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Original article

Plane of energy nutrition on blood metabolites, milk production and lamb growth for Friesian ewes

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ABSTRACT

This study was conducted to evaluate the effects of a low metabolizable energy (LME) and high metabolizable energy (HME) diet on twenty-two Friesian ewes, milk production and nutritional status and their lambs. On day 100 of gestation, ewes were divided into metabolizable energy (ME) groups and fed alfalfa hay and rolled corn that provided either 80% low metabolizable energy (LME) or 140% high metabolizable energy (HME) of recommended ME requirement based on published NRC (2007) values for 70 kg ewes carrying twins, nursing twins and producing 1.5 to 2.9 kg milk/day. Treatment period was from day -42 of gestation (approximately six weeks) to six weeks post parturition. Lamb treatments included nursing from ewes on HME, LME and lambs artificially reared (AR) on goat's milk. Body weight and backfat (BF) were measured weekly for each ewe and BW weekly for lambs. Blood samples were collected weekly from ewes during the experiment and from neonatal lambs. Blood glucose, plasma urea nitrogen (PUN), creatinine, total protein (TPP) and triglycerides were analyzed to assess the nutritional status of both ewes and lambs. Weekly milk samples for each ewe were analyzed for butter fat, protein, lactose, milk urea nitrogen (MUN), somatic cell count (SCC), and solids-not-fat (SNF). Ewe body weight was not different between treatments. There were differences in BF with the HME group having more BF than the LME group. Ewe blood glucose, PUN, and TPP were significant for week. Milk fat

(MF) percentage, daily fat produced, and lactose were affected by energy treatment. The LME group displayed both higher MF percentages and daily fat in milk while the HME group had higher concentrations of milk protein and lactose percentages. Lamb weight showed weekly and treatment affects for HME, LME and AR) with the HME group weighing the most by the end of the experiment. Concentrations of plasma glucose, PUN, and creatinine resulted in differences with the HME group having the highest concentration of each component. Our results indicate that perinatal nutrition effects both the ewe and lamb as well as milk production. Because of the lower energy intake of the LME group, we see that nutrient partitioning occurs enabling the ewe to allocate energy towards growth of the fetus and to produce enough milk to sustain growth of the lamb post placental drop. This partitioning of energy came at the expense of body condition for the LME group, and to a lesser extent to the HME group, in order to produce adequate milk for the offspring.

1. Introduction

During gestation and lactation, the endocrine system of the ewe distributes nutrients throughout the body to support the fetus and thereby causes major changes affecting metabolic processes (Charismiadou et al., 2000). In this way, prenatal ewe nutrition is vital to both the mother and potential offspring (Charismiadou et al., 2000). Consequently, animal performance is contingent on the intake of metabolizable and digestible nutrients (Mertens, 1994). Deficiency or overabundance of nutrients will affect the animal's productive capabilities. Though some ewes may be fed what is considered the appropriate mixed diet based on ewe breed, size, gestational stage, and milk production needs (NRC, 2007), there is a possibility that fetal growth could be reduced because of a placental limitation on the supply of nutrients (Mellor, 1983). When this occurs, nutrient restriction during gestation shift nutrient partitioning towards the uterus to foster growth of the fetus (Celi et al., 2008). Additionally, underfeeding pregnant sheep can result in a variety of adverse effects on fetal and newborn lambs such as affecting placental size, growth of the fetus, fetal fat reserves allocation for use after birth, udder development as well as colostrum and milk production (Mellor, 1983; 1988). Likewise, metabolism can vary due to the amounts and ratios of absorbed nutrients, as well as the individual, and the interaction of, biochemical pathways (Mertens, 1994). With the multitude of interactions occurring, it is important to keep in mind that differences in breed, diet, environment and management can also affect nutrient requirements and utilization by the animals (Galvani et al., 2008).

We hypothesize that metabolizable energy will affect ewe composition and milk composition and in turn affect lamb growth. Our objectives were, first, to determine the effects of low metabolizable energy (LME) and high metabolizable energy (HME) on Friesian ewe and lamb fed simple diets of alfalfa and corn. Second, the effects of ME on milk production during early lactation were also determined. Third, to compare natural rearing of lambs on ewes to artificially reared (AR) lambs fed goats milk.

2. Materials and methods

Twenty-two East Friesian ewes, between the ages of 2 and 5 years, were bred to East Friesian rams under the approval of the BYU IACUC (#16-1103). Rams were fitted with marking harnesses and as the ewes were marked the date was recorded. After 21 days, the marker color was changed and the new color marked ewes breeding recorded. Pregnancy was determined by ultrasound initially, and then confirmed by blood analysis (Utah Veterinary Diagnostic Laboratory, Logan, UT, USA). A farm ear tag identified each ewe. Three days after birth, each lamb was fitted with a farm tag. One day prior to beginning the experiment (third trimester), ewes were

vaccinated with a commercial 8-way product (Ultrabac 8®, Zoestis Animal Health, Parsppany, NJ, USA) and dewormed with a broad-spectrum anti-parasitic (Valbazen®, Zoestis Animal Health, Parsppany, NJ, USA).

Treatment groups were fed either an 80% (LME) or 140% (HME) of recommended ME requirement based on the Small Ruminant NRC (2007) for 70 kg ewes for late gestation and early lactation carrying or supporting twins producing 1.53 to 2.87 kg of milk per day. For the gestation period, the NRC ME requirement was 3.50 and 6.12 MCal for the LME and HME groups respectively. The lactation period NRC ME target was 4.38 for LME and 7.67 MCal HME. Ewes were evenly divided into treatment groups based on parity and age. For both groups each group had four ewes in their 3rd parity, four in their 2nd parity and 3 in their first parity.

During the first two trimesters of gestation, ewes were housed in a common paddock and fedalfalfa hay (*Medicago sativa*) (Table 1) at 0700. Water was provided throughout the experiment *ad libitum* and trace mineral salt blocks present in each paddock. On day 100 of gestation (approximately the beginning of the last trimester), ewes were randomly divided into ME treatment groups to ensure that ewe ages were equally represented in the two treatments, with 11 ewes per diet.

Table 1
Chemical composition[a] of the two diet components (alfalfa and corn) expressed on a percent dry matter basis.

	Alfalfa	Corn
Crude protein	21.4	8.9
NDF	37.1	11.0
ADF	27.9	4.1
Lignin	7.4	1.1
NFC	28.3	73.8
Starch	0.6	66.0
Fat	2.7	4.5
Ash	10.5	1.8
NEL, Mcal/kg	1.39	2.07

[a]Wet chemistry determination by Dairy One, Ithaca, NY.

Table 2
The diet formulation on dry matter basis of both the LME and HME groups adjusted for late gestation and early lactation.

	Gestation		Lactation	
	LME	HME	LME	HME
DMI, kg/d	1.59	2.10	1.95	2.58
Alfalfa, kg/d	1.350	1.786	1.459	1.932
Corn, kg/d	0.236	0.314	0.486	0.645
NFC, %	35.1	35.1	39.6	40.8
NDF, %	33.1	33.2	30.5	30.5
Protein intake, g/d	310	410	355	470

From day 100 of gestation to parturition (approximately day 145), ewes were fed daily (0700 hr) treatment diets (Table 1 and Table 2). During the treatment phase, the ewes were brought into the milking parlor at 0700 and given their individual daily allotment of corn. Hay was then given in the paddock feed bunks. Ewes were housed in two dry lot pens with access to shelter bedded with straw where the ewes gave birth. Prior to nursing ewes and lambs were sampled as outlined below. After parturition and sampling, ewes with lambs were moved to a 1.5 m x 1.5 m (crib) pen where they remained for three days to ensure "mothering-up" occurred. If a ewe had triplets (15 ewes), quadruplets (1 ewe), or it was determined the ewe was unfit to raise a lamb (2 ewes), the lamb or lambs were moved to the artificially reared (AR) lamb group, housed in a 4 m x 5.5 m pen. Artificially reared lambs received 240 ml of ewe colostrum within the first 6 hours postpartum. After the colostrum, the AR lambs were fed 75 ml of fresh goat milk four times per day until d-7. From d-8 to d-17 lambs were fed 120 ml four times per day.

From d-15 to d 21 lambs were fed 240 ml three times per day. From d-22 to d-42 lambs were fed 480 ml twice daily.

At parturition, ewes were weighed, BF measured, and blood drawn post placental drop, before lambs nursed and prior to putting the ewe and lambs into crib pens. At birth, lambs were weighed and 2ml of blood drawn prior to nursing and being put into the cribs with their mother, or in the case of the AR lambs, into the lamb nursery. After the three days in the crib, ewes and lambs were reintroduced back into the treatment group pen.

Ewes and lambs were weighed weekly from parturition to 6-weeks postpartum at 1000 hr on a platform scale, while lambs were weighed on a portable desktop scale until large enough (3000 g) to use the platform scale. Body condition was determined by backfat (BF) depth over the 12th rib using A-mode ultrasound (Preg-Alert Pro, Renco, Golden Valley, MN, USA). Blood was drawn (5 ml) weekly using a syringe and 20 ga. needle from the jugular vein of each ewe. The site of extraction was shaved and cleaned with alcohol prior to the blood draw. Plasma was harvested by centrifugation at 2,500 x g and 4 ˚C for 20 min, aliquoted and stored at -20 ˚C for later analysis. Twenty-four hr milk production was measured by holding the lambs from the ewes for 24 hr (0700 to 0700) three days after weight, blood and BF samples were collected. Milk weight was measured and a 20ml sample collected in milk analysis vials.

Plasma from both ewes and lambs was analyzed for glucose, urea nitrogen, creatinine, total plasma protein, and triglycerides using TECO colorimetric kits (TECO Diagnostics, Anaheim, CA, USA). Weekly milk samples from each ewe were analyzed for butter fat, protein, lactose, urea nitrogen, and somatic cell count by Rocky Mountain DHIA (Logan, UT, USA).

Statistical analysis was conducted with the proc Mixed module in SAS (2002). Fixed main effects included ME treatment and week, while animal was random to account for repeated measures. Least square means for treatment and week were determined to be significant at $P<0.05$. Model comparisons included weekly ME treatment comparisons for the response variables weight, BF, metabolites, milk production and milk composition. Main effect comparisons were also made between prepartum, parturition and postpartum stages. Treatment and week main effect comparisons were analyzed for the lamb response variables and expressed as least square means and determined significant at $P<0.05$.

3. Results and discussion

Two ewes (one from each treatment, both 3rd parity) did not complete the study due to bad utterand death during lambing. The LME groups produced 29 lambs while the HME group produced 21 lambs. Eleven lambs were moved to the AR group. Hay and corn grain were completely consumed by the ewes of both groups, leaving no feed residual, therefore feed intake for each group is that presented in Table 2.

Ewe body weight (Table 3) was not different between treatment groups. As expected, there was a sharp drop in weight at parturition for all ewes, with a difference of 20 kg between pre- and post-parturition (Table 4). Prepartum weights increased during the third trimester from 75.2 kg to 84. 5 kg for the LME group and from 76.1 kg to 84.2 kg for the HME group. After parturition there was no change in weight for either group. Postpartum weights averaged 68.7 and 67.2 kg for LME and HME respectively. Back fat (Fig.1) showed a difference by treatment. The LME group backfat steadily decreased from week -6 (3.0 mm) to week +6 (1.8 mm), while HME ewes increased from 3.3 to 3.6 mm between week -6 to week -3 then decreased to 2.7 mm at week -1 and maintained until week +4 where they decreased to 2.4 at week +6. Weekly blood metabolites for ewes (Table 3) showed no treatment effect for plasma glucose concentration however, there was a week effect. For both the HME and LME groups, parturition values differ ($P<0.05$) from the weeks prior and post parturition with a concentration of 9.43 mmol/l and 10.19 mmol/l; respectively. Average prepartum concentration for this study was 3.91 and 4.32 mmol/l for LME and HME respectively and 3.80 and 3.77 mmol/l postpartum (Table 4).

Plasma urea nitrogen varied significantly between treatment groups where LME PUN concentrations steadily increased from 4.3 mmol/l at week -5 to 7.0 mmol/l at week -1. During this period, HME concentrations fluctuated between 3.3 to 3.7 mmol/l. At parturition, both HME and LME were similar at 4.5 mmol/l. Postpartum concentrations averaged 4.3 and 4.9 mmol/l HME and LME. There were no differences in creatinine for treatment or week. Prepartum concentrations were 72.9 and 67.9 µmol/l for LME and HME, 77.0 and 69.9 µmol/l at parturition and 69.4 and 74.3 µmol/l postpartum.

Total plasma protein displayed a weekly effect in both the HME and LME groups. From week -5 to week -1 LME TPP decreased from 68.6 to 57.4 g/l, while, HME fluctuated between 73.2 to 65.3 mmol/l. At parturition, both

HME and LME groups increase to 73.6 and 69.3 mmol/l. The LME group remained at this level for the remainder of the experiment. At week +1 HME levels drop to 50.9 mmol/l before increasing to an average of 64.0 mmol/l for the remainder of the experiment. Prepartum triglyceride levels were 0.247 and 0.275 mmol/l for LME and HME, increasing to 0.280 and 0.291 mmol/l at parturition then dropping to 0.195 and 0.192 mmol/l.

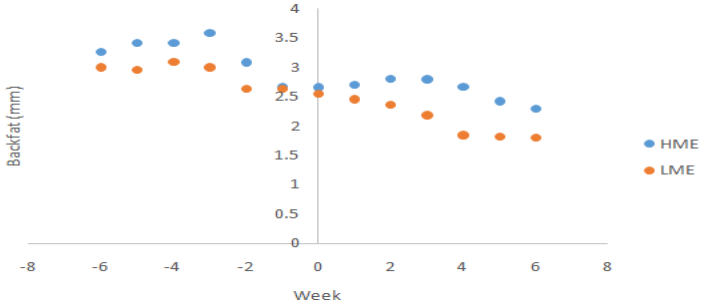

Fig. 1. Backfat measurements of ewes fed at 80% (LME) or 140% (HME) of NRC (2007) energy requirement. Treatment and week differences are significant at P<0.05 (SEM 0.22).

There was no difference in treatment or week effect for milk yield (Table 5), averaging 1.665 kg/d for HME and 1.779 kg/d for LME. Fat percentage was different (P<0.05) for treatment, 2.53% for HME and 4.43% for LME. Average daily milk fat was also only different between treatment groups, 44.8 g/d for HME and 87.7 g/d for LME. Milk protein percent was different for week where HME decreased from 4.93 to 4.44% and no change noted for LME (average 4.75%). Daily milk protein did not differ between treatment or week, averaging 75.0 and 85.0 g/d for HME and LME respectively. Milk lactose percent was different between treatment, 5.43% for HME and 5.12% for LME. Daily lactose averaged 89.9 for HME and 90.3 g/d for LME; no differences noted. No differences were determined for solids not fat (SNF) or MUN. Milk samples and weights were corrected for energy based on the eq. (Hemme, 2017):

ECM (g/d)= (0.327 x milk yield g/d) + (12.95 x fat g/d) + (7.2 x protein g/d)

Where EMC is energy-corrected milk. ECM was not different for treatment or week. The average for the two groups are 2279 g/d LME and 1793 g/d for HME.

Lamb weight (Fig.2) increased steadily for 6 weeks post parturition with lambs in the HME group increasing from 4.625 kg to 15.288 kg, a 231% increase. LME lamb weights increased from 4.180 kg to 13.221 kg (216% increase), while the AR weights increased from 4.256 kg to 12.300 kg (189% increase) over the six-week period. There is no difference in birth weight across the treatments and treatment differences do not become evident until weeks 5 and 6, where the HME group weights were 2.052 and 2.988 kg greater than the LME and AR respectively.

Lamb blood metabolite results are presented in Table 6. There is no treatment effect for glucose concentrations (Fig. 3) between the lamb groups. However, there is a weekly difference for blood glucose between week zero (at birth; from 2.37 to 3.48 mmol/L) increasing to between 8.32 to 9.57mmol/l at week 2 then decreasing to between.

Table 3
Ewe weight, backfat and blood metabolites of dairy sheep fed at 80% or 140% of energy requirement for six weeks prior, at, and six weeks post parturition.

		Weeks from Parturition														P<0.05[b]		
	Diet[a]	-6	-5	-4	-3	-2	-1	0	1	2	3	4	5	6	SEM	TRT	Week	TxW
Weight,	LME	76.1	79.1	81.9	83.8	85.6	84.2	66.9	66.6	69.5	68.6	67.0	65.0	66.1	2.47	ns	+	ns
kg	HME	75.2	78.1	80.0	81.5	84.2	84.5	67.6	69.7	69.7	65.8	65.3	65.3	64.5				
Backfat,	LME	3.0	3.0	3.1	3.0	2.6	2.6	2.5	2.5	2.4	2.2	1.6	1.8	1.8	0.22	+	+	ns
mm	HME	3.3	3.4	3.4	3.6	3.1	2.7	2.7	2.7	2.7	2.8	2.7	2.4	2.4				
Glucose,	LME	3.20	3.31	3.89	4.14	4.55	4.43	10.18	3.18	3.75	3.84	4.22	4.34	3.65	0.51	ns	+	ns
mmol/l	HME	3.81	3.91	4.13	4.76	4.49	4.81	9.43	4.10	3.05	3.56	3.97	3.72	4.22				
UreaN,	LME	4.80	4.33	5.26	6.35	6.84	7.02	4.55	3.44	3.54	3.78	4.84	5.00	5.01	1.28	ns	ns	ns
mmol/l	HME	4.04	3.77	3.44	3.73	3.89	3.30	4.59	3.48	4.87	4.54	4.81	5.90	5.18				
Creatinine,	LME	67.2	72.3	85.3	73.2	66.7	73.2	77.0	70.7	65.3	67.5	68.9	70.0	74.9	4.42	ns	ns	+
µmol/l	HME	64.3	67.8	63.0	67.2	69.1	75.4	69.9	72.9	72.7	75.4	69.9	79.7	75.3				
TPP,	LME	68.0	68.6	66.7	60.7	64.0	57.4	69.3	66.0	62.2	64.9	59.0	69.5	69.6	3.2	ns	+	ns
g/l	HME	73.2	73.3	68.1	65.3	66.6	65.3	73.6	50.9	65.4	62.7	65.9	66.2	70.2				
Triglycerides,	LME	0.240	0.255	0.254	0.264	0.243	0.227	0.280	0.194	0.174	0.203	0.199	0.216	0.184	0.018	ns	+	ns
mmol/l	HME	0.210	0.275	0.308	0.275	0.316	0.265	0.291	0.185	0.166	0.227	0.178	0.210	0.187				

[a]LME = Low energy diet; HME = High energy diet. [b]Symbol + Indicates significance.

Table 4
Weight and blood metabolite comparisons of pre- and post-parturition ewes fed 80 or 140% required energy intake.

		Stage				P<0.05		
	Diet[a]	Pre	Parturition	Post	SEM	TRT	Stage	TxP
Weight, kg	LME	81.8	66.8	67.2	5.11	ns	+	ns
	HME	80.7	67.5	68.7				
Backfat, mm	LME	2.89	2.55	2.05	0.12	+	+	ns
	HME	3.24	2.66	2.71				
Glucose, mmol/l	LME	3.92	10.19	3.80	0.22	ns	+	ns
	HME	4.32	9.43	3.77				
Urea N, mmol/l	LME	5.75	4.57	4.25	0.79	ns	ns	+
	HME	3.68	4.57	4.75				
Creatinine, mg/dL	LME	0.825	0.871	0.785	0.028	ns	ns	+
	HME	0.768	0.791	0.840				
TPP, g/l	LME	64.2	69.1	64.9	1.4	ns	+	ns
	HME	69.3	74.2	63.8				
Triglycerides, mmol/l	LME	0.247	0.280	0.195	0.009	ns	+	ns
	HME	0.275	0.291	0.192				

[a]LME = Low energy diet; HME = High energy diet. [b]Symbol + Indicates significance and ns Indicates no significance.

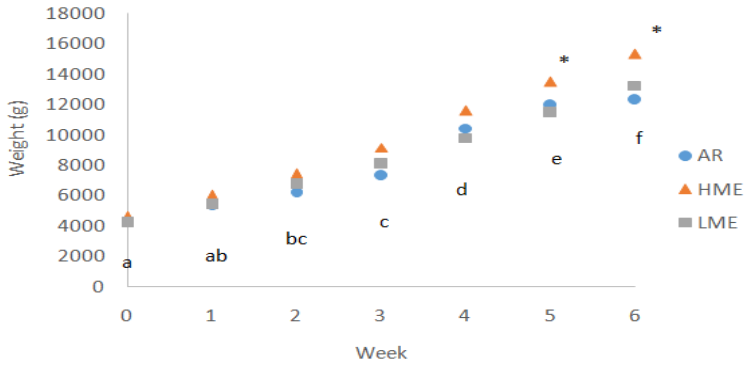

Fig. 2. Lamb weight changes from birth to six-weeks of age for artificially reared (AR), high energy (HME) and low energy (LME) lambs. Asterisk (*) indicates difference (P<0.05) between HME group and the other two (LME and AR), while "abcdef" indicate differences (P<0.05; SEM 2.47) between weeks.

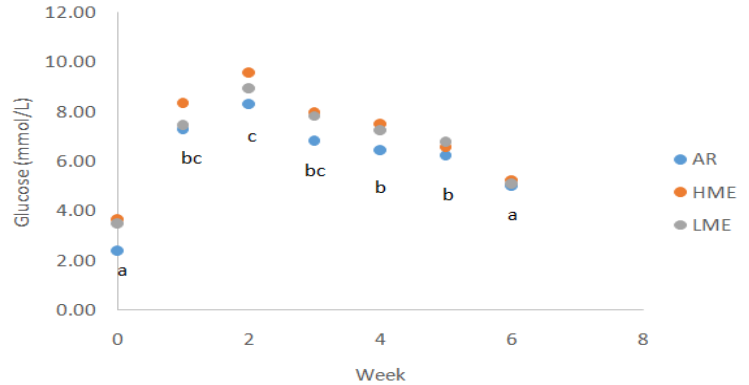

Fig. 3. Effects of maternal energy intake (80% vs. 140%) on blood glucose concentrations of lambs naturally reared on dams (HME=140%; LME=80%) or artificially reared (AR) on goats milk. Week means with differing "abc" are different at P<0.05 (SEM 0.52). There are no treatment differences.

5.0 to 5.26 mmol/l at week 6. Plasma urea nitrogen was significant (P<0.05) for week effect, where at birth levels were 4.8, 4.9 and 5.5 mmol/l for LME, HME and AR respectively. The LME and HME PUN levels increased to 6.4 mmol/l at week 1, while the AR group dropped to 2.6 mmol/l. Week 2 to 6 PUN levels fluctuated between 2.00 to 3.89 mmol/l.

Blood creatinine was not significant between treatments, but was for week with levels higher at birth ranging from 204.2 to 157.9 µmol/l. The levels decrease to an average of 55 µmol/l at week 2 and remain constant at this level for the remainder of the experiment. Total plasma protein was different for both treatment and week. At birth, the levels are 49.2, 42.2 and 46.8 g/l for HME, LME and AR respectively. The remainder of the experiment the levels fluctuated between 53 and 67 g/l, with LME most often being the highest and AR the lowest. Triglyceride concentrations were not different between treatments or weeks, ranging between 0.367 to 0.774 mmol/l.

Ewe body weights pre- and postpartum were not different between the two treatment groups. The short period (approximately 45 days) the energy diets fed may be the reason there was no difference between the weights of our ewes. Mora et al. (1996) demonstrated that goats have the ability to cope with moderate levels of malnutrition.

Table 5
Milk yield and milk composition of dairy ewes fed diets providing 80% or 140% of energy requirement.

		Week from parturition						P<0.05[c]		
	Diet[a]	1	2	3	4	5	SEM	TRT	Week	TxW
Milk yield	LME	1783	1838	1813	1886	1573	260	ns	ns	ns
g/d	HME	1667	1785	1657	1565	1650				
Milk Fat,	LME	5.00	3.95	3.94	4.52	4.74	0.61	+	ns	ns
%	HME	3.34	2.72	2.44	2.16	2.01				
Milk Fat,	LME	94.3	84.3	80.6	101.2	77.9	19.6	+	ns	ns
g/d	HME	64.3	46.4	42.2	35.4	35.6				
Milk Protein,	LME	5.00	4.63	4.67	4.62	4.85	0.13	ns	+	ns
%	HME	4.93	4.62	4.53	4.45	4.44				
Milk Protein,	LME	89.7	85.9	84.6	87.2	76.6	12.4	ns	ns	ns
g/d	HME	81.8	79.9	73.7	68.5	70.8				
Milk Lactose,	LME	5.03	5.08	5.29	5.06	5.16	0.11	+	ns	ns
%	HME	5.27	5.54	5.51	5.41	5.43				
Milk Urea,	LME	4.89	5.25	5.21	5.29	5.57	0.48	ns	ns	ns
mmol/l	HME	4.71	5.86	6.75	6.64	5.82				
ECM[b]	LME	2433	2334	2265	2547	2179	418	ns	ns	ns
	HME	1966	1762	1621	1462	1512				

[a]LME = Low energy diet; HME = High energy diet; [b]ECM = Energy corrected milk (g/d) = (0.327 x milk yieldg/d) + (12.95 x fat g/d) + (7.2 x protein g/d). [c]Symbol + Indicates significance.

Addah et al. (2017) suggest that sheep are able to compensate for sudden changes in nutrient restriction by increasing the efficiency of nutrient absorption and utilization, even though the sudden shift initially reduces average daily gain. Though there were no differences between weights of our two treatment groups, there was a difference in BF during the study. Backfat, used as a body condition estimate, is the last body fat reserve to be deposited, with internal deposited first followed by inter-muscular. These fat stores provide the animal with reserves that can be utilized to maintain substrate for required energy needs. When energy balance is negative lipolysis beginning with BF provides energy substrates to meet the body's energy needs. Though there is a numerical decrease in BF from the initiation of the study (approximately 0.5 mm for both treatments), differences do not become apparent until after parturition when the energy needs of lactation overcome the dietary supply. The sharpest decline of prepartum body condition for both groups was from week -3 to parturition suggesting that energy levels prior to parturition may not be adequate to meet the energy demands placed on the ewe for fetal growth and preparation for lactation. The postpartum decline of BF for the LME ewes and week +4 decline is further evidence of the effects of limiting energy requirements on lactating Friesian ewes.

Table 6
Effects of maternal energy intake (80% vs. 140%) on weight and blood metabolites of lambs naturally reared on dams or artificially reared on goat milk for six weeks post birth.

		Weeks from birth								P<0.05[b]		
	Diet[a]	0	1	2	3	4	5	6	SEM	TRT	Week	TxW
Weight, kg	LME	4180	5378	6722	8076	9771	11426	13221	520	+	+	ns
	HME	4625	5997	7442	9158	11575	13478	15288				
	AR	4256	5360	6161	7304	10416	11933	12300				
Glucose, mmol/l	LME	3.48	7.46	8.95	7.83	7.25	6.80	5.10	0.52	ns	+	ns
	HME	3.66	8.37	9.59	7.99	7.53	6.59	5.26				
	AR	2.37	7.30	8.32	6.82	6046	6.24	5.00				
Urea N, mmol/l	LME	4.91	6.39	2.00	1.98	2.40	3.26	3.65	0.64	ns	+	+
	HME	4.83	6.44	2.43	2.25	2.93	3.62	3.89				
	AR	5.54	2.61	2.93	2.17	2.85	2.92	3.25				
Creatinine, mmol/l	LME	157.9	74.1	46.0	64.4	49.1	57.9	57.9	11.5	ns	+	ns
	HME	204.2	111.8	56.2	68.4	58.8	55.2	54.0				
	AR	177.7	59.3	59.1	74.5	56.5	57.9	65.8				
TPP, g/l	LME	42.2	63.9	55.9	59.7	57.8	57.9	66.8	2.3	+	+	+
	HME	49.2	62.4	58.7	62.0	58.0	56.2	58.4				
	AR	46.8	54.3	53.3	56.5	53.0	53.0	56.7				
Triglycerides, mmol/l	LME	0.552	0.576	0.500	0.638	0.774	0.561	0.405	0.066	+	+	ns
	HME	0.554	0.531	0.596	0.580	0.668	0.598	0.570				
	AR	0.432	0.498	0.463	0.498	0.531	0.367	0.470				

[a]LME = Low energy diet; HME = High energy diet; AR = Artificially reared lambs. [b]Symbol + Indicates significance, ns: Indicates no significance.

Blood metabolite values provide an understanding of how various factors influence general nutritional status. The combination of these blood metabolites provides a picture of how administered treatments affect metabolic processes. In the case of this experiment, how does dietary energy level affect nutritional status of Friesian ewes and lambs. Burton et al. (2003) and Celi et al. (2008) report glucose responses in pre and postpartum alpacas and goats show a spike in blood glucose at parturition, similar to the response noted in our sheep. Leat (1974) also observed an increase in the glucose concentration in ewe plasma within 2 to 3 days prior to parturition followed by a decrease in levels 20 days postpartum. The period between late gestation and early lactation is an intense metabolic transition phase from providing nutrients to the fetus to lactogenesis. Bell (1995) concluded that the gravid uterus absorbs 30 to 50% of the ewe's glucose supply, thus putting stress on the ewe to maintain required glucose levels. Homeorhetic hormones (e.g., glucocorticoids, growth hormone, prolactin and estradiol) interact with homeostatic hormones (e.g., insulin and cortisol) to regulate glucose levels (Tucker, 1985). In the case of this experiment, with the fetus born, the large amount of maternal glucose going to the fetus has stopped and the glucose regulation has not yet adjusted. The ewe now must transition glucose to the needs of lactation.

When protein intake is in excess or energy is limiting, urea N levels will increase due to the catabolism of amino acids either for fat stores or for energy needs. Increases in protein and energy can increase retention of nitrogen in growing ruminant animals and may result in an increase of PUN (Tur et al., 2017). Recycling PUN via the rumen is important for microbial growth and function and improves nitrogen utilization (Wang et al., 2012). Urea N not taken up by the rumen is excreted in the urine. Excess concentrations of urea in the blood can affect multiple physiological processes including production of milk, immune function, embryo survivability and reproductive efficiency (Dominic et al., 2014). Several studies have stated that PUN serves as an indirect indicator of the energy or protein levels in the diet in conjunction with levels of energy required (Ramin et al., 2010). In this study, PUN levels for the LME group increased from approximately 4.5 to 7.0 mmol/l between week-5 and parturition, while the HME group PUN remained relatively constant between 3.5 and 4.0 mmol/l. This indicates the LME ewes may have shifted to protein catabolism to meet energy needs brought on by the dietary energy restriction.

Triglyceride concentrations in the blood provide an indication of fat metabolism, where low levels indicate malnutrition and high levels obesity. Prepartum triglyceride levels are higher compared to postpartum indicating

there is a shift in nutrient status and that the postpartum ewes have a higher energy demand than prepartum. This is brought out in the NRC (2007), where lactating ewes require higher energy than gestating ewes. What these metabolites in conjunction with the body condition indicate is that the requirements published in the NRC (2007) may be inadequate for Friesian dairy sheep.

Due to its nutritional composition, sheep milk contains more nutrients and a larger supply of total solids than cow or goat milk providing a source of proteins, lipids, calcium and phosphorous while balancing a similar quantity of carbohydrates, fat, and proteins (Recio et al., 2009). Several factors affect milk yield including stage of lactation, environmental factors, feed quality and intake, and genetics to name a few (Collier et al., 2017; Pulina et al., 2007). Lactose synthesis controls water secretion; thus, lactose determines milk volume osmotically (Miglior et al., 2006). Additionally, protein and fat concentrations in milk are largely determined by dietary protein, VFA production in the rumen and the water content driven by lactose (Henao-Velasquez et al., 2014).

The equation to determine ECM takes into account the grams of fat and protein as well as milk volume. Somewhat surprisingly, the LME group has a higher milk fat than the HME group, but when expressed on an ECM basis there are no differences between the groups. Cannas et al. (2013) found that ewes fed lower amounts of non-fiber carbohydrates (NFC) produced more milk than those fed more NFC. A comparable result occurred in this study where the ewes in the LME group produced more milk than those in the HME group. Like the ewes in the Cannas et al. (2013) study, this may be a result of ME being shuttled towards fat reserves rather than milk production. Milk fat varies greatly during the lactation period, between ewes, between daily milking, between milking sheep breeds, and due to season and climate (McDonald et al., 1995; Milis, 2008). This variation can be due in part to concentration of volatile fatty acids (VFAs) which originate in the rumen. The proportion and type of volatile fatty acids produced in the rumen depend on the substrate metabolized and the species of bacteria present (Dijkstra, 1994). Acetate and butyrate are the primary precursors for milk fat synthesis whereas propionate is glucogenic (Bergman, 1990; Urrutia and Haveratine, 2017). Our study did not focus on VFAs, however a difference in milk fat concentration may be attributed to differing levels and composition of VFAs. In goats, Eknæs and Skeie (2006) and Eknæs et al. (2006) concluded that milk yield was not only affected by the mobilization of tissue energy, but it also affected milk composition; specifically, the fatty acid profile. Other factors that affect milk fat concentration include energy balance of the ewes, neutral detergent fiber (NDF) fraction in forages consumed, NFC, as well as particle size of the feed, amount of feed consumed, and the fatty acid composition of dietary fat supplements (Pulina, 2006). Forage source has an impact on milk fat that is independent of energy intake (Goetsch et al., 2011). Milk fat synthesis is stimulated via diets rich in digestible fiber, likely through the enhanced supply of acetate to the mammary gland (Cannas et al., 2013). Milk fat yield in goats was found to be greater for diets consisting of higher forage (60 to 65%) content (Álvarez et al., 2007; Ngwa et al., 2009).

Unlike the findings of Alvarez et al. (2007) and Ngwa et al. (2009), this study found that milk fat was higher for ewes in the LME group. Forage source, rather than energy intake, has an impact on milk fat concentration (Goetsch et al., 2011). The LME sheep in our study were limit fed the alfalfa in addition to lower corn grain to achieve a level of 80% ME. The HME group was fed more than the required dry matter intake (NRC, 2007) and no hay refusal was noted, leading us to conclude that even the HME were limit fed to some degree. Amount of hay (forage) provided for each treatment group could still be too low for Eastern Friesian causing no difference in milk yield or milk fat concentrations.

Ewes in the HME group had on average higher backfat than those in the LME group, 3.0 and 2.5 mm respectively, supporting this assumption. Cannas further suggests that higher milk production in sheep with lower NFC could be the result of a more marked partitioning of dietary energy towards milk synthesis (Cannas et al., 2013). Our results indicate that ewes fed 140% ME (HME) provided an energy level for milk component production that required less body reserve energy, whereas those fed 80% ME (LME) used required more body reserves resources for milk production.

Urea nitrogen is a waste product derived by the breakdown of protein, synthesized in the liver, circulates in the blood and is excreted in the urine. Blood urea concentrations rapidly equilibrate with body fluid pools such as the mammary gland. In the secretory cells of the mammary gland, urea moves into the milk and becomes a non-protein nitrogen component of milk (Cannas, 1998; Gustafsson and Palmquist, 1993). MUN and blood urea nitrogen concentrations are used to evaluate diets fed to ruminants because they are considered to be adequate indicators of protein metabolism and intake (Jelinek et al., 1996; Roseler et al., 1993). Though there are no differences between MUN or PUN in our study, at week three and four (when there were high concentrations of MUN in the HME group; 13.5 mmol/l and 13.3 mmol/l), milk production decreased. Weeks 3 and 4 for the HME

group were the only times MUN concentrations exceeded 2.6 mmol/l. This could be a result of the alfalfa hay crude protein level. Diets used for this experiment were not isonitrogenous while CP was slightly below requirement for the LME group and well above requirement for the HME group.

Lactose concentrations were higher for the HME group throughout the 6-week collection period, with overall means of 5.43% and 5.12% for HME and LME respectively. Henao-Velasquez et al. (2014), stated that lactose levels differ daily in milk production and differ in concentration of fat, milk urea nitrogen, glucose availability and somatic cell count. Our findings were similar in that lactose levels followed a similar curve as the MUN levels, with a low concentration of both components at week one, a slight increase through subsequent weeks, and finally a decrease at week five. ECM was not significant for treatment, week or the interaction.

Fetal growth during the third trimester varies due to ewe nutritional status during late gestation (Robinson, 1980). The fetus however, does increase by nearly 75% during this time. Late gestation is recognized as a highly energy-inefficient physiological process for ruminants due partly to the high expenditure of energy for maintenance and growth of the fetus (Kiani, 2006; Lodge and Heany, 1970). Birth weight of lambs was not different across our three treatments. The AR group was a result of lambs born to ewes from both ME treatments who were unable to raise the lamb on their own. Because they were evenly a result of both groups coming from sets of twins or triplets, no differences were noted in birth weights between the groups. Lamb weight increased from birth to the end of our experiment (six weeks), with the HME group showing great weight gain despite no difference in milk yield, milk composition or ECM between the treatment groups. Ewes in this study were fed the alfalfa hay *ad libitum* prior to the initiation of the experiment. The lack of difference between birth weights of the two ME groups may be attributed to the LME utilizing feed more efficiently as explained by Lu et al. (2005) or due to fat reserves in the ewes that were able to compensate for the restriction in energy intake, or both.

Plasma glucose levels were different at parturition and weeks two and three displaying a weekly effect but no treatment effects. Glucose concentrations for each group were 6.08 mmol/l for AR, 7.00 mmol/l for HME and 6.70 mmol/l for LME. Milk lactose and other glucogenic compounds have been shown to increase blood glucose (Rauprich et al., 2000). One week after parturition, there was a sharp increase in the concentration of PUN for the LME and HME groups. At week two, the HME group and the AR group continued to exhibit high concentration of PUN, though the LME group's levels were significantly lower. Kirk and Walker (1976) stated that neonatal sheep have difficulty excreting urea the first few days of life. However, lambs become more efficient as they age, as evidenced by the PUN concentration beginning to level out six-weeks post-birth similar to alpaca cria (Burton et al., 2003).

Creatinine levels were higher overall in the HME group than in the LME and AR groups. There was a drop in creatinine levels one week following parturition for all three groups after parturition and concentrations leveled out without a significant increase. Burton et al. (2003) described how metabolic pathways are adjusted to new sources of substrate during this first week of life. Protein mobilization and kidney function may account for the high levels of creatinine during the first week of life (Burton, 2003).

4. Conclusion

The results of this study demonstrate that perinatal and postnatal nutrition affects ewe and offspring metabolic processes. Energy restriction in the LME group resulted in nutrient partitioning allowing ewes to produce milk that facilitate lamb growth such that they grew at a rate similar to those from the HME group. It is evident that ewes can adapt to a restricted diet, although body condition will be compromised so that adequate milk is produced for the lambs. The simple diet regime implemented to meet the needs of the HME ewes during three different stages of life (late gestation, parturition, and lactation) were not able to offset the use of body reserves. This indicates a redistribution of body reserves for lactation.

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