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Sheep gastrointestinal development in response to different dietary treatments

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Abstract

Physical maturation of the ruminal epithelium has previously been linked to ruminal production of VFA following the initiation of solid feed intake. This study was conducted to evaluate the effect of VFA administration and energy intake on sheep gastrointestinal development. Twelve lambs were removed from their dams at birth and trained to nurse on nipple buckets. All lambs consumed milk until 49 d of age and were subsequently assigned to one of four treatments: continued ad libitum intake of milk (M), ad libitum intake of a pelleted lamb starter (F), restricted intake of a pelleted lamb starter (P: paired to the energy intake of M lambs), or continued ad libitum intake of milk replacer plus an oral VFA solution (V; 55.2:36.9:7.2 mmol/100 mmol acetate:propionate:butyrate) via stomach tube to provide 10% of the predicted NE_g. At slaughter visceral organs were removed and separated. Ruminal and intestinal tissues were weighed and intestinal tissue length was determined. Subsections of the rumen, duodenum, jejunum, ileum, and the colon were used to determine total, epithelial and musculature DM, protein, DNA, and RNA. Data are presented as a percent of empty body weight (%EBW) unless otherwise noted. Both F and P stimulated increases ($P<0.05$) in rumen mass (2.232±0.077 and 2.126±0.238 %EBW, respectively), while V treatment did not (0.761±0.038 %EBW) in comparison to milk fed animals (0.88±0.104 %EBW). Small intestinal weights (%EBW) were unaffected by P and F relative to milk fed animals yet increased in V (3.32±0.982, 2.66±0.242, 3.122±0.354, and 4.061±0.158 %EBW for M, P, F, and V, respectively). The ratio of small intestinal length to empty body weight declined ($P<0.05$) with intake of solid feed and VFA treatment. However, wet weight per unit length of the small intestine was increased by F, P and V above that observed for M. Thus, although VFA treatment at this dose was insufficient to induce normal ruminal development, intestinal physical development was stimulated by oral VFA infusion in developing lambs.

Keywords: Rumen; Development; Sheep; Intestine; Volatile fatty acids

1. Introduction

At birth the rumen is a rudimentary nonfunctional sac. Normal development of the rumen requires the establishment of a viable microbial population and the formation of volatile fatty acids (Sander et al., 1959; Tamate et al., 1962). Establishment of ruminal microbial fermentation begins between two to four weeks of age as a result of the initiation of solid feed intake (Giesecke et al., 1979; Baldwin and Jesse, 1992). Ruminal development is characterized by tremendous increases in mass, volume and surface area. Tissue

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growth is accompanied by a differentiation which results in physical changes such as increased keratinization and papillary development (Tamate et al., 1962), and altered metabolic characteristics including decreased use of glucose with increased oxidation of butyrate and ketogenesis (Giesecke et al., 1979; Baldwin and Jesse, 1992). In addition to the importance in the morphological development of the rumen, VFA are the primary energy substrate of mature ruminants with upwards of 70% of the energetic requirements of the animal being met from ruminally absorbed VFA (Bergman, 1990). Thus, understanding the control of ruminal growth and differentiation is essential to the development of improved feeding regimes.

Surface area and total mass of the rumen are sensitive to changes in VFA production as well as energy intake in mature and developing ruminants (Mayer et al., 1986). Similarly, visceral organs generally increase in mass when energy intake is elevated and decrease in mass when energy intake is restricted (Freetly et al., 1995). Visceral organs can account for 30–60% of the energetic needs of the ruminant (Reynolds and Huntington, 1988; Reynolds et al., 1991). Thus, despite their important service to the animal, the visceral organs are using energy that could be available for production of meat and milk. Therefore, the mechanisms controlling visceral organ growth and energy use are important areas of research. The purpose of this study was to: (1) determine the effect of dietary energy intake and volatile fatty acids on the growth pattern of visceral organs of lambs, and (2) determine the effectiveness of oral VFA administration in stimulating ruminal and intestinal development.

2. Materials and methods

2.1. Animals and diets

Fourteen mixed breed lambs were separated from their dams at one day of age, placed in individual pens, and trained to nurse milk replacer from nipple buckets. Milk replacer (Ultra Fresh, Land O'Lakes, Fort Dodge, Iowa) was prepared fresh twice daily as directed by the manufacturer (185 g in a final volume of 1 l). Milk replacer was cold and maintained cold throughout the day using cold packs in the nipple buckets. Milk or feed intake was determined daily and body weight was measured weekly. Lambs were maintained solely on milk replacer (ad libitum) from birth to 49 days. After day 49, the lambs were randomly assigned to one of four treatment groups: continued milk feeding (M; n=3), continued milk feeding plus VFA infusions (V; n=5), weaned to a pelleted lamb starter (F; n=3), or weaned with feed offered restricted to the energy intake of the milk fed lambs (P; n=3). Animals were gradually weaned to the new dietary regime from 49 to 56 d and were maintained on their respective treatments until they were euthanized at 84 d. Treatments or feed intake were adjusted weekly from 49 to 84 d. Animal protocols were approved by the Beltsville Area Animal Care and Use Committee (protocol no. 94-058).

Lambs in the fed group were weaned following 49 days onto a pelleted lamb starter consisting of 330 g corn, 250 g barley, 167 g alfalfa meal (17% CP), 167 g soybean meal, 83 g molasses, and 3 g vitamin–mineral premix per kg of the mixture. Lambs had unlimited access to both pellets and water until slaughter. The pair-fed group lambs were fed the same pelleted starter except feed offered was limited to the same metabolizable energy intake per kg body weight$^{0.75}$ as the lambs in the milk-fed group consumed. Feed intake of the pair-fed animals was adjusted weekly. Lambs in the VFA infused group were allowed free access to milk replacer and infused ruminally, via stomach tube, with volatile fatty acids received approximately 10% NE_g requirements three times daily. The VFA solution consisted of sodium salts of acetate, propionate and butyrate in a ratio of 55.2:36.9:7.2 mmol/100 mol (buffered to pH 6.7). The initial goal of the experiment was to achieve 50% of the NE_g requirements coming from infused VFA following weekly adjustments in dose (i.e. 12.5%, 25% and finally 50%). However, two of the lambs which were moved from the 12.5% to the 25% dose experienced metabolic distress and were removed from the trial. Thus, the three lambs remaining were started and maintained at 10% of the estimated NE_g requirements throughout the experiment to ensure that the trial could be completed.

2.2. Procedures and measurements

Lambs were stunned with a captive bolt gun, exsanguinated, and the visceral organs removed. The reti-

culorumen complex was emptied and rinsed with warm tap water to remove digesta. Ruminal tissue was identified and separated from the reticulum and the ruminal epithelium was separated from underlying musculature and total, epithelial and musculature weights were determined. Sections (approximately 5 g) of the rumen were frozen in liquid nitrogen and stored (−80°C) until analyzed. Wet weights of the abomasum, omasum, reticulum, liver, kidneys, heart, and lungs were also recorded.

Small and large intestines were separated from mesentery, rinsed with saline (2 l), blotted and total wet weight was determined. Small and large intestinal lengths were determined by looping the intestine across a board fitted with pegs attached at 1 m increments without tension applied to minimize stretching. Two sections (15.24 cm) from the duodenum (1 m from the pyloric sphincter), jejunum (midpoint of the intestine), ileum (1 m from the ileal–cecal junction), and colon were removed. Section weights were recorded and one section from each tissue was split along its long axis. The cut section was laid on a glass plate and the width was measured at 10 randomly selected points. The mean width was recorded and the tissue was scraped with a glass slide to remove the epithelium. The epithelium and muscle tissue wet weights were recorded. Samples from the total section, scraped epithelium and muscle were frozen in liquid nitrogen and stored (−80°C) until analyzed for protein, RNA and DNA.

Tissue samples were dried (100°C) for 48 h and tissue protein was determined by micro-Kjeldahl digestion with automated procedures (AOAC, 1984). Additional 0.5 g samples were homogenized in 15 ml of cold extraction buffer (10 mmol/l Tris and 5 mmol/l EDTA) on ice for 3 min and aliquots were used for RNA and DNA determinations. Samples (3 ml) for RNA analysis were acid precipitated (1 ml 1.2 N perchloric acid) and centrifuged (10 000×g at 4°C) for 5 min. Supernatant was discarded and the pellet was raised twice in 0.2 N perchloric acid and centrifuged as above. Pellets were incubated (37°C) for 60 min in 3 ml of 0.3 N KOH. Following incubation 2 ml cold 1.2 N perchloric acid was added, samples were centrifuged (10 000×g at 4°C), the supernatant was saved and the pellet was washed two times with an additional 1 ml 0.2 N perchloric and all the supernatants were combined and saved. The optical density of the RNA hydrolysate was measured at 260 and 232 nm and μg RNA determined by the formula (39.1×optical density at 260 nm)−(15.5×optical density at 232 nm). Tissue DNA was determined by flourometric procedure using Hoechst Reagent and Calf Thymus DNA as a standard. The model used for the analysis of variance (PROC GLM; SAS, 1995) of data included the effects of treatment. Differences between means were determined by PDIFF and were considered significant at $P<0.05$.

3. Results

Initial lamb weights at 56 d were not significantly different between treatment groups (Table 1). By 84 d, the ad libitum starter pellet fed animals were significantly heavier ($P<0.05$) than all of the other groups and thus, average daily gain (ADG) was greater for F.

Table 1
Performance characteristics of lambs with four dietary treatments

Item	Treatment[a]				SEM
	M	F	P	V	
49 d wt. (kg)	8.8	12.4	12.4	10.7	1.2
56 d wt. (kg)	10.0	13.8	10.8	13.0	3.3
84 d wt. (kg)	11.8[c]	21.8[b]	14.8[c]	16.3[c]	3.3
ADG (g/d)	66.7[c]	291.9[b]	160.3[c]	120.6[c]	36.6
ME intake/$BW^{0.75}$ (MJ/d)	0.739[c]	0.976[b]	0.755[c]	0.827[b,c]	0.088
Feed intake (g/d)	–	601.3[b]	370.8[c]	–	45.4
Milk intake (ml/d)	1088	–	–	1501	163

[a] M, milk fed ad libitum; F, pellets ad libitum; P, pellets at restricted intakes; V, milk fed with VFA infusions.
[b,c] Means with different superscripts within rows are different ($P<0.05$; $n=3$ for all treatments).

Table 2
Tissue wet weights as a percentage of empty body weight and lengths as a ratio with empty body weight at slaughter from lambs with four dietary treatments[a]

Tissue	Treatment[b]				SEM
	M	F	P	V	
Rumen, total	0.88[c]	2.23[d]	2.13[d]	0.76[c]	1.68
Rumen, muscle	0.50[c]	0.84[d]	0.84[d]	0.45[c]	0.08
Rumen, epithelial	0.38[c]	1.39[d]	1.29[d]	0.31[c]	0.10
Reticulum	0.25[c,d]	0.34[d]	0.31[d]	0.17[c]	0.04
Omasum	0.11[c]	0.18[d]	0.21[d]	0.07[c]	0.02
Abomasum	0.62	0.60	0.50	0.47	0.10
Liver	2.77	2.40	2.34	2.08	0.26
Heart	0.77	0.67	0.71	0.70	0.06
Lungs	2.34	1.78	1.68	1.52	0.40
Kidney	0.69	0.59	0.59	0.56	0.11
Small intestine, (wt.) (g/EBW)	3.32[d]	3.12[d]	2.66[d]	4.06[c]	0.66
Small intestine length (m/EBW)	8.76[d]	4.90[c]	5.32[c,d]	6.77[d]	1.45
Large intestine (wt.) (g/EBW)	1.44	1.58	1.23	1.48	0.12
Large intestine length (m/EBW)	1.14	1.02	0.93	0.88	0.15

[a] Tissue wet weights are presented as a percentage of empty body weight (EBW).
[b] M, milk fed ad libitum; F, pellets ad libitum; P, pellets at restricted intakes; V, milk fed with VFA infusions.
[c,d] Means with superscripts that differ within rows are different ($P<0.05$; $n=3$ for all treatments).

Average daily intake of ME on a metabolic body weight basis was greatest ($P<0.05$) for F and lowest for M and P groups with V being intermediate. Lamb starter pellet intake (g/d) was reduced ($P<0.05$) by the restriction imposed and milk intake was not affected by VFA infusion.

Feeding lamb starter, both ad libitum and restricted to the ME intake of the milk fed animals, increased ($P<0.05$) total, epithelial and muscle wet weights of the rumen as a percentage of empty body weight (Table 2) compared with milk fed animals. Oral infusion of VFA in addition to milk consumption did neither affect the mass of the rumen epithelium nor the rumen musculature. The omasum responded in a similar manner to the rumen in that total epithelial and muscle weights were greater ($P<0.05$) in lambs from the P and F groups in comparison with M and V groups. However, the reticulum was not increased as a percentage of empty body weight in the fed and pair fed groups as compared to the milk fed group but were increased ($P<0.05$) as compared to the VFA infused group. Abomasum, liver, heart, kidney and lungs were unaffected by dietary treatment. Oral infusion of VFA increased ($P<0.05$) the small intestinal wet mass as percentage of empty body weight in comparison to the M, F, and P groups. The ratio of small intestine length to EBW was decreased ($P<0.05$) in the fed group in comparison with the milk fed and VFA infused groups with the pair-fed group being intermediate. Large intestinal tissue mass as a percentage of EBW did not change nor did the ratio of length to EBW.

Total, epithelial and musculature wet weight of duodenal sections (15.24 cm) was greater ($P<0.05$) in the VFA infused lambs relative to M with F and P being intermediate (Table 3). The width of the duodenal sections followed the same pattern. Jejunal section total and epithelial wet weights and widths were increased ($P<0.05$) in the VFA infused lambs with the fed lambs again being intermediate. Musculature of the jejunum was not affected by treatment. Total ileal section and epithelial tissue wet weights were increased ($P<0.05$) in the fed, pair-fed and VFA infused groups. Musculature weight of the ileum was increased in the fed animals with the pair-fed and VFA infused animals having intermediate weights. Ileal width was greatest ($P<0.05$) in the VFA infused group with the fed and pair-fed groups intermediate. Colon musculature and widths were not affected by treat-

Table 3
Weights and widths of intestinal sections[a] from lambs with four dietary treatments

	Treatment[b]				SEM
	M	F	P	V	
Duodenum					
Total section (g wet wt.)	2.33[c]	3.03[c,d]	3.30[c,d]	3.93[d]	0.39
Epithelial (g wet wt.)	1.53[c]	2.13[c,d]	2.13[c,d]	2.77[d]	0.31
Musculature (g wet wt.)	0.37[c]	0.43[c,d]	0.43[c,d]	0.60[d]	0.08
Width (cm)	1.60[c]	2.13[c,d]	1.90[c,d]	2.30[d]	0.26
Jejunum					
Total Section (g wet wt.)	2.07[c]	3.10[d]	2.37[c,d]	4.07[e]	0.35
Epithelial (g wet wt.)	1.43[c]	2.03[c,d]	1.97[c,d]	2.77[d]	0.31
Musculature (g wet wt.)	0.40	0.53	0.60	0.60	0.10
Width (cm)	1.63[c]	2.20[c,d]	2.43[c,d]	2.57[d]	0.26
Ileum					
Total section (g wet wt.)	4.00[c]	8.97[d]	8.13[d]	6.80[c,d]	1.11
Epithelial (g wet wt.)	2.83[c]	6.43[d]	6.20[d]	4.83[d]	0.70
Musculature (g wet wt.)	0.87[c]	1.63[d]	1.43[c,d]	1.43[c,d]	0.22
Width (cm)	2.20[c]	3.23[d,e]	2.77[c,d]	3.67[e]	0.25
Colon					
Total section (g wet wt.)	3.47[c]	4.37[c]	4.63[c]	7.10[d]	0.71
Epithelial (g wet wt.)	1.40[c]	1.67[c,d]	1.77[c,d]	2.47[d]	0.36
Musculature (g wet wt.)	1.57	2.13	1.77	1.93	0.26
Width (cm)	2.00	2.03	1.83	1.97	0.24

[a] Weights and widths from 6 in. (15.24 cm) tissue sections from the intestinal segments.
[b] M, milk fed ad libitum; F, pellets ad libitum; P, pellets at restricted intakes; V, milk fed with VFA infusions.
[c,d,e] Means with superscripts that differ within rows are different ($P<0.05$; $n=3$ for all treatments).

ment, however, total section and epithelial wet weights were increased ($P<0.05$) in the VFA infused group.

Feeding, both ad libitum and pair-fed groups, decreased ($P<0.05$) ruminal protein per unit DM relative to VFA and milk only treatments (Table 4). Ruminal RNA content and the ratio of RNA to protein were elevated in milk fed animals compared with the VFA infused group, while feeding the pelleted lamb starter resulted in intermediate values. Ruminal DNA was unaffected by dietary treatment, but the ratio of protein to DNA was increased ($P<0.05$) in the VFA treated animals compared with pair-fed animals. Duodenal protein was increased ($P<0.05$) in the milk fed and ad libitum fed groups compared to the pair-fed and VFA infused groups. Duodenal RNA was decreased ($P<0.05$) in the fed group compared with the milk-fed group and pair-fed, while the VFA infused groups had intermediate RNA concentrations. The ratio of duodenal RNA to protein was decreased ($P<0.05$) in the fed group in comparison to the milk fed group. Duodenal DNA was greater ($P<0.05$) in the pair-fed and VFA infused lambs compared to the milk-fed group. The ratio of duodenal protein to DNA was decreased ($P<0.05$) in the pair-fed and VFA infused lambs compared to the ad libitum fed and milk-fed lambs. Jejunal protein was decreased ($P<0.05$) in the VFA infused group and RNA was increased ($P<0.05$) in the milk-fed group. The ratio of jejunal RNA to protein was increased ($P<0.05$) in the milk fed group with no changes in the DNA concentration or the protein to DNA ratios. Ileal and colon protein, RNA and DNA were not affected by treatment. Feeding ad libitum increased ($P<0.05$) the tissue protein of the liver and pair-fed and VFA infused groups had elevated DNA per gram of dry weight compared with the milk-fed group. The DNA concentration of the *Longissimus dorsi* was increased in the pair-fed and VFA infused groups in comparison to the fed group.

Table 4
Visceral tissue protein, RNA, DNA and ratios of RNA to protein and protein to DNA from lambs with four dietary treatments

Tissue	Treatment[a]				SEM
	M	F	P	V	
Rumen					
Protein (mg/g dry wt.)	147.64[c]	105.55[b]	116.10[b]	144.11[c]	7.89
RNA (mg/g dry wt.)	16.57[c]	10.10[b,c]	8.72[b]	7.63[b]	2.48
DNA (mg/g dry wt.)	5.35	4.33	5.35	4.17	0.94
RNA:protein	0.11[c]	0.10[b,c]	0.08[b,c]	0.05[b]	0.02
Protein:DNA	27.90[b,c]	27.40[b,c]	22.50[b]	39.90[c]	5.99
Duodenum					
Protein (mg/g dry wt.)	125.37[c]	126.99[c]	107.16[b]	107.68[b]	4.87
RNA (mg/g dry wt.)	26.14[c]	16.94[b]	18.15[b,c]	19.35[b,c]	3.39
DNA (mg/g dry wt.)	10.67[b]	13.02[b,c]	20.03[c]	21.84[c]	3.41
RNA:protein	0.21[c]	0.13[b]	0.16[b,c]	0.18[b,c]	0.03
Protein:DNA	12.00[c]	12.30[c]	5.50[b]	5.20[b]	1.91
Jejunum					
Protein (mg/g dry wt.)	124.82[c]	128.90[c]	121.31[c]	110.05[b]	3.24
RNA (mg/g dry wt.)	27.74[c]	16.61[b]	15.32[b]	13.10[b]	2.96
DNA (mg/g dry wt.)	8.93	13.11	18.08	16.36	4.05
RNA:protein	0.22[c]	0.13[b]	0.13[b]	0.12[b]	0.03
Protein:DNA	14.40	12.60	8.80	7.60	2.93
Ileum					
Protein (mg/g dry wt.)	131.89	132.00	124.77	122.01	3.91
RNA (mg/g dry wt.)	23.18	47.93	19.06	17.26	13.29
DNA (mg/g dry wt.)	10.39	11.43	18.28	22.15	6.23
RNA:protein	0.18	0.36	0.15	0.14	0.10
Protein:DNA	14.50	15.10	8.50	10.00	4.35
Colon					
Protein (mg/g dry wt.)	81.33	73.44	62.83	42.06	15.61
RNA (mg/g dry wt.)	9.11	7.71	6.23	5.02	2.04
DNA (mg/g dry wt.)	4.05	4.70	6.11	4.28	1.25
RNA:protein	0.11	0.11	0.10	0.12	0.01
Protein:DNA	21.10	16.60	10.60	10.50	4.07
Liver					
Protein (mg/g dry wt.)	103.26[b]	113.87[c]	101.93[b]	98.24[b]	4.05
RNA (mg/g dry wt.)	17.69	15.41	12.83	14.44	2.11
DNA (mg/g dry wt.)	6.94[b]	7.98[b,c]	11.73[c]	14.85[d]	1.78
RNA:protein	0.17	0.14	0.13	0.15	0.02
Protein:DNA	15.30	16.60	8.80	6.90	2.36
Muscle					
Protein (mg/g dry wt.)	132.74	122.42	127.67	124.49	6.42
RNA (mg/g dry wt.)	4.32	4.41	3.62	3.09	0.88
DNA (mg/g dry wt.)	3.23[b,c]	2.71[b]	4.46[c]	4.47[c]	0.64
RNA:protein	0.03	0.04	0.03	0.03	0.01
Protein:DNA	44.50	50.50	29.80	28.20	6.75

[a] M, milk fed ad libitum; F, pellets ad libitum; P, pellets at restricted intakes; V, milk fed with VFA infusions.
[b,c] Means with superscripts that differ within rows are different ($P<0.05$; $n=3$ for all treatments).

4. Discussion

As expected, the lambs weaned to ad libitum intake of starter pellets consumed more ME and thus, gained weight at higher rates through the 28 d feeding trial. Also, the ME intake of the milk and pair fed animals was equivalent for the trial. Volatile fatty acid infusion resulted in a numerically increased ME intake/day on a metabolic body weight basis and did not appear to affect milk intake in these lambs. Although at higher doses of VFA infusion (25% estimated NE_g requirement) the lambs ceased milk intake and had to be removed from the trial, the 10% dose did not negatively influence the intake of milk.

When compared with grain and hay fed animals, neonatal ruminant animals maintained solely on milk during the first months of life exhibit limited ruminal development with respect to rumen weight (Tamate et al., 1962), capacity (Smith, 1961; Tamate et al., 1962), papillary growth (Warner et al., 1956; Tamate et al., 1962), degree of keratinization (Gilliland et al., 1962), pigmentation (Tamate et al., 1962) and musculature development (Warner et al., 1956; Smith, 1961; Tamate et al., 1962; Hamada et al., 1976). This lack of development is most likely due to the effective shunting of milk directly to the abomasum by the reflexive closure of the esophageal groove (Warner et al., 1956), thus preventing substrate from entering the rumen and establishing a ruminal microbial fermentation. In this study ruminal development was not stimulated by VFA infusion. This is likely due to inadequate concentrations of VFA being present in the ruminal lumen. Ruminal acetate concentration was the only VFA significantly elevated by VFA infusion in this experiment and acetate has been shown to have the least stimulatory effect on rumen epithelial development (Sander et al., 1959; Tamate et al., 1962). Either the quantity of VFA infused was insufficient to keep the rumen concentration elevated, or alternatively, the animals could have shunted VFA past the reticulorumen via closure of the esophageal groove (Warner et al., 1956). Because development of the omasum is also limited in these lambs, VFA shunted past the reticulorumen would pass directly into the abomasum, and presumably into the small intestine. Volatile fatty acid concentrations in the intestine were not measured in this experiment. However, this possibility would explain some of the effects of VFA infusion on intestinal mass.

Use of ruminally inert materials such as nylon bristles (Warner et al., 1956), plastic sponges (Tamate et al., 1962), wood shavings (Smith, 1961), and plastic cubes (Hamada et al., 1976) to simulate the physical stimulus of feed in the rumen results in increased rumen muscle but not papillary development. Increasing amounts of concentrate in the diet do not result in a change in rumen muscularity but in increased papillae density and papillae height in calves (Stobo et al., 1966) and in lambs (Rickard and Ternouth, 1965). Consistent with these observations, the physical development of the rumen, both weight and papillary development, were not different between the ad libitum fed lambs and the restricted lambs. However, the change in energy delivery from milk to pelleted lamb starter caused substantial changes in ruminal muscle development, implicating bulk as an important factor but not eliminating chemical factors.

Changes in tissue mass of the kidneys, liver, heart and lungs (Johnson et al., 1990) of ruminant animals and in the gastrointestinal tract of rats (Ferrell and Koong, 1986) has been previously demonstrated with increased DM intake and this has been largely attributed to the concomitant increase in energy intake. The service oriented tissues examined in the current experiment were not affected by changes in energy intake as a percentage of EBW, and intestinal size, which declines as a percentage of EBW from birth to maturity, was not further reduced by feed intake. Changes in liver mass of feed-restricted and re-fed lambs have been shown to occur in as little as three days (Wester et al., 1995). Furthermore, in feed-restricted and re-fed lambs portal drained visceral oxygen consumption returns to the consumption of fully fed control animals in as little as 28 days (Freetly et al., 1995), suggesting that enough time on treatment was provided in the current experiment to realize these effects. However, in contrast to the mature animals in previous studies, the lambs used in this experiment were presumably undergoing growth due to changes in the form of energy delivery in addition to growth due to the normal maturation process of a 12 week old lamb. Thus, changes in visceral organ mass occurring due to metabolizable energy intake may have been masked by the effects of tissue differentiation to meet

the new absorptive and metabolic requirements associated with solid feed intake.

In the current experiment, VFA infusions increased small intestinal mass as a percentage of EBW and the length of the intestine in the VFA infused lambs was numerically the longest of all of the groups but as a ratio of EBW the small intestine length was reduced. Additionally, the duodenal and jejunal sections from VFA infused lambs increased in weight and width relative to the milk fed controls. This was not due to increases in tissue water as there were no changes in epithelial dry matter. Cell size of the duodenal tissue in the VFA infused lambs, as determined by protein:DNA ratio, was reduced and in jejunal tissue this ratio was numerically reduced. Thus, a possible explanation, to account for the increased tissue mass observed, is that cell proliferation in the first two segments of the small intestine were stimulated by VFA administered in this manner. The VFA have been shown to be stimulatory towards cell proliferation in the rumen in vivo (Sander et al., 1959; Tamate et al., 1962) and in other tissues including colonic mucosa (Roediger et al., 1993). The response of the colon in this study is also consistent with this contention that luminal VFA could be stimulatory towards epithelial cell proliferation. Thus, although oral administration of VFA does result in significant changes in intestinal growth characteristics in developing ruminants, as a model for the investigation of ruminal development in immature sheep this model is ineffective because of the lack of an increase in ruminal VFA concentrations. Also, in mature ruminants it is questionable whether the VFA effects noted here would occur because of the capacity for the omasum to remove VFA from the lumen of the digestive tract prior to their appearance in the small intestine (Bergman, 1990).

5. Conclusions

In developing neonatal ruminants, intake of solid feed is necessary to promote normal ruminal development. In the present study, oral infusion of VFA did not stimulate ruminal development, however, intestinal tissue growth was stimulated. Additionally, energy alone is not the sole determining factor regulating visceral organ size during development in weaning age animals. Further research is required to determine the specific effects of nutrition on the energy metabolism of visceral organs and to elucidate the factors and mechanisms which control these important processes.

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