73.0	95.0
CP	47	81.2	0.73	65.8	92.4
Fat	47	86.8	1.07	73.2	98.3
ADF	47	32.3	2.56	1.4	62.3
NDF	47	38.0	3.45	0.0	70.1
Starch	47	79.3	3.17	43.1	99.6
Trial 3b					
DM	24	83.0	0.38	77.5	86.5
OM	24	84.3	0.36	80.3	88.5
CP	24	84.4	0.47	80.0	88.5
Fat	24	82.1	0.62	75.5	87.7
ADF	24	62.7	1.02	52.1	71.4
NDF	24	62.5	0.97	49.9	70.5
Starch	24	94.2	0.41	90.5	98.1

¹Total-tract digestion was measured at 3, 6, and 8 wk (trial 1); 5 and 8 wk (trial 2a); 11, 13, and 16 wk (trial 2b); 5, 7, and 8 wk (trial 3a); and 11 and 15 wk (trial 3b).

Table 5. Estimates of ME at production intake (MEcs, Mcal/kg of DM) in calf starters (CS) fed to calves

Dependent variable ¹	No of obs.	Intercept		lnccsNFCI ²		PEL ³		TEX ³		PEL × lnccsNFCI		TEX × lnccsNFCI		Probability ⁴	
		Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	lnccsNFCI	Form Int.
dDMcs	207	0.5750	0.1763	0.0604	0.0442	-0.1845	0.1698	-0.1696	0.1684	0.0603	0.0478	0.0888	0.0441	0.03	0.56 0.11
dCPcs	207	0.7074	0.2399	0.0268	0.0591	-0.3296	0.2378	-0.0421	0.2377	0.1076	0.6702	-0.0130	0.0613	0.01	0.001 0.004
dEEcs	207	0.8834	0.2886	-0.0218	0.0803	-0.2123	0.2778	-0.3808	0.2723	0.0916	0.0789	0.1226	0.0724	0.43	0.15 0.23
dNDFcs	207	0.3904	0.1472	0.0262	0.0391	-0.0909	0.1484	-0.2630	0.1462	0.0789	0.0422	0.0826	0.0385	0.06	0.003 0.10
dNFCcs	207	0.9351	0.0829	0.0047	0.0209	-0.3486	0.0784	-0.3226	0.0775	0.1348	0.2212	0.1272	0.0203	0.01	0.001 0.001
DEcs ⁵	207	2.7309	0.4219	0.2203	0.1208	-0.6863	0.4337	-0.2599	0.4252	0.3135	0.1232	0.2049	0.1109	0.03	0.003 0.001
DEcs ⁶	147	2.3468	0.1429	0.1429	0.0470									0.04	
DEcs ⁷	60	2.9961	0.7006	0.1995	0.1661									0.44	
MEcs ⁵	207	2.3186	0.4278	0.2297	0.1225	-0.6628	0.4398	-0.2708	0.4312	0.2960	0.1249	0.2093	0.1125	0.03	0.007 0.06
MEcs ⁶	147	1.9327	0.1356	0.4694	0.0925									0.04	
MEcs ⁷	60	2.3086	0.1306	0.2648	0.0318									0.001	
MEratio ⁵	207	0.9690	0.1387	0.0149	0.0398	-0.3983	0.1427	-0.3419	0.1399	0.1571	0.0405	0.1201	0.0366	0.04	0.02 0.001
MEratio ⁶	147	0.6051	0.0327	0.1465	0.0307									0.04	
MEratio ⁷	60	0.9576	0.0644	0.0319	0.0404									0.57	

¹Dependent variable: dDMcs = DM digestibility (%) in CS; dCPcs = CP digestibility (%) in CS; dEEcs = ether extract digestibility (%) in CS; dNDFcs = NDF digestibility (%) in CS; dNFCcs = NFC digestibility (%) in CS; DEcs = digestible energy (Mcal/kg) in CS; MEcs = ME (Mcal/kg) in CS; MEratio = MEcs/MEncr (ME calculated using NRC, 2001, equations).

²Natural logarithm of cumulative calf starter NFC intake (kg) from d 0 of the study to the end of each digestibility period.

³Form of starter used in each study: PEL = pelleted, TEX = texturized. Coefficients for TMR = 0.

⁴Probability of a significant effect of the natural logarithm of cumulative NFC intake from CS (kg; lnccsNFCI); form of CS (form), and lnccsNFCI × form of CS interaction (int.).

⁵Equation using all records.

⁶Equation using data from trials 1, 2a, and 3a only.

⁷Equation using data from trials 2b and 3b only.

Figure 1. Effect of cumulative NFC intake from calf starter on calf starter nutrient digestibility in calves fed pelleted (PEL) or textured (TEX) calf starters without or with (TMR) 5% grass hay. Values are adjusted as described by St-Pierre (2001). Panels a to e: DM, CP, ether extract (EE), NDF, and NFC digestibilities, respectively.

terion of preparation for weaning, if cumulative intake also contributes to gastrointestinal development and increased digestibility.

Most feeds used in this data set were high-starch, TEX without added hay. Few data in our data set included high fiber by-products, and no diets included forage before 8 wk of age. Further, it is unclear whether inclusion of other types of feeds, including a greater use of forage, would influence these calculations. Also, differences in NFC composition including sugar, starch, and pectins could influence our calculations. For example, Suárez et al. (2006) reported that veal calves consuming diets

containing more NDF consumed more DM compared with calves fed diets containing pectins. Further, rumen fermentation characteristics varied among calves fed diets with carbohydrates derived mainly from starch, NDF, or pectins. More data are warranted to evaluate effects of varying nutrient content, physical form, and feed management on energy predictions.

The MERatio was slightly more correlated with InccsDMI ($r = 0.817$) compared with InccsNFCI ($r = 0.815$). Therefore, we modeled the effect of InccsDMI on MERatio during the first 56 d, when MERatio increased to approximately 100%. The equation was

Figure 2. Effect of cumulative NFC intake from calf starter on calf starter digestible energy (DE) in calves fed pelleted (PEL) or textured (TEX) calf starters without or with (TMR) 5% grass hay. Values are adjusted as described by St-Pierre (2001). Panel a includes all observations in the data set from d 0 to 112 ($n = 207$). Panel b includes only data from d 0 to 56 ($n = 147$).

Figure 3. Effect of cumulative NFC intake from calf starter on calf starter ME in calves fed pelleted (PEL) or textured (TEX) calf starters without or with (TMR) 5% grass hay. Values are adjusted as described by St-Pierre (2001). Panel a includes all observations in the data set from d 0 to 112 ($n = 207$). Panel b includes only data from d 0 to 56 ($n = 147$).

$ME_{ratio} = 0.5038 + 0.1486 \times \ln_{cscsDMI}$. The standard errors for intercept and slope were 0.05814 and 0.02998, respectively (Figure 5). Both intercept and slope were significant ($P < 0.001$). The ME_{ratio} reached 100% at 28.5 kg of cumulative DMI, which is consistent with 15 kg of cumulative NFC intake, assuming that the percent NFC in CS used in our studies at approximately 53%. Because NFC content of CS may not be known in on-farm situations, the use of cumulative DMI may be a more practical method to estimate the point at which $ME_{cscs} = ME_{nrc}$. The equation could potentially

Figure 4. Effect of cumulative NFC intake from calf starter on ratio of calculated ME in calf starter to ME calculated by NRC (2001) in calves fed pelleted (PEL) or textured (TEX) calf starter without or with (TMR) 5% grass hay. Values are adjusted as described by St-Pierre (2001). Panel a includes all observations in the data set from d 0 to 112 ($n = 207$). Panel b includes only data from d 0 to 56 ($n = 147$).

Table 6. Effect of changing CP digestibility and ether extract in milk replacer on calculated ME in calf starter

Item	ME_{cscs}^1	
	Mean	%
dCPmr ²		
60%	2.55	117
70%	2.45	112
80%	2.24	102
81.8%	2.19	100
90%	1.86	85
100%	1.69	77
dEEmr ³		
60%	2.34	107
70%	2.34	107
80%	2.33	107
90%	2.30	105
96.8%	2.19	100
100%	2.07	94

¹ ME_{cscs} = ME (Mcal/kg of DM) in calf starter.

²Digestibility of CP in milk replacer. Mean dCPmr = 81.8% was used in model development.

³Digestibility of ether extract in milk replacer. Mean dEEmr = 96.8% was used in model development.

be used to discount ME_{nrc} and allow prediction of the actual ME available to the calf using cumulative DMI.

One criticism of our approach was the need to partition CP and EE digestibility between MR and CS before weaning. Errors in estimates of MR digestibility would affect prediction of dCPcs and dEEcs and influence prediction of ME_{cscs} before weaning. Constant values for dCPmr and dEEmr (81.8 and 96.8% of DM,

Figure 5. Effect of cumulative DMI from calf starter on ratio of calculated ME in calf starter to ME calculated by NRC (2001) for the first 56 d of the trial ($n = 147$). Model was $ME_{ratio} = 0.5038 + 0.1486 \times \ln_{cscsDMI}$. Standard errors for intercept and slope were 0.05814 and 0.02998, respectively. Effect of form of diet was not included in the model.

respectively) were used in model development. Table 6 demonstrates effect of changing digestibility of CP and EE in MR on calculated MEcs before weaning. Generally, as digestibility of CP or EE was reduced in MR, calculated energy values in CS increased, as the model required that digestibility of CP or EE in CS would increase to maintain TTD of CP or EE. Although partitioning CP and EE between CS and MR adds a potential source of error to these calculations, we believe the effects on the overall results were not large. However, additional data are needed to corroborate or refute this assumption.

CONCLUSIONS

Before weaning, calves obtain less energy from CS than predicted by existing NRC (2001) models. Development of the gastrointestinal system to efficiently digest nutrients, but particularly carbohydrates, is required. Cumulative intake of NFC from CS appears to be a critical factor in the development of digestibility of NDF and NFC and, thus, DE and ME in CS. In this study, when calves consumed a minimum of 15 kg of cumulative NFC from CS, digestibility of nutrients improved to the point at which MEcs were similar to MENrc, suggesting that gastrointestinal maturation developed sufficiently to allow calves to extract energy from CS. Accumulated intake of 15 kg of NFC from CS would equate to 30 kg of a 50% NFC starter or 60 kg of NFC from a 25% NFC starter. Adjustment of NRC calculations of energy values of CS for calves from birth to approximately 4 mo of age appears warranted.

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