Effects of solid feed level and roughage-to-concentrate ratio on ruminal drinking and passage kinetics of milk replacer, concentrates, and roughage in veal calves

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ABSTRACT

Effects of solid feed (SF) level and roughage-to-concentrate (R:C) ratio on ruminal drinking and passage kinetics of milk replacer, concentrate, and roughage were studied in veal calves. In total, 80 male Holstein-Friesian calves (45 ± 0.2 kg of body weight) were divided over 16 pens (5 calves per pen). Pens were randomly assigned to either a low (LSF) or a high (HSF) SF level and to 1 of 2 R:C ratios: 20:80 or 50:50 on a dry matter (DM) basis. Roughage was composed of 50% corn silage and 50% chopped wheat straw on a DM basis. At 27 wk of age, measurements were conducted in 32 calves. During the measurement period, SF intake was 1.2 kg of DM/d for LSF and 3.0 kg of DM/d for HSF, and milk replacer intake averaged 2.3 kg of DM/d for LSF and 1.3 kg of DM/d for HSF. To estimate passage kinetics of milk replacer, concentrate, and straw, indigestible markers (CoEDTA, hexatriacontane C₃₆, Cr-neutral detergent fiber) were supplied with the feed as a single dose 4, 24, and 48 h before assessment of their quantitative recovery in the rumen, abomasum, small intestine, and large intestine. Rumen Co recovery averaged 20% of the last milk replacer meal. Recoveries of Co remained largely unaffected by SF level and R:C ratio. The R:C ratio did not affect rumen recovery of C₃₆ or Cr. Rumen fractional passage rate of concentrate was estimated from recovery of C₃₆ in the rumen and increased from 3.3%/h for LSF to 4.9%/h for HSF. Rumen fractional passage rate of straw was estimated from Cr recovery in the rumen and increased from 1.3%/h for LSF to 1.7%/h for HSF. An increase in SF level was accompanied by an increase in fresh and dry rumen

contents. In HSF calves, pH decreased and VFA concentrations increased with increasing concentrate proportion, indicating increased fermentation. The ratio between Cr and C₃₆ was similar in the small and large intestine, indicating that passage of concentrate and straw is mainly determined by rumen and abomasum emptying. In conclusion, increasing SF level introduces large variation in passage kinetics of dietary components, predominantly in the rumen compartment. The SF level, rather than the R:C ratio, influences rumen recovery of concentrate and roughage. Our data provide insight in passage kinetics of milk (Co representing the milk replacer) and SF (Cr and C₃₆ representing roughage and concentrate, respectively) and may contribute to the development of feed evaluation models for calves fed milk and SF.

Key words: calves, passage rate, nutrient utilization, forage-to-concentrate ratio

INTRODUCTION

Provision of a minimum amount (50 to 250 g/d) of fibrous feed for veal calves is compulsory according to guidelines of the European Union (97/2/EC Directive by the EU Council). Solid feed (SF) provision reduces abnormal oral behaviors (Kooijman et al., 1991; Veissier et al., 1998; Webb et al., 2012), and therefore contributes to improved calf welfare. Furthermore, an economic incentive exists to replace MR by SF in veal calf diets due to increasing prices of milk replacer (MR) ingredients. With increasing amounts of SF provided, products from rumen fermentation contribute to maintenance requirements and growth at the expense of nutrients from MR. In a previous study, we showed that the contribution of SF and MR to BW gain of veal calves largely follows its contribution to digestible energy supply, but effects of age exist (Berends et al., 2012a, 2014). Underlying mechanisms are not

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clear, but it is likely that variation in rumen passage kinetics of SF components and ruminal drinking largely contributes to variation in digestible energy supply. No information exists on passage kinetics of dietary components throughout the gastrointestinal tract in veal calves fed a combination of MR and SF. In dairy calves, it was shown that reducing MR intake (up to 60% compared with a control) had only minor effects on rumen passage kinetics of SF (Broesder et al., 1990). In addition, roughage-to-concentrate (**R:C**) ratio (Colucci et al., 1982; Poore et al., 1990; Rotger et al., 2005), as well as SF level (Colucci et al., 1990), may affect passage kinetics, as observed in ruminants fed only SF. In calves, MR is generally assumed to bypass the reticulorumen by means of the esophageal groove reflex. However, MR may leak into the rumen due to a failure of the esophageal groove reflex or backflow of MR from the abomasum, referred to as ruminal drinking, which can be substantial in dairy calves (0–25%; Guilhermet et al., 1975; Abe et al., 1979) and veal calves (14 to 35%; Suárez et al., 2007; Berends et al., 2012b). The objective of the current study was to assess the effects of SF level and R:C ratio on ruminal drinking and passage kinetics of dietary components in veal calves fed MR, roughage, and concentrate.

MATERIALS AND METHODS

This study was conducted at the research facilities of VanDrie group (Scherpenzeel, the Netherlands). Procedures complied with the Dutch Law on Experimental Animals and the ETS123 (Council of Europe 1985 and the 86/609/EEC Directive) and were approved by the Animal Care and Use Committee of Wageningen University.

Animals, Experimental Design, and Housing

Eighty male Holstein-Friesian calves (2 wk of age; 45 ± 0.2 kg of BW) were purchased from commercial dairy farms and selected based on uniformity and clinical health. Calves were allocated to pens (5 calves per pen; 16 pens) based on BW. Pens were randomly assigned to 1 of 2 SF levels—a low SF level (**LSF**) or a high SF level (**HSF**)—and to an R:C ratio of either 20:80 or 50:50 (Table 1). Upon arrival, calves were adapted to the designated SF levels at a fixed R:C of 50:50 until wk 10. During the experimental period (wk 11 to 27 after arrival), calves were exposed to their assigned SF level and R:C ratio. During the last 2 d of the experimental period, passage kinetics were measured in 32 calves originating from 16 pens.

During the experimental period, calves were housed in groups of 5 calves in pens (3×3 m) equipped with

wooden-slatted floors and fences and without bedding material. During the last 2 d of the experimental period, 2 calves per pen were randomly selected and housed in individual pens placed inside the group pen to facilitate individual feeding and monitoring. Individual pens measured 0.9×2.0 m and allowed audio-visual contact with group mates. Throughout the experiment, calves were exposed to daylight and artificial light from 0500 to 2300 h and to darkness during the remainder of the day. Animal health was checked daily by visual appraisal. Hemoglobin concentration in blood was measured across the trial at wk 11, 15, 19, and 23 and corrected by iron injection to comply with the minimum European Union level of 4.5 mmol/L at the end of the fattening period.

Diets and Feeding

The calves in the current study were selected from another experiment, which has been described by Berends et al. (2014). In short, roughage was composed of 50% corn silage (Table 2) and 50% chopped (3 ± 2 cm) wheat straw (Table 2) on a DM basis. Provision of SF increased biweekly and linearly during the experimental period (wk 11–27), and averaged 780 g of DM/d for LSF and 2,000 g of DM/d for HSF.

Daily DMI from MR during the measurement period is shown in Table 1. The concentration of MR (Table 3) was 188 g/L throughout the experimental period. The MR was supplied in buckets at 40 to 41°C, provided twice daily in equally sized meals at 0600 and 1600 h, respectively. Calves were allowed 15 min to consume the milk; refusals were collected.

The SF was prepared in a mixing wagon (Easymix 2, Vliebo, Veenendaal, the Netherlands), and provided as a mixture in a long feed trough in front of the pen directly after MR provision and collection of MR refusals. Solid feed refusals were removed and weighed once daily before the MR meal in the morning. During the experimental period, calves had free access to water provided via drinking nipples. During the 2-d measure-

Table 1. Daily DM provision of solid feed (SF) and milk replacer (g of DM/calf per day) in calves ($n = 8$ per treatment combination) fed at 1 of 2 levels of SF intake, at 1 of 2 roughage-to-concentrate ratios (R:C)¹ at 27 wk of age

Type of feed	Low SF		High SF	
	20:80	50:50	20:80	50:50
Solid feed		1,170		3,000
Milk replacer	2,224	2,370	1,058	1,458

¹Roughage consisted of 50% corn silage and 50% chopped wheat straw on a DM basis.

ment period (wk 27), calves were provided with water in buckets for 15 min at 1200 and 2200 h.

Measurements

Feed Intake and Performance. Milk replacer intake and SF intake were measured daily. Calves were weighed every 2 wk.

Markers. Indigestible markers were used to estimate kinetics of MR, concentrate (hexatriacontane), and straw along the digestive tract of calves. Passage kinetics were assessed by measuring the recovery of external markers from 4 compartments of the gastrointestinal tract at slaughter; reticulorumen, abomasum, small intestine, and large intestine. Each marker was provided as a pulse dose and in a proportionate mixture with the other SF components corresponding to the treatment. To assess passage kinetics of roughage, chromium-mordanted fiber straw with similar particle size of 3 ± 2 cm (**Cr-NDF**; 50 g/calf) was provided with the SF 48 h before slaughter. In total, most ($n = 27$) calves consumed the pulse dose with Cr-NDF within 120 min. The Cr-NDF was prepared as described by Udén et al. (1980) with the same straw as included in the SF. To assess ruminal drinking and passage kinetics of MR, 36 g of cobalt(II)EDTA (**CoEDTA**; Udén et al., 1980) was dissolved into the final MR meal and provided to each calf at 4 h before slaughter. Calves were allowed 15 min to consume the meal. To assess passage kinetics of concentrate particles, 6% of hexatriacontane (**C₃₆**; >95.0% wt/wt, Minakem, Beuvry-la-Forêt, France) was included in the concentrate (Table 2). The enriched concentrate was provided with the SF 24 h before slaughter. In total, 88% of calves consumed the pulse dose with C₃₆ within 60 min.

Slaughter Procedure. At the end of the measurement period, calves were slaughtered at the experimental facilities over 2 consecutive slaughter days. Euthanasia by pentobarbital was directly followed by exsanguination. To avoid reflux of MR from the abomasum into the forestomachs at slaughter, calves were lifted by the forelegs immediately following exsanguination. Subsequently, ligations were made at the level of the thoracic entrance, the omasal-cardia of the abomasum, and the reticulo-omasal orifice. The gastrointestinal tract was divided into 4 segments: reticulorumen, abomasum, small intestine, and large intestine. The weight of each segment was recorded with and without contents. Rumen contents were quantitatively collected and solid and liquid phases were separated using a metal sieve (1.5 mm). After weighing the solid and liquid phase, a proportionate sample of rumen contents was prepared by reconstituting samples of the liquid and solid phases,

Table 2. Analyzed nutrient composition (% of DM, unless otherwise indicated) of concentrate, corn silage, and straw

Nutrient	Concentrate ¹	Corn silage	Wheat straw
DM, % of product	89.8	29.7	93.1
CP ²	13.7	6.9	3.1
Crude fat	6.7	2.9	0.9
Starch	42.9	31.2	1.1
NDF	12.7	42.1	79.4

¹Concentrate composition: 36.2% corn, 20.6% lupins, 20.3% barley, 12.5% carob meal, 4.4% corn gluten meal, 6% premix (lactose carrier). Provided per kilogram of concentrate: vitamin A, 4,000 IU; vitamin D, 500 IU; vitamin E, 100 IU; zinc (ZnSO₄), 25 mg; manganese (MnSO₄), 20 mg; iodine (KI), 0.8 mg; iron (FeSO₄), 63 mg; selenium (Na₂SeO₃), 0.15 mg; copper (CuSO₄), 15 mg; cobalt, 0.1 mg; 1.13 g of magnesium (magnesium sulfate), 3.0 g of sodium (NaCl), 8.6 g of calcium (CaCO₃), and 3.9 g of potassium (KH₂PO₄).

²N $\times$ 6.25.

which was oven-dried and stored for analysis. A sample of the rumen liquid was used for pH measurement, then acidified with H₃PO₄ (5%) and stored at -20°C pending analysis of VFA. After mixing, samples of abomasal contents, small intestinal contents, and large intestinal contents were taken and stored at -20°C pending analysis. The length of small intestine was measured.

Table 3. Ingredient composition and analyzed nutrient composition of the experimental milk replacer

Item	Amount
Ingredient, %	
Fat-filled whey powder ¹	39.4
Whey protein concentrate	19.4
Whey	14.3
Delactosed whey	13.5
Soy protein isolate	3.8
Soy protein concentrate	2.5
Acidified whey ²	2.0
Pregelatinized wheat starch	2.0
Vitamin and mineral premix ³	1.0
Calcium formate	1.0
L-Lysine-HCl	0.5
DL-Methionine	0.3
Citric acid	0.2
Mono-ammonium phosphate	0.1
L-Threonine	0.02
Nutrient, % of DM (unless otherwise stated)	
DM, % of product	97.0
CP ⁴	21.0
Crude fat	21.2
Starch	2.2

¹Contained 50% fat, palm oil and coconut oil (80/20, wt/wt).

²Acidified with lactate, provided 5.9 g of lactate/kg of the experimental diet.

³Provided per kilogram of the experimental diet: 16.6 g of K, 15.5 g of Cl, 8.3 g of Fe, 6.1 g of P, 5.9 g of Cu (CuSO₄), 5.7 g of Na, 1.3 g of Mg (MgO), 25,000 IU of vitamin A, 4,000 IU of vitamin D₃, and 100 IU of vitamin E.

⁴Calculated as N $\times$ 6.25.

Chemical Analyses. Samples of MR, concentrate, corn silage, and wheat straw were collected weekly. Corn silage samples were pooled monthly; other samples were pooled over the experimental period. Feed components (MR, corn silage, concentrate, straw) were analyzed for DM, ash, N, starch, NDF (except for MR), and crude fat content. For determination of DM content, corn silage and concentrate samples were freeze-dried. Concentrate, straw, and corn silage samples were ground to pass a 1-mm screen. Dry matter content was determined by drying to a constant weight according to ISO 6496 (ISO, 1998). Kjeldahl N content was determined according to ISO 5983 (ISO, 1997). Starch content was determined enzymatically as described by Rijnen et al. (2001). The NDF content was analyzed according to Van Soest et al. (1991). Crude fat content was determined after acid hydrolysis according to ISO 6496 (ISO, 1999). Concentrations of VFA in rumen liquid were quantified by GC (Fisons HRGC Mega 2, CE Instruments, Milan, Italy) according to Pellikaan et al. (2011).

The Cr and Co concentrations were determined in the contents from each gastrointestinal compartment by atomic absorption spectrometry according to Pellikaan et al. (2013). Extraction and analysis of *n*-alkanes was carried out according to Bezabih et al. (2011). Ground samples were pulverized using a ball mill (MM 2000; 4 min at 80 Hz; Retsch Technology GmbH, Haan, Germany) before extraction and analysis, as described by Mayes et al. (1986) with modifications of Salt et al. (1992) using tetratriacontane as an internal standard. The extracted samples were analyzed for C_{36} using a GC. The concentration of C_{36} was calculated from peak areas using an internal standard (Bezabih et al., 2011).

Calculations. Rumen fractional passage rates were assumed constant and estimated for concentrate and straw from rumen recoveries of C_{36} and Cr, respectively, according to the formula:

$$C_t = C_0 \times e^{-kp \times t},$$

where C_t is the marker concentration at time t , C_0 is the marker concentration at time 0, kp is the fractional passage rate, and t is time in h.

Statistical Analysis. The data set included 32 observations. For Co recovery, 8 calves were excluded because of MR refusals exceeding 10% (1 LSF 50:50; 5 LSF 20:80; 2 HSF 50:50). Dependent variables were analyzed by mixed model analysis in PROC MIXED (SAS 9.20 by SAS Institute Inc., Cary, NC) for continuous data, with calf as experimental unit, pen as random effect, and SF level, R:C ratio, and day of slaughter as fixed effects, and the interaction between SF level and

R:C ratio. Results are presented as least squared means and their standard error of the mean. Differences were considered significant at $P < 0.05$.

RESULTS

During the experimental period (wk 11 to 27), LSF calves consumed 93 ± 2.9 and 94 ± 0.3 kg of DM of SF and 251 ± 6.2 and 232 ± 1.4 kg of DM of MR for R:C 50:50 and 20:80, respectively. In the same period, HSF calves consumed 239 ± 0.9 (R:C 50:50) and 248 ± 1.6 kg of DM of SF (R:C 20:80) and 184 ± 1.7 and 150 ± 0.9 kg of DM of MR, respectively. Final BW was greater ($P < 0.05$) for calves fed HSF (259 ± 4.2 kg) than for calves fed LSF (245 ± 5.9 kg), but growth performance was not affected by R:C ratio.

Recovery of Co in the rumen averaged $20 \pm 4.0\%$. Rumen and small and large intestinal Co recovery was unaffected by SF level and R:C ratio (Table 4). Abomasal Co recovery was greater ($P = 0.01$) in LSF calves than in HSF calves. Rumen recovery of C_{36} was unaffected by R:C ratio, but decreased by 15% points ($P < 0.001$) with SF level. This difference was reflected in the cumulative C_{36} recovery. Rumen recovery of Cr was unaffected by R:C ratio, but decreased by 8% points ($P = 0.002$) with SF level. This difference was reflected in the cumulative Cr recovery. Recoveries of Cr and C_{36} in abomasum and small intestine were generally low ($<5\%$). For the abomasum, recoveries of Cr and C_{36} increased with roughage inclusion for the LSF calves, and decreased with roughage inclusion for the HSF calves. For the small intestine, recoveries of Cr and C_{36} decreased with roughage inclusion for the LSF calves, whereas the opposite was true for the HSF calves (SF $\times$ R:C interaction, $P = 0.01$).

At high SF intake, a low R:C ratio resulted in a 1-point lower pH ($P = 0.004$; Table 5) and a higher total VFA concentration (37 mmol/L; SF $\times$ RC, $P = 0.04$). The SF level did not affect empty weights of the gastrointestinal compartments, but rumen contents (fresh as well as dry) increased ($P < 0.001$) in response to an increase in SF level. DM content of digesta in the rumen and abomasum decreased in 20:80 compared with 50:50 (both $P < 0.05$). The empty weight of the abomasum increased ($P = 0.01$) in 50:50 compared with 20:80. Small intestinal weight, contents, and length were unaffected by SF level or R:C ratio. The empty weight of the large intestine increased in 20:80 compared with 50:50 in HSF calves only (interaction SF $\times$ RC, $P = 0.05$).

From rumen recoveries of Cr and C_{36} , the fractional rates of passage were estimated (Table 6). Ruminal fractional passage rate of C_{36} , representing concentrate,

Table 4. Effects of level of solid feed (SF; low vs. high) and roughage-to-concentrate ratio (R:C; 20:80 vs. 50:50) on the recovery of pulse-dosed markers, Co, Cr, and hexatriacontane (C_{36}), in gastrointestinal compartments of veal calves¹

Item	Low SF		High SF		SEM	P-value		
	20:80	50:50	20:80	50:50		SF	R:C	SF × R:C
Co recovery, %								
Rumen	18.3	11.4	16.3	34.4	9.59	0.23	0.52	0.15
Abomasum	11.2	14.8	9.2	3.3	3.11	0.01	0.64	0.06
Small intestine	27.6	44.7	39.4	31.0	8.05	0.89	0.53	0.08
Large intestine	23.1	16.7	20.4	17.9	4.89	0.86	0.32	0.66
Total	78.4	86.2	84.0	85.6	3.17	0.38	0.11	0.25
C_{36} recovery, %								
Rumen	48.4	44.2	30.0	32.4	4.10	<0.001	0.75	0.26
Abomasum	1.2	2.0	2.0	1.6	0.47	0.55	0.44	0.09
Small intestine	3.3	1.7	2.6	4.5	0.91	0.12	0.75	0.01
Large intestine	13.5	14.3	14.5	13.5	2.43	0.95	0.94	0.61
Total	66.4	62.2	49.1	52.1	4.74	<0.001	0.86	0.29
Cr recovery, %								
Rumen	55.6	53.6	48.4	42.2	3.78	0.002	0.14	0.44
Abomasum	1.6	2.2	1.6	0.6	0.79	0.33	0.57	0.01
Small intestine	1.6	0.9	0.9	2.2	0.51	0.41	0.49	0.01
Large intestine	5.2	6.9	5.0	5.3	1.23	0.30	0.25	0.47
Total	63.9	63.5	56.9	51.1	3.78	0.001	0.25	0.32

¹Dietary treatments included low or high level of solid feed (SF). The SF included 1 of 2 roughage-to-concentrate ratios (R:C; 20:80 vs. 50:50 on DM basis) and was fed in addition to a milk replacer. Cobalt was pulse-dosed as CoEDTA with milk replacer at 4 h before slaughter; C_{36} was pulse-dosed with concentrate in SF at 24 h before slaughter; Cr was pulse-dosed as Cr-NDF with wheat straw in SF at 48 h before slaughter.

increased ($P < 0.001$) with SF level, from 3.3%/h for LSF to 4.9%/h for HSF calves. Ruminal fractional passage rate of Cr, representing straw, increased ($P = 0.003$) with SF level, from 1.3%/h for LSF to 1.7%/h for HSF calves. Ruminal passage rates of C_{36} and Cr were unaffected by R:C ratio.

DISCUSSION

Ruminal Drinking and Passage of MR

Although the majority of MR is assumed to bypass the rumen by means of the esophageal groove reflex,

Table 5. Effects of level of solid feed (SF; low vs. high) and roughage-to-concentrate ratio (R:C; 20:80 vs. 50:50) on weights of gastrointestinal compartments, contents, and DM content in veal calves¹

Item	Low SF		High SF		SEM	P-value		
	20:80	50:50	20:80	50:50		SF	R:C	SF × R:C
Rumen								
Ruminal pH	6.4	6.5	6.0	6.9	0.19	0.81	0.004	0.02
Total VFA, mmol/L	125	127	161	124	9.3	0.08	0.06	0.04
Empty weight, kg	5.1	4.6	5.4	6.0	1.00	0.10	0.92	0.23
Contents, kg	16.9	15.7	23.4	22.9	2.04	<0.001	0.56	0.81
DM content, g/kg	137	152	163	174	12.1	<0.001	0.04	0.73
Abomasum								
Empty weight, kg	1.8	2.4	2.0	2.1	0.16	0.84	0.01	0.03
Contents, kg	1.5	2.6	2.5	1.2	0.47	0.46	0.76	0.001
DM content, g/kg	44	69	81	83	11.0	<0.001	0.03	0.01
Small intestine								
Empty weight, kg	5.0	5.4	5.0	5.0	0.35	0.47	0.44	0.48
Contents, kg	3.7	4.0	4.7	3.8	0.52	0.35	0.40	0.14
DM content, g/kg	66	65	61	74	7.7	0.74	0.29	0.19
Length, m	28.2	29.9	29.5	28.4	0.65	0.96	0.84	0.37
Large intestine								
Empty weight, kg	2.4	2.5	2.6	2.2	0.19	0.72	0.11	0.05
Contents, kg	2.0	1.7	2.1	2.1	0.18	0.05	0.34	0.33
DM content, g/kg	113	130	143	137	11.0	0.02	0.48	0.15

¹Dietary treatments included low or high level of solid feed (SF). The SF included 1 of 2 roughage-to-concentrate ratios (R:C; 20:80 vs. 50:50 on DM basis) and was fed in addition to a milk replacer.

Table 6. Effects of level of solid feed (SF; low vs. high) and roughage-to-concentrate ratio (R:C; 20:80 vs. 50:50) on estimated fractional ruminal passage rate (Kp) for C₃₆ (concentrate) and Cr-NDF (straw) in veal calves¹

Item	Low SF		High SF		SEM	P-value		
	20:80	50:50	20:80	50:50		SF	R:C	SF × R:C
Kp C ₃₆ , concentrate, %/h	3.2	3.4	5.1	4.8	0.45	<0.001	0.96	0.39
Kp Cr-NDF, straw, %/h	1.3	1.3	1.5	1.8	0.16	0.003	0.18	0.32

¹Dietary treatments include low or high level of solid feed (SF). The SF included one of two roughage-to-concentrate ratios (R:C; 20:80 vs. 50:50 on DM basis) and was fed in addition to a milk replacer.
P* < 0.01; *P* < 0.001.

ruminal drinking is frequently observed in veal calves (Suárez et al., 2007; Berends et al., 2012b). In the current study, ruminal recovery of Co, supplied with the MR, averaged 20%, which is similar to previous marker studies (Suárez et al., 2007; Berends et al., 2012b) but exceeds estimates from other marker studies (<7%; Labussière et al., 2014). Although SF level and R:C ratio did not affect ruminal Co recovery, the large variation in ruminal Co recovery complicates interpretation of the effect of SF level and R:C ratio on passage of MR through the remaining part of the digestive tract. To gain more insight in the gastrointestinal transit of MR, Co recovery in the abomasum, small intestine, and large intestine was expressed as a percentage of the oral dose corrected for rumen recovery (Figure 1), thereby neglecting passage of the marker from the rumen compartment within the 4-h period between administration and slaughter. These data showed that postrumen pas-

sage kinetics of MR were hardly affected by SF intake or R:C ratio. In the current study, a large contrast in MR intake was observed between treatments, with LSF 50:50 calves receiving the largest amounts of MR and HSF 20:80 receiving the lowest amounts of MR. In ruminants, abomasal volume and the rate of digesta flow from the abomasum and along the small intestine are linearly related to the level of intake (Gregory et al., 1985). For MR, abomasal emptying rate is negatively related to meal volumes (Bell and Razig, 1973). Therefore, the reduction in abomasal recovery in HSF is likely related to the associated reduction in MR intake. Total Co recovery averaged 84%. The incomplete recovery indicates that CoEDTA may be partly absorbed. Although this marker has been used successfully to estimate passage kinetics (Huhtanen and Kukkonen, 1995), abomasal emptying rate (Holtenius et al., 2000), and ruminal drinking (Suárez et al., 2007; Berends et

Figure 1. Cobalt recovery as a percentage (means ± SE) of the dose administered, corrected for rumen Co recovery. Abomasal Co recovery was affected by level of solid feed (SF; *P* < 0.01), but not by roughage-to-concentrate (R:C) ratio or the interaction. Recoveries in small and large intestine were unaffected by SF level, R:C ratio, or the interaction. The low SF 50:50 (R:C) treatment is represented by a dotted bar, low SF 20:80 by a white bar, high SF 50:50 by a light gray bar, and high SF 20:80 by a dark gray bar.

al., 2012b), Co excretion via urine was found to be 2 to 3% in ruminants (Udén et al., 1980), suggesting that some amounts of Co could be absorbed from the digestive tract.

Passage Rates of Concentrate and Straw

From marker recovery data in the current study, we calculated fractional rumen passage rates assuming an exponential decay as commonly done in ruminant studies (e.g., Tamminga et al., 1989). Fractional passage rates of concentrates and straw were generally lower than previously reported for dairy calves around weaning (Hart and Polan, 1984; Lallès and Poncet, 1990; Vazquez-Anon et al., 1993) and adult ruminants fed only SF (Owens and Goetsch, 1986; Colucci et al., 1990). This could be due to the relatively low SF intake in our study, because calves obtained the vast majority of digestible energy from MR. Potentially, differences could be explained by a different particle size of the pulse-dosed straw compared with previously mentioned studies.

The observed increase in ruminal fractional passage rate with increasing SF intake and decreasing MR intake was previously observed in dairy calves (Broesder et al., 1990) and with increasing SF intake in adult ruminants (Owens and Goetsch, 1986; Robinson et al., 1987; Colucci et al., 1990). However, other studies found no effect of increasing SF intake on passage of particles in young ruminants (Hodgson, 1971a; Lallès and Poncet, 1990). The increase in SF intake also increased rumen contents in the current study, which is in accordance with the positive relationship observed between rumen fluid volume and SF intake in young calves during weaning (Hodgson, 1971b) and in dairy cows (Owens and Goetsch, 1986). A greater rumen volume enables a longer retention time and thus greater feed degradation, which may partly compensate for the increase in fractional passage rate.

Ruminal fractional passage rates of concentrate are typically greater than those of roughages, such as straw (Colucci et al., 1990), which can be explained by increased time for rumination and comminution to decrease particle size of roughages. The absence of an effect of R:C ratio on passage rates of concentrate (Poore et al., 1990; Warner et al., 2013) and roughage (Poore et al., 1990; Rotger et al., 2005) has been demonstrated before, as reviewed by Offer and Dixon (2000) for cattle. A negative effect of concentrate proportion on rumen volume, as observed in adult ruminants (Owens and Goetsch, 1986), was absent in our study.

The relationship between C_{36} and Cr recovery in the different postrumen compartments was highly significant ($P < 0.001$) and strong ($R^2 \geq 0.80$) for the tubular

parts of the gut (Figure 2), but this was less clear for the abomasum ($R^2 = 0.49$; Figure 2) and the rumen ($R^2 = 0.40$; results not shown). These results suggest that rumen and abomasal emptying differ between concentrate and roughages, whereas passage through the remaining part of the gut is similar for concentrate and straw. This observation is similar to previous studies on passage behavior of solid and liquid markers through the postrumen sections of the gastrointestinal tract in dairy cows (Wylie et al., 2000; Pellikaan, 2004).

In conclusion, the low passage rates found for concentrate and straw in the current study can be explained by the low SF intake (or high MR intake). An increase in SF intake coincided with an increase in rumen volume. The ratio between Cr and C_{36} was similar in the small and large intestine, indicating that passage of concentrate and straw is mainly determined by rumen and abomasum emptying.

Gastrointestinal Development

Ruminal VFA concentrations observed in the current study were similar to VFA concentrations observed in growing calves and heifers provided with similar R:C ratios (Vazquez-Anon et al., 1993; Rotger et al., 2005; Moody et al., 2007). The highest ruminal VFA concentrations were observed in calves fed a high level of SF with a 20:80 R:C ratio. This interaction ($P = 0.04$) indicates greater rumen fermentation with large amounts of readily degradable fiber originating from concentrate. The increase in total VFA concentration was accompanied by a reduction in rumen pH in these calves. Abomasal weight increased with roughage inclusion, especially in LSF calves, but it remains unclear why this effect was less pronounced in HSF calves.

CONCLUSIONS

Ruminal drinking, as indicated from recovery of Co in the rumen, was not affected by SF intake and R:C ratio in veal calves. On average, 20% of the MR was recovered in the rumen. An increase in SF intake increased rumen passage rates of concentrates and straw as well as rumen volume. The differences in passage of concentrate and straw are mainly induced by variation in rumen and abomasum emptying, as indicated from the constant ratio between Cr (marker for straw) and C_{36} (marker for concentrate) in the small and large intestines. These data provide insight in passage kinetics of MR, roughage, and concentrate, and the interactions between SF intake and R:C ratio. The current findings may be used for the development of mechanistic models simulating digestion of MR and SF and predicting growth in veal calves.

Figure 2. Relationship between hexatriacontane (C_{36}) recovery and chromium (Cr) recovery in abomasum ($\square$; $y = 0.86x + 0.42$; $R^2 = 0.49$), small intestine (Δ ; $y = 0.49x - 0.08$; $R^2 = 0.80$), and large intestine ($\circ$; $y = 0.49x - 1.17$; $R^2 = 0.80$). Cobalt was pulse-dosed as CoEDTA with milk replacer at 4 h before slaughter; C_{36} was pulse-dosed with concentrate at 24 h before slaughter; Cr was pulse-dosed as Cr-NDF with straw at 48 h before slaughter. Recoveries were determined in gastrointestinal compartments of veal calves. For each segment, the estimated regression coefficient was highly significant ($P < 0.001$).

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