Altering ewe nutrition in late gestation: II. The impact on fetal development and offspring performance[1]

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ABSTRACT: The present study was conducted to evaluate the effects of offering Belclare X ewes a single diet rationed to 80, 100, or 120% of recommended ME requirements from d 119 of gestation to parturition, with concurrent changes in other dietary nutrients. The effects on the development of the fetus and subsequent offspring performance to weaning were monitored. Sixty twin-bearing ewes were allocated to 1 of 3 dietary treatments based on Agricultural and Food Research Council recommendations (AFRC, 1993) as amended by Robinson et al. (2002a) as follows: 80% of predicted ME requirement, 100% of predicted ME requirement, and 120% of predicted ME requirement. Ewes were individually fed for the final 4 wk of gestation. Diets fed were grass silage based; however, when silage intake failed to meet ME requirements, ewes were offered varying quantities of concentrates, on an individual basis, to ensure they met their required daily ME allocation. Concentrates offered were composed of 40% barley, 22% beet pulp nuts, 20% distillers' dried grains, and 14% soybean meal, on a DM basis. At birth, lambs were weighed, behavioral and skeletal measurements were recorded, and plasma blood samples were collected. At 1 h postpartum, a subset of lambs (*n* = 10) per treatment was euthanized to assess organ weight and intestinal morphology. At birth, there was no effect of treatment on lamb live weight at birth ($P = 0.31$), although lambs born to ewes offered 120% ME had a larger thoracic circumference ($P = 0.05$). Lambs born to ewes offered the excess energy treatment (120% ME) were quickest to stand and attempt to suckle after birth, in addition to having a greater live weight at weaning ($P = 0.01$) and ADG from birth to weaning ($P = 0.05$). Nutritional treatment had no effect on the organ weights ($P \geq 0.11$) or the ileal morphology ($P \geq 0.62$) of the lamb measured at 1 h postpartum. In summary, the impact of applying a dietary alteration to ewes in late gestation is not directly reflected in organ weight or total live weight at birth but is present at weaning, therefore outlining the poor reliability of using birth weight as an indicator of maternal nutrition during late gestation.

Key words: fetal programming, lamb performance, maternal gestational nutrition, neonatal development, sheep

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INTRODUCTION

External factors influencing in utero and early life development of the fetus have long lasting effects on the animal's health, specifically their response to internal parasites and immune development and productivity in later life (Barker et al., 2002; Kenyon and Blair, 2014). The in utero environment experienced by the fetus, from the earliest stages of gestation, has been shown to impact fetal skeletal development, male and female reproductive function, and

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relative organ size, thus influencing fetal birth weight and postpartum growth rate (Wallace et al., 2000; Rhind, 2004; Blair et al., 2011).

Maternal size, nutrition, and litter size are 3 of the primary extrinsic factors influencing the developing fetus and subsequent neonatal performance (Kenyon and Blair, 2014). Studies have reported that altering the level of maternal nutrition up to d 130 of gestation can affect fetal growth, influencing birth weight (Caton et al., 2009) and postnatal growth (Kenyon et al., 2009). Optimum ewe and lamb behavior at parturition is crucial to the well-being and survival of the neonate, with Dwyer et al. (2003) reporting that maternal nutrient restriction impairs the duration of ewe grooming behavior expressed immediately after lambing, thus weakening the ewe–lamb bond.

Therefore, if altering the maternal diet is to have a positive, influential impact on offspring performance, the results must be evident during the period of detailed nutritional management (i.e., late gestation). We tested the hypothesis that altering the level of nutrition offered to the ewe during the late gestational phase would directly impact fetal skeletal development, thus influencing growth performance in the postpartum period. Therefore, the objectives of this study were 1) to identify the impacts of nutritional restriction versus excess on the development of the fetus at parturition and 2) to identify the effects, if any, this would have on growth and performance at subsequent weaning.

MATERIALS AND METHODS

All procedures involving ewes and lambs in this study were conducted under experimental license from the Irish Department of Health in accordance with the Cruelty to Animals Act of 1876 and the European Communities (Cruelty to Animals Act, 1876) Regulations, 1994. The euthanasia of lambs was conducted under experimental license from the Irish Medicines Board in accordance with the European Union (protection of animals used for scientific purposes) regulations 2012 (statutory instrument number 543 of 2012). This study was conducted at University College Dublin, Lyons Research Farm, Newcastle, County Dublin, Ireland.

Pre-Experimental Animal Management

The management of ewes from mating until d 105 of gestation is detailed in a companion paper (McGovern et al., 2015). Six weeks before the mean predicted lambing date, 60 mature twin-bearing ewes were selected for this study and were randomly allocated to 1 of 3 nutritional treatments ($n = 20$ per treatment). Before selection, the ewes were blocked on the basis of live weight (mean of 79.2 kg [SEM 1.87]) and balanced for BCS (3.3 ± 0.06 BCS), age (3 ± 0.84 yr of age), and both ewe and lamb sire breed. Body condition score assessments were made by a trained technician and ewes were scored on a scale of 0 to 5, with 0 being emaciated and 5 obese (Russel, 1984).

Nutritional Treatments

Ewes were allocated to 1 of 3 nutritional treatments based on Agricultural and Food Research Council recommendations (AFRC, 1993) as amended by Robinson et al. (2002a) as follows: 1) 80% of predicted ME requirement, 2) 100% of predicted ME requirement, and 3) 120% of predicted ME requirement. Metabolizable energy requirements, based on those outlined by the Agricultural and Food Research Council Technical Committee (AFRC, 1993; and amended by Robinson et al., 2002a) were calculated individually for each ewe as follows:

$$\text{Total energy requirement} = \text{maintenance} + \text{fetal requirements},$$

$$\text{ME requirement} = (F + A)/K_m,$$

$$\text{Fetal energy requirement} = E_c/K_c,$$

$$\text{Energy content of the gravid fetus } (E_t) = \log10(Et) = 3.322 - 4.979e\ {-0.00643t}, \text{ and}$$

$$\text{Daily energy retention in the fetus } (E_c) = 0.25Wo[Et\ (0.07372^{-0.00643t})],$$

in which F = fasting metabolism, A = the activity allowance of the animal, K_m = the efficiency factor for the utilization of ME for maintenance, K_c = the efficiency of energy utilization for conceptus gain, t = the number of days from conception, and W_o = the total expected litter weight at birth (kg).

The Agricultural and Food Research Council equation for fetal energy requirement was amended according to Robinson et al. (2002a) to account for the efficiency of energy utilization for conceptus gain. The initial BW of the ewe, recorded at the beginning of the study, and the total expected litter weight (10 kg; Boland et al., 2006) were used as constants in the calculation of the ME requirement for the duration of the feeding period, whereas individual requirements were revised on a weekly basis to allow for the increasing fetal energy demands as gestation progressed. Once calculated the requirements were amended according to specific treatment allocation. On d 119 of gestation, ewes were housed in individual pens with 33 ewes penned on wooden slats and the remaining 27 ewes penned on expanded metal slats with floor type balanced across treatments. A detailed description of the feeding management and the data collection of the ewes for the final 4 wk of gestation and at lambing is provided in a companion manuscript (McGovern et al., 2015). The chemical composition of feedstuffs offered is outlined in Table 1.

Table 1. Chemical composition of silage and concentrate offered to ewes during late gestation

Item	Silage	14% CP[1] concentrate	18% CP[1] concentrate
DM, % as fed	25.4	84.5	85.0
CP, % DM basis	11.5	13.8	17.9
NDF, % DM basis	41.7	30.8	26.9
ADF, % DM basis	25.8	14.3	13.4
ADL, % DM basis	4.4	–	–
Starch, % DM basis	–	22.1	20.8
Ether extract, % DM basis	2.8	2.5	1.9
GE, MJ/kg DM	16.6	16.4	17.0
ME, MJ/kg DM	10.6	11.9	12.7

[1] Percentage of CP in the concentrate.

Ewe Measurements and Lambing Data

All ewes lambed in their individual pens where they remained with their lambs until 24 h postpartum. Within 1 h of birth, the navel of each lamb was dipped in a 10% iodine solution, following which time live weight at birth and sex were recorded for each lamb. At 24 h postpartum, all lambs were ear tagged.

Following hand milking of ewes at 1, 10, and 18 h postpartum, lambs were fed colostrum from their dam via a stomach tube. Depending on the yield of colostrum collected, lambs received the maximum amount of colostrum available, after sampling, within the range of 20 to 50 mL colostrum per kilogram of lamb birth weight. When colostrum production was insufficient to provide a minimum of 20 mL/kg lamb birth weight, lambs received substitute colostrum, pooled per treatment, up to the maximum allowance of 50 mL/kg lamb birth weight.

Behavior at Parturition

Neonatal behavioral data were recorded including time of birth, the length of time spent attempting to stand, the length of time taken from birth to successfully standing, and the length of time taken from birth to making an initial attempt at suckling. The definitions of behaviors recorded are similar to those outlined by Dwyer et al. (2004).

Lamb Blood Sample Collection

Before stomach tubing, at 1 h postpartum, 2 plasma (5 mL each) blood samples were collected via jugular venipuncture in heparinized vacutainers (Becton, Dickinson and Company, Plymouth, UK; reference numbers 367,880 and 368,921, respectively) from all lambs. At 24 h postpartum, serum blood samples were collected via jugular venipuncture using nonheparinized vacutainers (Becton, Dickinson and Company; reference number 368,975). All plasma blood samples were immediately placed on ice and centrifuged at 1,800 × *g* for 15 min at 4°C after which the plasma was pipetted into separate pour-off tubes and frozen at –20°C until further analysis. Serum blood samples were stored at room temperature for 1 h after collection before being transferred to a refrigerator where they remained for 24 h at 4°C. Samples were subsequently centrifuged, collected, and stored as outlined above.

Skeletal Measurements, Organ Collection, and Small Intestinal Morphology

At 1 h postpartum (and before euthanasia, where appropriate), all lambs had their thoracic circumference, crown to rump length (Neville et al., 2010), and fore and hind leg length measured (Blair et al., 2011). A subgroup of 30 lambs (*n* = 10 per treatment) were then euthanized (at 1 h postpartum) by lethal injection using Euthatal (pentobarbitone sodium B.P.; Merial Animal Limited, Dublin 1, Ireland) at a rate of 1 mL/kg birth weight. All lambs selected for euthanasia were female and had an average birth weight of 4.64 ± 0.594 kg. This resulted in 10 ewes per treatment rearing twin lambs and 10 ewes per treatment rearing single lambs (defined hereafter as rearing rank twin = 2 and single = 1).

Following euthanasia, the liver, spleen, kidneys, kidney fat, heart, lungs, thyroid, brain, and digestive tract were dissected and weighed. Intestinal tissue from the middle section of the ileum, approximately 10 cm from the ileocecal junction, was aseptically isolated, flushed with 0.9% salt solution, and fixed in 10% phosphate buffered formalin. The preserved intestinal segments were prepared using standard paraffin embedding techniques. Cross-sections at 5 μm thickness of each ileal sample were stained with hemotoxylin and eosin (Pierce et al., 2006). Villus height and crypt depth were assessed on the stained sections (100x) using a light microscope fitted with an image analyzer (Image Pro-Plus 9.1; Media Cybernetics, Rockville, MD). Measurements of 20 well-orientated intact villi and crypts were assessed for each animal. The villus height was measured from the crypt–villus junction to the tip of the villus and the crypt depth was measured from the crypt–villus junction to the base.

Lamb Weight and Factory Data Collection

All remaining lambs were weighed every 7 d from d 14 to 28 inclusive postpartum and once every 14 d thereafter until slaughter. Lambs were weighed using an electronic scales (Prattley, Temuka, New Zealand) and BW were electronically recorded (Tru-Test Group, Auckland, New Zealand). Lambs were weaned on d 98 postpartum and drafted for slaughter at 44 to 46 kg of BW. All lambs had their days to slaughter corrected for preslaughter BW of 45 kg before statistical analysis. At slaughter, lamb HCW was recorded and subsequently used to calculate kill-out percentage.

Chemical Analysis

Lamb plasma samples were analyzed for glucose (interassay CV = 0.20), NEFA (mmol/L), urea (mmol/L), and total protein (g/L) content as outlined in a companion paper (McGovern et al., 2015).

Total serum immunoglobulin concentration (g/L) was determined using the zinc sulfate turbidity test (McEwan et al., 1970). These results were then reduced by a factor of 0.09 to provide the IgG-only content of the serum (Larson et al., 1974).

Statistical Analysis

Data were analyzed as a completely randomized block design using the mixed model procedure in SAS (SAS, version 9.4; SAS Inst. Inc., Cary, NC). Individual ewe was the experimental unit for all parameters analyzed. Data distributions were analyzed to fit the assumptions of normality using the UNIVARIATE procedure. The data were tested for the linear and quadratic effects of energy inclusion in the diet using the general linear model procedure. Where a significant linear effect was present ($P \leq 0.05$), the R^2 value is reported in the text in conjunction with the associated P-value. Quadratic effects were nonsignificant ($P > 0.05$) and, therefore, are not reported.

The model used for all variables included the fixed effect of treatment, breed, and ewe age and the random effect of ewe. Date of birth was fitted as a covariate for all lamb parameters analyzed and a repeated measure analysis was performed on lamb BW data, specifically weaning weight and weekly BW data. The repeated measures were fit using variance–covariance structures, with the most appropriate (lowest Bayesian information criterion values) used for each analysis. In addition, the fixed effects of lamb age (as the repeated time measure), sex, rearing rank, and the 2-way interactions of ewe nutritional treatment × lamb age and lamb age × rearing rank were significant and included in the model. The interaction ewe nutritional treatment × rearing rank was not significant ($P > 0.05$); therefore, it was not included as a fixed effect from the model before final analysis. Lamb birth weight was included as a covariate in the analysis of lamb growth rate data. All data presented in the tables are expressed as least squares means ± SEM. The probability value, which denotes statistical significance, was $P \leq 0.05$, and values tending toward significance were discussed at $0.05 < P < 0.10$.

RESULTS

Behavioral Data

Ewe nutritional treatment had no effect ($P \geq 0.55$) on the combined length of time both lambs spent attempting to stand after birth or the length of time from birth until they stood successfully (Table 2). There tended to be an effect ($P = 0.09$) of birth rank, where the first lamb born in each twin set spent less time attempting to stand and successfully stood quicker than their latter born twin mate.

The combined length of time from birth to when both lambs made an initial attempt at suckling was affected ($P = 0.04$) by ewe nutritional treatment, where lambs born to ewes offered the 80% ME diet made a successful attempt at suckling quicker than lambs born to ewes on either of the other 2 treatment groups (Table 2). Similarly, the first lamb born in each twin set made an initial attempt at suckling quicker than their twin mate ($P = 0.04$).

Colostrum Data

Treatment had an effect on the volume of colostrum fed to lambs, with those born to ewes offered 80% ME having a lesser intake than those born to ewes offered 100 or 120% ME, at 1 h postpartum ($P = 0.01$; Table 3). At 10 h postpartum, lambs born to ewes offered 120% ME tended to have a greater intake of colostrum when compared with the 80% ME progeny ($P = 0.06$). Lambs born to ewes offered 120% ME had a greater total intake of colostrum up to 18 h ($P = 0.05$). However, there was no effect of treatment ($P = 0.29$) on the volume of colostrum fed per kilogram of lamb birth weight within the first 18 h postpartum, with treatment means of 136 ± 3.2, 137 ± 3.2, and 142 ± 3.2 mL per kilogram birth weight for the 80, 100, and 120% ME treatments, respectively.

Table 2. The effect of prepartum nutritional treatment on lamb behavior within the first hour after parturition (least squares means ± SEM)

	Treatment[1]				Birth rank[3]			*P*-value		
Lamb behavior, s	80% ME	100% ME	120% ME	SEM[2]	1	2	SEM[2]	Treatment	Birth rank	Treatment × birth rank
Attempt to stand	374	272	418	129	313	476	94.1	0.55	0.09	0.40
Time to successful stand	773	914	805	185	915	1,152	96.9	0.72	0.09	0.62
Time to first suckling attempt	1,038[a]	1,393[b]	1,366[b]	207	1,201	1,483	102.7	0.04	0.04	0.20

[a,b]Within a row, means without a common superscript differ ($P < 0.05$).[1]Diets fed at 80 (80% ME), 100 (100% ME), or 120% (120% ME) of metabolic energy requirements (AFRC, 1993; amended by Robinson et al. 2002a).

[2]Standard error of the treatment mean.

[3]Birth rank: 1 and 2, where 1 is the first lamb born and 2 is the second.

Blood Metabolite Concentration

Ewe nutritional treatment had no effect on plasma glucose ($P = 0.38$) or plasma urea ($P = 0.77$) concentrations of lambs at 1 h postpartum (Table 4). There was a negative linear relationship ($R^2 = 0.71$, $P = 0.01$) between prepartum ewe nutritional treatment and plasma NEFA concentrations of lambs at 1 h postpartum. Lambs born to ewes offered the 120% ME treatment had a lesser ($P = 0.01$) plasma NEFA concentration when compared with lambs born to ewes offered 80 or 100% ME, at 1 h postpartum. The plasma total protein concentration of lambs born to ewes offered 100% ME was greater ($P = 0.04$) than that of lambs born to ewes offered 80 or 120% ME at 1 h postpartum. In addition, there was no effect ($P = 0.73$) of treatment on serum IgG concentration of lambs at 24 h postpartum.

Skeletal Measurements

Prepartum ewe nutritional treatment had no effect on lamb crown to rump length ($P = 0.52$) or hind leg length ($P = 0.74$; Table 5). Lambs born to ewes offered 80% ME had narrower thoracic circumferences ($P = 0.05$) whereas lambs born to ewes offered the 100% ME diet had ($P = 0.02$) a shorter fore leg length when compared with lambs born to ewes offered the 120% ME diet.

Organ Weights and Intestinal Morphology

Prepartum dietary treatment had no effects on any of the organ weights ($P \geq 0.11$) collected from lambs at 1 h postpartum (Table 5). Histological examination of the ileum indicated there was no effect ($P \geq 0.62$) of maternal dietary prepartum treatment on villus height, crypt depth, or the villus height to crypt depth ratio at 1 h postpartum (Table 5).

Lamb Performance

Body Weight. Ewe nutritional treatment had no effect ($P = 0.31$) on individual lamb birth weight with treatment means of 4.65 ± 0.161, 4.71 ± 0.161, and 4.87 ± 0.161 kg for the 80, 100, and 120% ME treatments, respectively. Prepartum ewe nutritional treatment influenced ($P \leq 0.04$) lamb BW from d 14 to 91 postpartum, with lambs born to ewes offered 100 or 120% ME weighing more than lambs born to ewes offered the 80% ME diet (Table 6). Lambs born to ewes offered the 120% ME diet remained heavier ($P \leq 0.05$) than lambs born to ewes offered the 80% ME diet until d 98. There was a significant effect of rearing rank ($P = 0.01$) from d 14 until weaning on d 98, where single-reared lambs remained heavier than those reared as twins.

Average Daily Gain. Ewe nutritional treatment affected lamb ADG, where lambs born to ewes offered the 120% ME diet had greater ADG from birth to d 21 postpartum and, subsequently, from birth to weaning when compared with lambs born to ewes offered 80% ME ($P = 0.02$; Table 6). However, from d 91 to 98, lambs born to ewes offered 80% ME tended to have a greater ADG than those born to ewes offered 120% ME ($P = 0.09$). An effect of rearing rank was apparent from birth to d 35 postpartum ($P = 0.01$) and from birth to slaughter ($P = 0.05$), with lambs reared as singles having greater ADG than those reared as twins.

Slaughter Data. There was no effect ($P \geq 0.26$) of ewe nutritional treatment on the ADG of lambs from birth to slaughter and from weaning to slaughter, the kill-out percentage, or the carcass weight of lambs at slaughter (Table 6). Lambs born to ewes offered the 120% ME treatment tended ($P = 0.09$) to reach their preslaughter BW quicker than lambs born to ewes offered the 100% ME diet. Rearing rank had an effect ($P = 0.01$) on days to slaughter, with lambs reared as singles reaching their final preslaughter BW (45 kg) 14 d earlier than lambs reared as twins.

DISCUSSION

The impact of external factors such as litter size, maternal nutrition, and dam size on the in utero and early life development of the ovine neonate must be

Table 3. The effect of prepartum nutritional treatment on lamb colostrum intake up to 18 h postpartum (least squares means ± SEM)

Lamb colostrum intake, mL	Treatment[1] 80% ME	100% ME	120% ME	SEM[2]	*P*-value
1 h[3]	222^{a}	216^{a}	251^{b}	8.8	0.01
10 h	225^{x}	243^{xy}	250^{y}	9.2	0.06
18 h	228	228	241	9.1	0.54
Total intake to 18 h	676^{a}	687^{a}	742^{b}	22.3	0.05
Intake/kg BW	136	137	142	3.2	0.29

[a,b] Within a row, means without a common superscript differ significantly ($P < 0.05$).

[x,y] Means within a row with different superscripts differ ($P < 0.10$).

[1] Diets fed at 80 (80% ME), 100 (100% ME), or 120% (120% ME) of metabolic energy requirements (AFRC, 1993; amended by Robinson et al. 2002a).

[2] Standard error of the treatment mean.

[3] Hours postpartum.

Table 4. The effect of prepartum nutritional treatment on lamb plasma glucose, NEFA, urea, and total protein concentration at 1 h postpartum and serum IgG concentration at 24 h postpartum (least squares means ± SEM)

Blood metabolite concentration, mmol/L	Treatment[1] 80% ME	100% ME	120% ME	SEM[2]	*P*-value
Glucose	5.05	5.17	4.41	0.467	0.38
NEFA	1.47^{d}	1.40^{d}	1.23^{c}	0.061	0.01
Urea	5.11	5.19	4.92	0.321	0.77
Total protein	37.61^{a}	41.22^{b}	37.67^{a}	1.157	0.04
Serum IgG concentration, g/L	25.4	24.2	26.0	1.72	0.73

[a–d] Within a row, means without a common superscript differ significantly ($P < 0.05$).

[1] Diets fed at 80 (80% ME), 100 (100% ME), or 120% (120% ME) of metabolic energy requirements (AFRC, 1993; amended by Robinson et al. 2002a).

[2] Standard error of the treatment mean.

given serious consideration (Kenyon and Blair, 2014). Although previous studies have investigated the effects of gestational nutrition on fetal development (Kenyon et al., 2009, 2011a,b; Blair et al., 2011), this study focused on assessing offspring performance after individual ewe feeding, where daily feed intake of the ewe, as opposed to group feeding, was monitored, thus allowing for a more accurate individual energy intake calculation on a daily basis.

Although there was a lack of difference observed in lamb birth weight, organ weight, and glucose concentration, significant effects from the nutritional imbalance were observed in lamb thoracic circumference, fore leg length, and lamb behavior, measured at birth. These differences, coupled with a greater ADG and BW at weaning, led us to accept the hypothesis that altering the level of nutrition offered to the ewe during this late gestational phase would directly impact fetal skeletal development, thus influencing postpartum growth and performance.

Due to the relative ease with which it can be practically measured on farms, lamb birth weight is often considered the first measure of maternal nutrition during gestation (Wu et al., 2006). Studies have outlined the influence of both maternal BCS and gestational nutrition on lamb birth weight (Gardener et al., 2005; Kenyon et al., 2009; Caton and Hess, 2010; Meyer et al., 2010), highlighting its importance in the detection of fetal growth restriction and/or adequate maternal nutrition. In the present study, despite the difference in ewe DMI and BCS (McGovern et al., 2015), there was a lack of difference observed in lamb birth weight. Initially, this highlighted the apparent adequacy of nutrition received by the ewes on each of the 3 dietary treatments and contradicted the earlier findings of Russel et al. (1977), who reported that a moderate degree of undernourishment in late gestation resulted in the reduced weight of twin lambs at birth. However, despite no difference observed in birth weight in the present study, elevated growth rates from birth to weaning and consequently heavier weaning weights were observed in lambs born to ewes fed in the 120% ME treatment during the prepartum period.

The development and, ultimately, the functioning of major organ systems during fetal development is governed by the maternal plane of nutrition (Godfrey and Barker, 2000; Wu et al., 2006; Caton et al., 2007). Throughout embryogenesis, organs develop from different embryonic origins over a period of time (McGeady et al., 2006). Consequently, the critical windows of development occur during different periods of gestation (Brendolan et al., 2007), as various organ systems have differing growth trajectories and maturating time points (Caton and Hess, 2010). The critical period of development for spleen growth has been identified during early gestation (Brendolan et al., 2007), although this early phase has also been shown as the pivotal phase in the development of the gastrointestinal tract (Reed et al., 2007) and, hence, the lack of difference observed not only in gastrointestinal tract weight but also in villus height, crypt depth, and the villus height:crypt depth ratio in the current study. This, in part, explains the lack of difference observed in organ weight in the present study, as the maternal dietary manipulation was applied for the final 4 wk of gestation, at which point the majority of fetal organ systems have undergone primary development (Kenyon et al., 2011b). This is in agreement with the findings of Caton and Hess (2010), who reported that the degree of compromised organ growth is more severe with increasing extremes of a dietary manipulation and that manipulation during the early- to

Table 5. The effect of prepartum nutritional treatment on lamb skeletal measurements, organ weights, and morphology data (least squares means ± SEM)

	Treatment[1]				
Parameter	80% ME	100% ME	120% ME	SEM[2]	*P*-value
Skeletal measurement, cm					
Crown to rump length	41.06	40.23	40.41	0.564	0.52
Thoracic circumference	37.39[a]	38.56[ab]	38.50[b]	0.538	0.05
Fore leg length	25.75[ab]	24.91[a]	26.58[b]	0.419	0.02
Hind leg length	29.80	29.20	29.56	0.731	0.74
Organ weight, g					
Liver	86.44	93.38	92.78	5.608	0.40
Spleen	6.05	5.43	6.51	0.576	0.49
Kidney	17.16	17.42	16.77	1.420	0.87
Kidney fat	18.64	18.10	20.10	0.808	0.23
Heart	31.15	31.51	30.29	1.202	0.74
Lungs	79.19	81.59	72.22	6.141	0.38
Thyroid	0.95	1.05	1.06	0.218	0.75
Brain	47.37	48.15	45.88	0.894	0.11
Digestive tract	244	211	236	18.827	0.33
Histological measurements, µm					
Villus height	168.2	163.3	173.8	19.49	0.87
Crypt depth	59.6	64.2	60.1	8.17	0.62
Villus height to crypt depth ratio	3.89	4.09	3.80	0.373	0.87

[a,b]Within a row, means without a common superscript differ significantly ($P < 0.05$).

[1]Diets fed at 80 (80% ME), 100 (100% ME), or 120% (120% ME) of metabolic energy requirements (AFRC, 1993; amended by Robinson et al. 2002a).

[2]Standard error of the treatment mean.

midpregnancy phase is the most likely period within which organ growth and development can be influenced.

Previous studies have found that manipulating the level of maternal nutrition throughout gestation can result in perturbed fetal growth and alterations in skeletal size at birth (Caton et al., 2009; Neville et al., 2010). In particular, restricting the plane of nutrition offered to the ewe has been shown to result in the diversion of nutrients toward essential organs and tissues to maintain their growth and development at the expense of less important ones (Quigley et al., 2008). Such limitations to the development of the fetus have been associated with a narrower thoracic circumference at birth (Quigley et al., 2008), which can subsequently lead to a decline in postnatal productivity. Therefore, the reduced growth rate by 80% ME progeny in the current study is potentially reflective of the narrowerthoracic circumference observed in these lambs.

Fetal demand for glucose markedly increases as gestation progresses (Morriss et al., 1974), with glucose acting as a primary energy source for the growing fetus, providing 30 to 40% of the energy required for growth (Bell and Bauman, 1997). Previous research has found that there is a linear relationship between maternal and fetal plasma glucose concentrations throughout gestation (Silver et al., 1973; Hammon et al., 2012). Consequently, fetal glucose can be examined as a determinant of maternal energy supply during gestation. Previous studies have demonstrated the utilization of body fat reserves by the ewe to preserve circulating concentrations of glucose during periods of nutrient restriction, thus maintaining fetal growth (Tygesen et al., 2008). This is supported, in the present study, by a marked reduction in BCS between ewes allocated to the restricted and excessive energy treatments (McGovern et al., 2015) coupled with the lack of difference seen in blood glucose concentration, organ size and, ultimately, birth weight of the offspring. It may be that the ewe yielded her own body reserves to ensure optimal fetal growth during the final stage of gestation.

The mobilization of body fat reserves is indicated through an elevation of plasma NEFA concentrations (Robinson et al., 2002b). According to Girard et al. (1992), fatty acid oxidation rapidly increases in the ruminant neonate after birth whereas Steinhoff-Wagner et al. (2011) has shown that the newborn calf is equipped with the ability to mobilize body fat, thus providing NEFA for internal energy supply within the first 24 h of birth. The elevated plasma NEFA concentrations, seen in the present study in lambs born to ewes restricted during the prepartum period, is, therefore, acting as an indicator of a shortage in energy availability to the lamb despite the lack of difference in plasma glucose concentration.

Neonatal survival is crucial to the viability and ultimate efficiency of any animal production enterprise (Redmer et al., 2004). In precocious species, such as sheep, the role of neonatal behavior after birth has been deemed critically important to the survival of the animal (Dwyer et al., 2003), with Alexander and Peterson (1961) stating that up to 33% of lamb deaths occur as a direct result of poor behavior by the lamb itself. For successful suckling to take place, the lamb must be able to stand and then move toward the udder. As a result, the speed at which the lamb undergoes behaviors such as righting, standing, and udder seeking determines how quickly after birth suckling is achieved (Dwyer et al., 2003). Findings from the present study are in agreement with the above statement, where the lamb that was quicker to stand after birth was also quicker at making a successful attempt at suckling. In addition, the quicker attempt at suckling made by lambs born to undernourished ewes in this study may be partially explained by work performed by Corner et al. (2010), where lambs born to nutritionally restricted ewes were perceived as being more aggressive in terms of maternal recognition and consequently were quicker to move toward the ewe after birth. In contrast to previous studies where a nutritional restriction during gestation negatively affected maternal behavior at parturition (Dwyer et al., 2003),

Table 6. The effect of prepartum nutritional treatment on lamb weight, ADG, days to slaughter, kill out percentage, and carcass weight (least squares means ± SEM)

	Treatment[1]				Rearing rank[3]			*P*-value		
Parameter	80% ME	100%ME	120% ME	SEM[2]	1	2	SEM[3]	Treatment	Rearing rank	Treatment × rearing rank
Days postpartum										
Day 0[4]	4.65	4.71	4.87	0.161	–	–	–	0.31	–	–
Day 14	9.11^{c}	10.76^{d}	10.40^{d}	0.256	10.81	9.38	0.220	0.01	0.01	0.96
Day 28	13.02^{c}	14.55^{d}	14.86^{d}	0.342	15.41	12.88	0.290	0.01	0.01	0.88
Day 42	16.62^{a}	18.59^{b}	19.04^{b}	0.469	19.71	16.46	0.393	0.04	0.01	0.95
Day 77	26.43^{c}	28.35^{d}	28.94^{d}	0.670	29.75	26.06	0.558	0.01	0.01	0.96
Day 98[5]	31.07^{a}	32.59^{ab}	33.48^{b}	0.767	34.41	30.35	0.638	0.02	0.01	0.90
ADG between days, g/d										
Day 0–14	289^{a}	310^{a}	344^{b}	13.7	349	279	9.81	0.02	0.01	0.94
Day 14–21	244^{a}	280^{b}	304^{b}	13.4	308	237	12.61	0.02	0.01	0.90
Day 0–35	291^{a}	304^{a}	334^{b}	10.2	349	270	12.61	0.02	0.01	0.97
Day 91–98	295^{y}	259^{xy}	225^{x}	28.7	203	196	13.01	0.09	0.73	0.87
Day 0–98	266^{a}	283^{ab}	289^{b}	7.3	296	263	13.10	0.05	0.08	0.92
Day 98 to slaughter[6]	204	181	191	11.4	188	194	13.41	0.39	0.75	0.96
Day 0 to slaughter	256	251	248	6.9	259	244	5.54	0.74	0.05	0.83
Slaughter data,										
Days to slaughter	157^{xy}	161^{y}	154^{x}	3.1	149	163	3.0	0.09	0.01	0.42
Kill out %	45.18	45.27	45.16	0.236	45.20	45.04	0.284	0.97	0.60	0.85
Carcass weight, kg	20.63	21.20	20.70	0.274	20.89	20.10	0.262	0.26	0.97	0.90

$^{a–d}$Within a row, means without a common superscript differ significantly ($P < 0.05$).

^{x,y}Within a row, means without a common superscript differ significantly ($P < 0.05$).

[1] Diets fed at 80 (80% ME), 100 (100% ME), or 120% (120% ME) of metabolic energy requirements (AFRC, 1993; amended by Robinson et al. 2002a).

[2] Standard error of the treatment mean.

[3] Rearing rank: 1 and 2, where 1 is a single-reared lamb and 2 is a twin-reared lamb.

[4] Day 0 = birth.

[5] Day 98 postpartum = weaning.

[6] Lambs were drafted for slaughter when they reached 45 kg BW.

the same was not evident in this study, with no apparent effect on maternal behavior observed (McGovern et al., 2015). However, imposing a more severe restriction for a longer interval before or during gestation may have more profound effects on maternal behavior, as seen in studies performed by Dwyer et al. (2003) and Hernandez et al. (2010).

The ability of the ewe to produce milk is a key driver of early lamb growth and, ultimately, survival (Morgan et al., 2007; Tygesen et al., 2008). The strong correlation identified between lamb growth rate and ewe milk production (Snowder and Glimp, 1991) allowed for the estimation of milk yield in the present study, using an equation as determined by Robinson et al. (1969). The greater estimated milk production observed from ewes offered the 120% ME treatment (McGovern et al., 2015) is reflected in increased growth rates from their offspring during the first 3 wk of life. Similar to observations made in the current study, greater milk yields in early lactation have been previously shown to give lambs a weight advantage that remains present up until weaning (Morgan et al., 2007). In contrast, lambs born to ewes that received the 80% ME treatment were disadvantaged by reduced milk yields in early lactation but had the potential to achieve growth rates equivalent to their counterparts from wk 4 until weaning.

The ability of the lamb to undergo compensatory growth postweaning has been demonstrated by Hatcher et al. (2008). Similarly, Galvani et al. (2014) reported that lambs reared by low milk yielding ewes had the greatest DMI and subsequently growth rate throughout the postweaning period. In agreement with the present study, lambs born to ewes offered the restricted treatment (80% ME) prepartum were lightest at weaning; however, there was no difference observed in the length of time it took them to reach the desired preslaughter BW, indicating a partial compensatory growth effect despite the lack of significant difference in ADG from weaning to slaughter.

Rearing rank significantly affects lamb growth rate (Morgan et al., 2007), primarily due to the volume of milk available to the lamb (Kenyon et al., 2011a). In a study performed by Galvani et al. (2014), lambs that had a 20% increase in milk intake had a 33% increase in growth rate from birth to weaning. In addition, Thompson et al. (2011) reported that lambs born and reared as singles had growth rates of only 10 g/d more than those born as twins and reared as singles, thus providing evidence that it is the availability of milk rather than pregnancy rank that primarily governs growth rate in the preweaning period. In the current study, the increased growth rates observed from lambs reared as singles in comparison with those reared as twins is, therefore, in agreement with previous studies (Kenyon et al., 2011a; Thompson et al., 2011), supporting the hypothesis that in addition to lamb birth weight, nutrient supply in the early postpartum period is a primary driver of lamb performance.

In conclusion, altering the level of ME offered to the ewe in late gestation (final 4 wk) had no significant influence on lamb birth weight, various organ weights, intestinal morphology, or plasma glucose concentrations, indicating that the lambs born in this study, regardless of ewe nutritional treatment, had a similar potential to grow at birth. However, the elevation of plasma NEFA concentration at 1 h postpartum and the decline in ADG and BW to weaning highlight the negative impact of imposing a maternal nutritional restriction during the late gestational phase. Therefore, this study indicates that individual lamb birth weight is a poor predictor of early life growth and performance to weaning and, therefore, should not be relied on as a primary indictor of maternal nutritional adequacy during gestation.

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