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The effect of maternal nutrition level during mid-gestation on postnatal muscle fibre composition and meat quality in lambs

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Abstract. Maternal nutrient intake during early- and mid-gestation can alter fetal growth and development with long-term consequences on the postnatal productivity and health of offspring. The aim of this study was to investigate the effects of maternal nutrition level during mid-gestation on postnatal growth rate, carcass composition, muscle fibre characteristics and meat quality in lambs. Ewes were fed from Days 30 to 80 of gestation as follows: 100% (control group, C), 50% (undernutrition, UN) or 175% (overnutrition, ON) of their daily requirement. During the rest of the gestation, the ewes in all groups were fed 100% of their daily requirements. Birth and weaning (at Day 90) weights of lambs born to ewes in nutritional groups were similar, but slaughter weights (at Day 150) and daily weight gain during finishing period of lambs born to the UN group were lower ($P < 0.05$). Similarly, a decrease in weights of semitendinosus (ST), semimembranosus and gastrocnemius muscles was observed in the lambs born to the UN group ($P < 0.05$). Lambs born to the ON group had a higher ($P < 0.05$) concentration of DNA in longissimus dorsi (LD) and ST muscles than UN groups, but they had a lower ($P < 0.05$) total protein and other proteins concentrations in LD and ST muscles than those to C and UN groups. Protein to DNA ratio in LD and ST muscles of lambs born to ON group were lower than those to C and UN groups ($P < 0.05$). However, lambs born to the ON group had a higher number of Type IIA and IIB muscle fibres in ST muscles but not in LD muscles than those in the C and UN groups ($P < 0.05$). Additionally an increase in the number of fibres/mm^2 muscle area in lambs born to the ON group was observed in LD and ST muscles ($P < 0.05$). There were no significant differences between treatment groups in terms of meat quality parameters studied. This study confirms that maternal nutrition level during mid-gestation alters the postnatal growth and muscle fibre development of lambs.

Additional keywords: lamb, maternal nutrition, meat quality, muscle fibre, postnatal growth.

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Introduction

Uterine environment can be manipulated by maternal nutrition level during gestation and this may affect fetal development, which subsequently may alter postnatal productive life, postnatal skeletal muscle growth and meat quality of the meat-producing animals (Rehfeldt *et al.* 2011; Kenyon and Blair 2014). Intrauterine growth retardation (IUGR) can be defined as impaired growth and development of the mammalian fetus during gestation (Wu *et al.* 2006). Inadequate maternal nutrition is one of the primary causes of IUGR (Zhu *et al.* 2006). There is evidence to suggest that IUGR is associated with altered composition of the whole body and muscle, as well as the distribution of muscle fibre type of the offspring (Wu *et al.* 2006; Zhu *et al.* 2006). For example, maternal dietary restriction during early- and mid-gestation can decrease the number of muscle fibres formed, which tends to be associated with decreased growth rates and increased adiposity (Daniel *et al.* 2007; Rehfeldt *et al.* 2011). This is because skeletal muscle has a lower priority in nutrient partitioning compared with the brain and heart in response to the challenges the fetus faces during development, rendering it particularly vulnerable to nutrient deficiency (Zhu *et al.* 2006). In addition, the fat and connective tissue contents of skeletal muscle mass as well as muscle fibre characteristics are major factors that affect the postmortem quality of meat (Wu *et al.* 2006).

It is well known that the prenatal period is crucial for skeletal muscle development, because no net increase in the number of muscle fibres occurs after birth (Du *et al.* 2010). It is possible that nutrition interventions at an earlier stage of development during muscle fibre genesis can alter cellular function of muscles affecting birthweight, postnatal muscle growth and possibly meat quality at commercial slaughter weight. Hyperplasia of fetal muscle fibres in sheep begins ~30 or 32 days of gestation and is completed ~85–90 days of gestation (Brameld

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and Daniel 2008). The prenatal development of muscle fibres and adiposities may, therefore, have a profound impact on meat quality when the animal is slaughtered at or near adult bodyweight (BW).

The sheep is a seasonal breeder and allowed to graze pasture in rangeland and consume forages (an extensive system). Therefore, pasture grazing is the most common practice for managing sheep flocks worldwide with little or no supplement provided (Zervas and Tsiplakou 2011). However, the breeding season of sheep in the northern hemisphere coincides with the early autumn months, which is a time when grass growth is decreasing. This means the nutrition intake of the ewes is very low (especially in Mediterranean regions) because the quality of rangeland is often very poor (Ocak *et al.* 2006). Moreover, poor quality of grass at this time decreases its digestibility resulting in insufficient nutrition in pregnant ewes unless they are supplemented with protein and/or energy (Ocak *et al.* 2006). Failure to supply the adequate amount of nutrients to meet fetal demand, for example due to maternal malnutrition, results in inadequate placental function (Sen *et al.* 2013). Therefore, maternal nutrition level during the first half of gestation, when myoblast proliferation and myofibre genesis occur, is critical and malnutrition during this period may alter fetal development and lead to long-term or permanent changes in the structure or function of the body (Du *et al.* 2010; Kenyon and Blair 2014). Skeletal muscle is particularly vulnerable to nutrient availability during fetal development, thus the level and the period of nutrient restriction is very important.

The present study was, therefore, designed to investigate the effect of maternal nutrition level during the period of muscle fibre development on birthweight, postnatal growth performance, carcass composition, muscle fibre characteristics (number and types) and meat quality of the lamb after weaning at the end of the finishing period using a local sheep breed, Karayaka. Karayaka sheep are well suited to the harsh climate, poor pasture and severe conditions that are the characteristics of the hills and uplands of the local raising region (Sen *et al.* 2011). The breed is well known in Turkey with its high quality meat. They are classified also as a carpet-wool breed. The Karayaka breed is considered to be of low fecundity (0.66) and small breed (~45 kg). They are usually maintained on rangeland without roughage or compound feed supplementation during the day from weaning to breeding season (Olfaz *et al.* 2010).

Materials and methods

Animals

The experimental procedures were approved by the Local Animal Care and Ethics Committee of Gaziosmanpasa University, Tokat, Turkey ensuring compliance with EC Directive 86/609/EEC for animal experiments. The study was conducted within the normal seasonal breeding cycle of the ewes in Turkey (September–March). Experimental animals of second and third parity were from the Karayaka breed, 3–5 years of age, and maintained at the sheep farm of Gaziosmanpasa University, Tokat, Turkey (40°31′N, 36°53′E, 650 m above sea level). Ewes were individually housed at Day 25 of gestation and they were allocated randomly into one of three treatment groups at Day 30 of gestation. The groups were balanced for BW, muscle depth (MD) and fat depth (FD) of longissimus dorsi (LD) muscle. All the ewes were fed with a diet to meet 100% of global daily requirement up to Day 30 of gestation, when their diet was increased to 175% (overnutrition group; ON), or decreased to 50% (undernutrition group; UN) of global daily requirement until Day 80 of gestation followed by 100% of their daily requirement until parturition. Ewes in the control group (C) were fed with a diet to meet 100% of their daily requirement throughout gestation. The average gestation length of ewes in ON, C and UN groups were 147 ± 1.0, 147 ± 0.8 and 149 ± 0.6, respectively. The daily requirements of ewes throughout this study were calculated on an individual ewe BW basis (AFRC 1993). Diets were composed of concentrate (89.5% DM, 23.4% crude protein and 10.9 MJ ME/kg DM), and good quality alfalfa hay (88.4% DM, 16.8% crude protein and 8.2 MJ ME/kg DM). Diets were given daily in two equal meals at 0830 hours and 1630 hours. Ewes were weighed every 2 weeks and the amount of feed adjusted for BW. Water and minerals were freely available throughout the study. The distribution numbers of ewes by nutritional treatments and lambs by sex, birth type and mortality rate until weaning are presented in Table 1.

Growth and finishing of lambs

Four ewes in the ON group gave birth to twin lambs, but all ewes in other groups gave birth to single lambs. Following lambing, lambs were kept with their dams from birth to 2 weeks. Starting from Day 15 after birth, lambs were kept in a sheepfold during the day time, ewes were allowed to pasture during the day time and lambs were allowed to suckle over the nights in the sheepfold. When all lambs were 15 days old, in addition to the suckled ewe's milk, they were fed *ad libitum* with a creep-feed concentrated diet (containing 88% DM, 15% crude protein and 10.2 MJ ME/kg DM; Guven Yem A. S., Corum, Turkey) and good quality alfalfa fed to appetite. At Day 90 after birth, lambs were weaned and shorn. Feed and water were withdrawn

Table 1. The distribution numbers of ewes by nutritional treatments and lambs by sex, birth type and mortality rate until weaning

ON, overnutrition (175% of their daily requirement); C, control (100% of their daily requirement); UN, undernutrition (50% of their daily requirement)

Traits	Treatment groups		
	ON	C	UN
Ewes	10	12	22
Gave birth to singles	6	12	22
Male lambs	4	7	12
Female lambs	2	5	10
Gave birth to twins	4	–	–
Male lambs	3	–	–
Female lambs	5	–	–
Mortality rate of lambs until weaning (%)			
Male lambs	28.6 (2/7)	14.3 (1/7)	8.0 (1/12)
Female lambs	42.9 (3/7)	40.0 (2/5)	0.0 (0/10)
Fattened and slaughtered lambs			
Male lambs	5	6	11
Female lambs	4	3	10

overnight for determination of fasting liveweight in the next morning at weaning. After weaning all lambs were subjected to a finishing period for 60 days and slaughtered at 150 days of age as described by Sen *et al.* (2011).

Measurements and muscle sample collection

At the end of the finishing period, feed and water were withdrawn overnight for determination of fasting liveweights the next morning. Then, all lambs were transported to an abattoir. Before slaughter, MD, FD and muscle area of LD muscle at the third lumbar vertebrae were measured using an ultrasonic linear probe (Falco Vet. linear prop 8.0 MHz, Pie Medical, Maastricht, Netherlands) and lambs were slaughtered following a standard commercial slaughter procedure. Warm carcass weights were recorded after removing all internal organs. Spleen, lungs, liver, kidney, empty reticulo rumen and empty intestine were weighed. Fresh weights of internal fat, pelvic fat, kidney fat, semitendinosus (ST), semimembranosus (SM) and gastrocnemius (GN) muscles from the right side of the carcasses were also recorded and carcasses were chilled for 24 h at 4°C.

Within 30 min of slaughter, approximate 50–75-g muscle samples from the central part of the mid-section of the whole LD and ST muscles were excised from the right side of the carcasses for histochemical analysis of muscle fibres. These samples were trimmed of subcutaneous fat and fascia, frozen in liquid nitrogen and stored at −80°C until histochemical analysis of muscle fibres. For determination of meat quality, additional approximate 100–150-g muscle samples were taken from the central part of the mid-section of the whole LD and ST muscles from the left side of the carcasses. These samples were trimmed of subcutaneous fat and fascia before storage at 4°C for meat quality analysis.

Determination of muscle cellular characteristics

The concentration of DNA in fresh minced ST and LD muscles was extracted by using a commercial DNA Purification Kit as suggested by the manufacturer (Fermentas Pure Extreme K0512, Istanbul, Turkey). The calibration curve was prepared by using calf thymus DNA (Sigma Chemical Co., Istanbul, Turkey) as the standard. The DNA concentration was measured based on the absorbance at 260 nm using a spectrophotometer.

Protein extraction of fresh minced LD and ST muscles was performed in two steps resulting in water-soluble (sarcoplasmic proteins) and salt-soluble (myofibrillar proteins) fraction by the methods of Ahhmed *et al.* (2007) with some modifications. Approximately 4 g of minced LD and ST muscles samples were homogenised in 40 mL of buffer 1 (50 mM KH_2PO_4, 4°C, pH 7.0) using an Ultra Thurrax (13 500 rpm, 15 s) and centrifuged at 10 000*g* for 30 min at 4°C. The supernatant was filtered through glass wool and the volume was made up to 50 mL with buffer 1. The filtered supernatant contained the sarcoplasmic proteins. The pellet was resuspended in 40 mL of buffer 2 (50 mM KH_2PO_4, 0.6 M KCl, pH 7.0) using an Ultra Thurrax (13 500 rpm, 5 s) and centrifuged again at 10 000*g* for 30 min at 4°C. The supernatant was decanted through glass wool and the volume was made up to 50 mL with buffer 2. The filtered supernatant contained the myofibrillar proteins. The procedure was conducted once for each sample. Protein concentrations in the extracts were determined in triplicate in suitable dilutions of both fractions by the method of Bradford (1976) with bovine serum albumin as a standard. Mean values were calculated from six replicates.

The total protein concentration of fresh minced LD and ST muscles was determined on the basis of total nitrogen content (N × 6.25) by the Kjeldahl method (AOAC 1990). Other proteins including stromal protein concentration of LD and ST muscles were calculated by subtracting myofibrillar and sarcoplasmic protein concentrations from total protein concentration. Protein to DNA ratio was calculated by dividing total protein concentration to concentration of DNA.

Meat quality analyses

All meat quality parameters (drip loss, cooking loss, shear force, pH, colour and intramuscular fat content) were analysed as described by Sen *et al.* (2011). Fresh minced LD and ST muscles were analysed by AOAC (1990) procedures for DM and ash.

Histochemical determination of muscle fibre type composition

Contractile type (Type I, IIA and IIB) of muscle fibres in LD and ST muscles were determined using myosin ATPase staining technique described by Brooke and Kaiser (1970) with some modifications. At least four transverse serial muscle sections (10 µm thick) were obtained using a cryostat at −20°C (Cryotome E, Thermo Electron Corporation, Basingstoke, UK). Sections were allowed to dry and then stained for myosin ATPase after pre-incubation for 12 min at 4°C at pH 4.2 in 1N formic acid buffer. Sections were then washed twice for 1 min each time at pH 7.4 with 18 mM $CaCl_2$ and 100 mM Tris. Sections were then incubated for 60 min at 37°C in 18 mM $CaCl_2$, 20 mM Tris buffer (pH 9.4), and 2.7 mM ATP. After the incubation, sections were washed twice for 5 min each time in 1% $CaCl_2$ solution followed by 3 min of incubation in 2% $CoCl_2$ solution at room temperature. Sections were then washed in distilled water before being stained with 1% ammonium sulfide (wt/vol; Fluka, Istanbul, Turkey) solution for 2 min. The stained sections were finally washed for 10 min with distilled water. Sections were then dehydrated for 15 s in ethanol (80%, 95% and 100%) and acetone (100%). The coverslips were mounted onto glass slides with Canada balsam (Fluka 60610) before viewing under a microscope.

Metabolic type (oxidative and glycolytic) of muscle fibres in LD, ST and SM muscles was determined using the succinate dehydrogenase staining technique described by Nachlas *et al.* (1957). Myofibres were viewed using a microscope (×10; Nikon Eclipse E600, Nikon Corporation, Tokyo, Japan) linked to an image capture system (Clemex, Image Analysis Software, Vision Lite, Montreal, Canada). Four areas were selected randomly from the sections to determine fibre type composition and myofibre diameter. Myofibre diameter was measured from ~25 fibres of each fibre type from each area counted. Images of muscle fibres from LD and ST muscles stained for myosin ATPase (pH 4.2) and succinate dehydrogenase are presented in Figs 1 and 2, respectively.

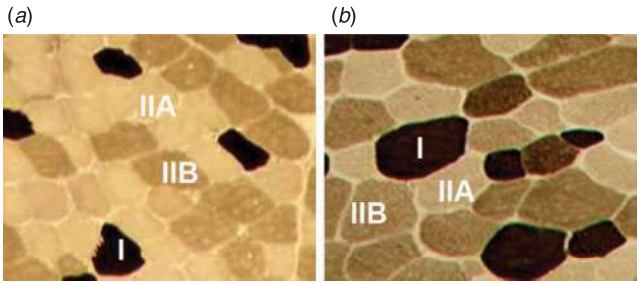

Fig. 1. Pictures of myosin ATPase staining (pH 4.2) of (*a*) longissimus dorsi muscles and (*b*) semitendinosus muscle. The darkest muscle fibre is Type I, intermediate muscle fibre is Type IIB and the lightest muscle fibre is Type IIA.

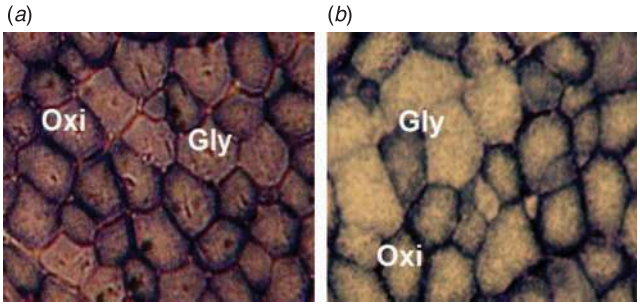

Fig. 2. Pictures of succinate dehydrogenase staining of (*a*) longissimus dorsi muscles and (*b*) semitendinosus muscle. The darkest blue muscle fibre is oxidative (oxi; Type I) and the lightest blue muscle fibre is glycolytic (gly; Type IIA and Type IIB).

Statistical analyses

The effect of maternal nutrition levels during mid-gestation on postnatal growth rate, carcass composition, muscle fibre characteristics, meat quality of lambs and other traits were analysed as a complete randomised design using the general linear model of the Statistical Analysis System (Minitab 1998). The birth type and sex of lambs were used as cofactor in the model to eliminate their effects on data. The differences in the mean values were compared by the Tukey's multiple comparison tests and results were computed as mean ± s.e.m. Statistical significance was considered at $P < 0.05$ and $P < 0.01$.

Results

Effect of maternal nutrition levels from Day 30 to Day 80 of gestation on the mean BW of ewes are presented in Fig. 3. Ewes in the ON, C and UN groups had similar BW at mating (50.9 ± 1.03 kg, 49.9 ± 1.12 kg and 48.8 ± 1.29 kg, respectively), and Day 30 of gestation (51.9 ± 1.08 kg, 50.4 ± 0.91 kg, 49.2 ± 1.07 kg, respectively). However, BW of ewes differed significantly between nutritional groups during the feeding period. Ewes in the ON group gained more BW than ewes in C groups, with ewes in the UN group losing BW ($P < 0.01$) from Day 30 to Day 80 of gestation. Similarly, there was a decrease ($P < 0.05$) in MD and FD values of LD muscle in UN ewes until Day 80 of gestation, resulting in an increase in

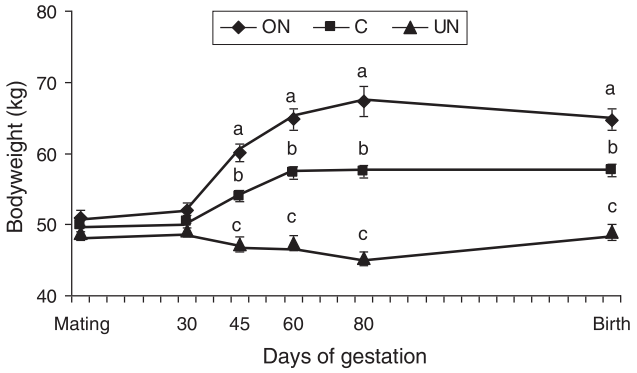

Fig. 3. Effect of maternal nutrition levels from Day 30 to Day 80 of gestation on the mean bodyweight of ewes. ON, overnutrition (175% of their daily requirement); C, control (100% of their daily requirement); UN, undernutrition (50% of their daily requirement). Symbols with different letters are significantly different at $P < 0.01$. The error bars represent the standard error of the mean.

MD to FD ratio of LD muscle ($P < 0.05$) compared with ewes in the ON and C groups (data not shown).

Growth performance and carcass characteristics of lambs at 150 days of age born to ewes that were fed at different levels from Day 30 to Day 80 of gestation are presented in Table 2. Although the level of maternal nutrition did not appear to affect lamb birthweights and weaning weights at 90 days of age, lambs born to ewes in the ON group tended to be heavier ($P = 0.084$) at birth compared with the C and UN groups. There was an effect ($P < 0.05$) of maternal nutrition level on final slaughter weight at 150 days of age, with lambs born to ewes in the UN group being lighter than those lambs born to ewes in the C group. They also had a lower average daily gain up to slaughter ($P < 0.05$). Lambs born to ewes in the UN group had lower average hot carcass weights ($P < 0.05$). There were no significant differences between lambs born to ewes in nutritional groups in terms of LD muscle characteristics.

Relative weights of some muscles, organs and carcass fat depots of lambs at 150 days of age born to ewes that were fed at different levels from Day 30 to Day 80 of gestation are presented in Table 3. Lambs born to ewes in the UN group had reduced ($P < 0.05$) whole muscle weights for ST, SM and GN (173.1 g, 43.7 g and 95.7 g, respectively), than lambs born to ewes in C (202.6 g, 47.7 g and 107.0 g, respectively) or ON (186.9 g, 49.6 g and 115.3 g, respectively), but there were no significant differences between groups in terms of relative muscle weights (g/kg of BW) for ST, SM and GN muscles. All lambs had similar heart, liver, lung, kidney, spleen, empty small intestine and empty reticulo rumen weights. There were no significant differences between lambs born to nutritional groups in terms of internal, pelvic, kidney and total fat as a percentage of slaughter weights, but internal fat weight of lambs born to ewes in the UN group tended to be higher ($P = 0.094$) than that of ewes in the C and ON groups (data not shown).

Muscle cellular characteristics of LD and ST muscles in 150-day-old lambs born to ewes that were fed at different levels from Day 30 to Day 80 of gestation are presented in Table 4. Lambs born to the ON group had higher ($P < 0.05$) concentrations of DNA in LD and ST muscles than those born to UN groups, but

Table 2. Growth performance and carcass characteristics of lambs at 150 days of age born to ewes that were fed at different levels from Day 30 to Day 80 of gestation

a,b, Different letters in the same row indicate significant difference ($P < 0.05$). ON, overnutrition (175% of their daily requirement); C, control (100% of their daily requirement); UN, undernutrition (50% of their daily requirement); PSE, pooled standard error

Traits	Treatment groups			PSE	*P*-values
	ON	C	UN		
Lamb weights (kg)					
Birth	4.34	3.81	3.69	0.09	0.08
Weaning	18.5	20.1	18.3	0.4	0.20
Slaughter	34.6ab	35.4a	32.0b	0.7	0.04
Average daily gains (g/day)					
Birth to weaning	161	180	161	4	0.20
Weaning to slaughter	266a	258a	228b	10	0.05
Birth to slaughter	204ab	210a	188b	5	0.05
Longissimus dorsi muscle characteristics					
Fat depth (mm)	3.62	3.60	3.30	0.15	0.60
Muscle depth (mm)	21.6	20.8	21.2	0.5	0.88
Muscle area (cm^2)	7.65	7.64	7.51	0.24	0.97
Muscle depth (mm) to fat depth (mm) ratio	5.96	5.79	6.19	0.37	0.93
Hot carcass weights (kg)	16.5a	16.3a	15.0b	0.4	0.04

Table 3. Relative weights (g/kg of bodyweight) of some muscles, organs and non-carcass fat depots in 150-day-old lambs born to ewes that were fed at different levels from Day 30 to Day 80 of gestation

ON, overnutrition (175% of their daily requirement); C, control (100% of their daily requirement); UN, undernutrition (50% of their daily requirement); PSE, pooled standard error

Traits	Treatment groups			PSE	*P*-values
	ON	C	UN		
Muscles					
Semitendinosus	5.61	5.59	5.51	0.15	0.88
Semimembranosus	1.49	1.34	1.41	0.04	0.43
Gastrocnemius	3.37	3.03	3.02	0.09	0.16
Organs					
Heart	4.24	4.21	4.37	0.08	0.38
Liver	20.8	19.8	20.4	0.4	0.71
Lung	14.7	12.7	13.3	0.4	0.29
Kidney	3.24	2.96	3.33	0.06	0.11
Spleen	1.79	1.81	2.14	0.07	0.10
Small intestine	20.5	19.6	21.5	0.6	0.38
Reticulo rumen	26.3	29.2	27.7	0.9	0.59
Non-carcass fat depots					
Internal fat	10.1	9.73	11.7	0.6	0.18
Pelvic fat	4.96	4.20	4.30	0.43	0.98
Kidney fat	2.75	2.62	2.56	0.22	0.35
Total fat	17.8	16.6	18.8	1.2	0.54

they had lower ($P < 0.05$) total protein and other proteins concentration in LD and ST muscles than those born to the C and UN groups. Protein to DNA ratio in LD and ST muscles of lambs born to the ON group was lower ($P < 0.05$) than those born to C and UN groups. There were no significant differences between lambs born to ewes in nutritional groups in terms of myofibrillar and sarcoplasmic protein concentrations in LD and ST muscles.

Table 4. Muscle cellular characteristics of longissimus dorsi and semitendinosus muscles in 150-day-old lambs born to ewes that were fed at different levels from Day 30 to Day 80 of gestation

a,b, Different letters in the same row indicate significant difference ($P < 0.05$). ON, overnutrition (175% of their daily requirement); C, control (100% of their daily requirement); UN, undernutrition (50% of their daily requirement); PSE, pooled standard error, IMF, intramuscular fat

Traits	Treatment groups			PSE	*P*-values
	ON	C	UN		
DNA (μg/g)					
Longissimus dorsi	843a	801a	632b	86	0.04
Semitendinosus	1019a	574ab	461b	98	0.02
Myofibrillar protein (mg/g)					
Longissimus dorsi	62.3	60.7	60.4	1.6	0.73
Semitendinosus	65.6	64.5	64.0	0.5	0.81
Sarcoplasmic protein (mg/g)					
Longissimus dorsi	39.9	35.9	34.5	2.1	0.54
Semitendinosus	29.5	29.7	30.1	0.8	0.78
Other proteins (mg/g)					
Longissimus dorsi	74.4b	112a	111a	2	0.03
Semitendinosus	80.1b	110a	110a	3	0.03
Total protein (mg/g)					
Longissimus dorsi	177b	208a	206a	8	0.04
Semitendinosus	175b	204a	204a	2	0.04
Protein (g): DNA (μg)					
Longissimus dorsi	248b	307b	406a	28	0.04
Semitendinosus	214c	464b	608a	61	0.01
IMF (%)					
Longissimus dorsi	2.14b	2.62b	2.90a	0.28	0.05
Semitendinosus	1.90	2.24	2.23	0.18	0.26
IMF (g): DNA (μg)					
Longissimus dorsi	3.27b	3.55b	5.64a	0.44	0.04
Semitendinosus	2.31c	4.96b	7.04a	0.79	0.05
Dry matter (%)					
Longissimus dorsi	24.77	24.52	25.31	0.23	0.87
Semitendinosus	24.20	24.17	24.37	0.16	0.95
Ash (%)					
Longissimus dorsi	1.09	1.17	1.08	0.05	0.54
Semitendinosus	1.16	0.99	1.08	0.03	0.36

There were no significant differences between lambs born to ewes in nutritional groups in terms of meat quality parameters such as pH, colour, drip loss, cooking loss, and shear force (data not shown). DM and ash ratio of LD and ST muscles in lambs from different treatment groups were similar, but lambs born to ewes in the UN group had a higher intramuscular fat content in LD (but not ST) muscle than those born to ewes from C and ON groups. Additionally, intramuscular fat to DNA ratio in LD and ST muscles of lambs born to the UN group was higher ($P < 0.05$) than those born to C and UN groups.

Effect of maternal nutrition levels from Day 30 to Day 80 of gestation on number of Type I, IIA and IIB fibres/mm^2 muscle area in LD and ST muscles of lambs are presented in Fig. 4 and

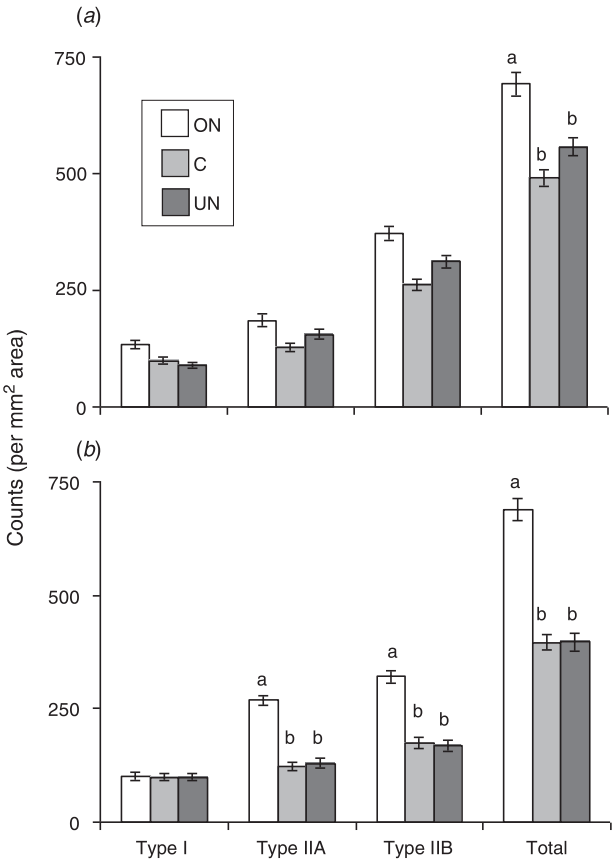

Fig. 4. Effect of maternal nutrition levels from Day 30 to Day 80 of gestation on the mean number of Type I, IIA, and IIB fibres/mm^2 muscle area in (*a*) longissimus dorsi and (*b*) semitendinosus muscles of lambs at 150 days of age. ON, overnutrition (175% of their daily requirement); C, control (100% of their daily requirement); UN, undernutrition (50% of their daily requirement). The error bars represent the standard error of the mean and bars with different letters are significantly different at $P < 0.05$.

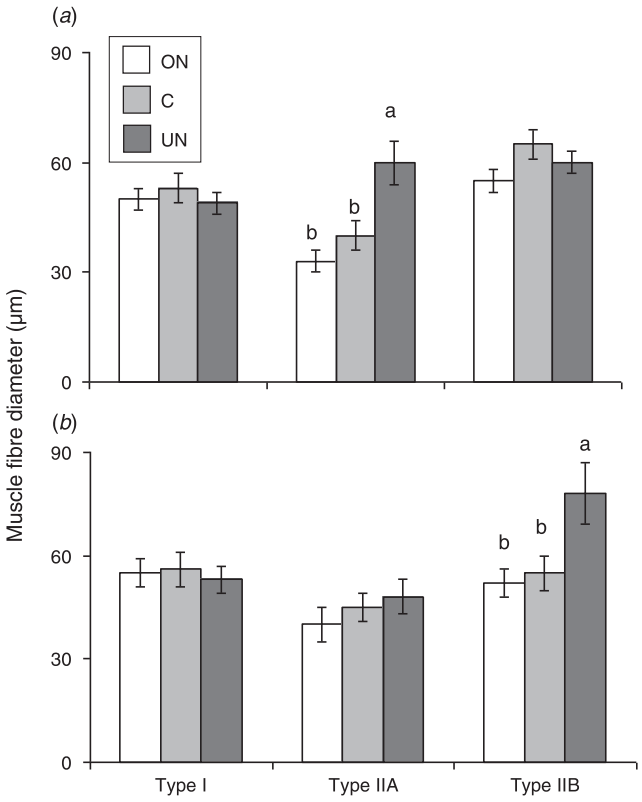

Fig. 5. Effect of maternal nutrition levels from Day 30 to Day 80 of gestation on the mean diameter of Type I, IIA, and IIB fibres in (*a*) longissimus dorsi and (*b*) semitendinosus muscles of lambs at 150 days of age. ON, overnutrition (175% of their daily requirement); C, control (100% of their daily requirement); UN, undernutrition (50% of their daily requirement). The error bars represent the standard error of the mean and bars with different letters are significantly different at $P < 0.05$.

Fig. 5, respectively. Maternal overnutrition resulted in an increase in the number of Type I, IIA, and IIB fibres/mm^2 muscle area in ST muscles of lambs ($P < 0.05$). There were, however, no significant differences between lambs in terms of number of Type I, IIA and IIB fibres/mm^2 muscle area in LD muscle, but an increase was observed in the number of total fibres/mm^2 muscle area in LD muscle of lambs born to ewes in the ON group ($P < 0.05$). There were no significant differences between lambs born to ewes in nutritional groups in terms of the diameter of Type I and IIB muscle fibre in LD muscle, but maternal undernutrition during mid-gestation resulted in an increase ($P < 0.05$) in diameter of Type IIA muscle fibre in LD muscle. Maternal nutrition level during mid-gestation did not affect the diameter of Type I and IIA muscle fibre in ST muscle of lambs, but lambs born to UN ewes had higher ($P < 0.05$) diameter of Type IIB muscle fibre in ST muscle than those of lambs born to ewes in other nutritional groups.

Effect of maternal nutrition levels from Day 30 to Day 80 of gestation on the mean number of oxidative and glycolytic fibres/mm^2 muscle area in LD and ST muscles of lambs are presented in Fig. 6. The level of maternal nutrition did not appear to affect metabolic properties of muscle fibres in lambs. There were no significant differences between lambs in terms of the mean number of oxidative and glycolytic fibres/mm^2 muscle area in LD and ST muscles.

Discussion

The present study demonstrates that maternal nutrition level during mid-gestation (from 30 to 80 days) influences growth performance, muscle fibre types and number, muscle fibre cellular characteristics and carcass characteristics, but not birthweight and meat quality of the lamb after weaning at the end of finishing period. Additionally, maternal nutrition level during mid-gestation changes BW, MD and FD values of LD muscle in ewes, reflecting the effects of nutritional treatments.

Maternal BW or condition at the start of gestation may play a role in feto-placental growth in early gestation (Sen *et al.* 2013). Moreover, lower maternal weight or body condition at mating and maternal undernutrition during early- and mid-gestation may have negative effects on placental and fetal growth (MacLaughlin *et al.* 2005; Sen *et al.* 2013). In the present study, there were no significant differences at the beginning of the feeding period between ewes in ON, C and UN groups in terms of the BW, MD and FD values of LD

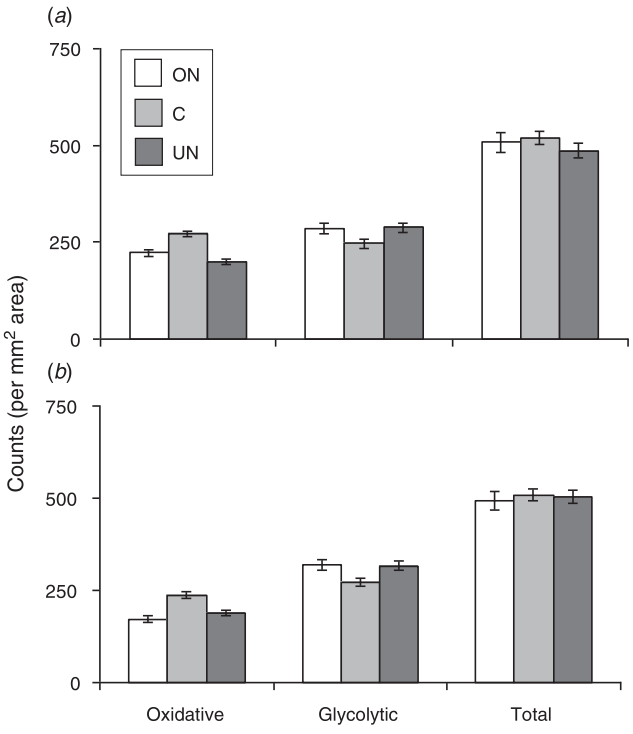

Fig. 6. Effect of maternal nutrition levels from Day 30 to Day 80 of gestation on the mean number of oxidative and glycolytic fibres/mm^2 muscle area in (*a*) longissimus dorsi and (*b*) semitendinosus muscles of lambs at 150 days of age. ON, overnutrition (175% of their daily requirement); C, control (100% of their daily requirement); UN, undernutrition (50% of their daily requirement). The error bars represent the standard error of the mean.

muscle as expected, maternal undernutrition during mid-gestation caused a decrease in BW and body reserves of ewes, resulting in a decrease in MD and FD values of LD muscle at the finishing of the feeding period of the ewes. BW did progressively decline in ewes in the UN group than that of ON and C ewes from Days 30 to 80 of gestation. During the experimental feeding period, BW of ewes in the ON and C groups increased 29.7% and 14.1%, respectively, whereas ewes in the UN group lost 8% of their BW on average. These results indicated that maternal undernutrition during mid-gestation induced an increase in body reserve mobilisation of ewes in the UN group compared with ewes in the ON and C groups, and body reserves in pregnant ewes depend on nutritional intake level. These findings are similar to Osgerby *et al*. (2002) in which UN ewes (on the 70% diet) between Days 26 and 135 of gestation had lower BW and body condition scores compared with the well fed ewes (on the 100% diet) by Day 135 of gestation. Additionally, Muñoz *et al*. (2008) reported that increasing the plane of nutrition (2.0 × maintenance) from Day 0 to Day 39 resulted in increases in BW and in BW changes during early pregnancy, but during mid-pregnancy (from Day 40 to Day 90), ewes offered low diet (0.6 × maintenance) gained more BW than ewes offered high diet, with ewes offered maintenance being intermediate.

Tygesen *et al*. (2007) reported that maternal undernutrition (60% of requirements for maintenance) during the last 6 weeks of gestation reduced birthweights of lambs. In addition, Muñoz *et al*. (2009) reported that lambs born from 1- and 2-year-old ON ewes (200% of requirements for maintenance) were heavier at birth than lambs from C (100% of requirements for maintenance) and UN ewes (60% of requirements for maintenance). In contrast, Fahey *et al*. (2005*a*) and Daniel *et al*. (2007) demonstrated that lamb birthweight was not affected by maternal nutrient restriction during early- and mid-gestation. In the present study, we did not observe any influence of the maternal nutrition levels from Day 30 to Day 80 of gestation on birthweight of lambs. These results indicate the importance of the timing of any maternal nutrition intake on lamb birthweights. In particular, maternal nutrition levels in late gestation can have effects on birthweight. However, additive effects of maternal nutrient levels during early- and mid-gestation on postnatal growth and adult size of offspring should not be ignored. Postnatal growth of lambs may be more sensitive to alterations in maternal nutrition intake during early- and mid-gestation and an association between prenatal environment and postnatal growth of offspring may occur (Fahey *et al.* 2005*a*, 2005*b*; Daniel *et al.* 2007).

In the present study, lambs from ewes in the UN group grew slower from weaning to slaughter. Therefore, they were lighter and had lower average hot carcass weights at slaughter (150 days of age). This finding agrees with previous work by Daniel *et al.* (2007) in which lambs from dietary restricted (70%) ewes during early- and mid-gestation (from 30 to 70 days) grew more slowly and were therefore lighter at slaughter (at 24 weeks of age) than those from well nourished ewes. Similarly, Nordby *et al*. (1987) reported that lambs from ewes restricted to 70% from Day 30 before breeding and the first 100 days of gestation took several days longer to reach the required slaughter weight. On the contrary, Krausgrill *et al*. (1999) showed that lambs from dams restricted from mating to Day 70 of gestation reached their target slaughter weight (35 kg) no later than those from C ewes. These data suggest that the timing of the nutritional insult and the age or weight of follow-up study may be important in terms of effects being studied. Certainly, the timing and duration of dietary restriction seem to be important factors in determining permanency and extent of reduced body size.

The lighter net weights of ST, SM and GN muscles were observed in lambs from UN ewes compared with lambs from C ewes. These results are consistent with the findings of Daniel *et al.* (2007) who reported male lambs from Days 30 to 70-restricted dams had the lighter LD and vastus lateralis muscle compared with males from C. Nordby *et al.* (1987) showed that feeding ewes 70% for the first 100 days of gestation resulted in lambs with heavier ST muscle weights than lambs from adequately fed ewes. This suggests that there may be complex interactions involving the specific timing the degree of nutrient restriction that impact upon any compensatory growth that may occur to overcome previous diet restriction.

Maternal nutrient restriction or overnutrition throughout pregnancy leads to alteration in adiposity of offspring (Symonds *et al.* 2010). A few studies have been carried out on the effects of maternal nutrition on adiposity of offspring in sheep. In the present study, maternal nutritional status during mid-gestation did not influence non-carcass fat of lambs, but average weight of internal fat tended to be higher in lambs born to UN ewes and also they had ~25% higher intramuscular fat

content and higher intramuscular fat to DNA ratio in the LD and ST muscles. Nordby *et al.* (1987) reported that maternal malnutrition (70% of C) from 30 days before breeding until 100 days' gestation had no effect on body fat at slaughter (58.5 kg liveweight) of lambs (Nordby *et al.* 1987). However, Bispham *et al.* (2002) showed that drastic malnutrition (50% C) during early- to mid-gestation (28–80 days' gestation) results in increased perirenal (PR) adipose tissue weights of the fetal lamb. Additionally, Long *et al.* (2012) reported that maternal overnutrition (150%) from Day 60 before conception to Day 135 of gestation increased PR adipose tissue weights as a percentage of fetal weights and subcutaneous fat thickness compared with C fetuses. This finding shows that maternal nutrition level especially undernutrition during mid-gestation may increase postnatal adiposity of lambs. Moreover both non-carcass fat content and intramuscular fat content may alter muscle fibre development, cellular characteristic and chemical composition of the muscle.

Growth processes are correlated with concentrations of DNA and protein, and protein-DNA ratio in skeletal muscle (Greenwood *et al.* 2006*a*). The ratio of protein to DNA (the so-called DNA unit) is an index of cell size in syncytial tissues such as muscle (Greenwood *et al.* 2006*b*). Quigley *et al.* (2005) reported that maternal feed intake during the peri-conception period (from 18 days before until 6 days after ovulation) did not influence total concentrations of DNA and protein in the ST muscle of singleton fetuses at 75 days of gestation. However, protein to DNA ratio in the ST muscle of fetuses from ON (1.5 × maintenance) ewes was higher compared with fetuses from UN (0.5 × maintenance) ewes in their study (Quigley *et al.* 2005). Greenwood *et al.* (2000) reported that low birthweight newborn lambs had less had less muscle DNA than their large counterparts and they also had a lower ratio of muscle protein to DNA at birth. In the present study, although maternal nutrition level during mid-gestation did not influence lamb birthweight, lambs from ewes in the UN group had significantly lower concentrations of DNA in LD and ST muscles compared with lambs at slaughter age from ewes in the C and ON groups. Additionally, protein to DNA ratio was significantly higher in LD and ST muscles of lambs from ewes in the UN group than lambs at slaughter age from ewes in C and ON groups. These findings support observations in the present study that maternal undernutrition during mid-gestation decreases muscle fibre number whereas it increases muscle fibre diameter in LD and ST muscles of lambs.

Muscle proteins are categorised as sarcoplasmic (30%), myofibrillar (50–60%) and stromal (10–20%) proteins based on their solubility. Myofibrillar proteins are salt soluble and responsible for the actual contraction of the muscle. Two basic functional categories of myofibrillar proteins are structural and contractile proteins. Sarcoplasmic proteins are water soluble and these proteins are almost all enzymes. Myoglobin, a common sarcoplasmic protein that is important in meat colour. Stromal proteins include proteins of connective tissues and they are insoluble in both water and salt. These insoluble proteins form the harness that holds together the muscle fibres and amount of stromal proteins affect meat tenderness (Aberle *et al.* 2001). In the present study lambs from nutrition groups had similar myofibrillar and sarcoplasmic protein concentrations, and also meat colour characteristics, in LD and ST muscles, but lambs from ON ewes had lower other proteins concentration. Therefore, decreased in total protein concentration of lambs from ON ewes may be caused by lower other proteins concentration in all muscles. Keever (2011) reported that salt-soluble proteins contents as a percentage of wet weight were significant difference between species. In the present study lambs from nutrition groups had low sarcoplasmic protein concentration in muscles than different species and breed such as beef (~55 mg/g in LD muscle; Rowe *et al.* 2004), chicken (~85 mg/g in breast fillets; Bowker and Zhuang 2013), pork (~64 mg/g in LD muscle; Wilson and Van Laack 1999) and lamb (~45 mg/g in ST muscle of Poll Dorset · Border Leicester–Merino; Warner *et al.* 2014). These differences may be explained by species and breed differences because the protein concentration of meat can vary depending on the species and breed (Heinz and Hautzinger 2007). Additionally, the sheep breed used in this study has very low BW, which may have a different ratio of other proteins in their carcasses.

Drastic maternal malnutrition throughout gestation or during early-, mid- and late-gestation has been shown to reduce myofibre number in fetal lambs. Zhu *et al.* (2004) showed that fetus (Day 78 of gestation) from UN ewes (0.5 × maintenance) from Day 28 to Day 78 of gestation had fewer secondary myofibres in LD muscle compared with C. Fahey *et al.* (2005*a*) reported that maternal malnutrition (0.5 × maintenance) from Day 30 to Day 70 of gestation did alter the muscle fibre composition of 14-day-old lambs by reducing the numbers of Type II fibres in both the LD muscle. Furthermore, this study reported that maternal malnutrition (0.5 × maintenance) during (from Day 55 to Day 95 of gestation) and after (from Day 85 to Day 115 of gestation) muscle fibre formation did not alter the muscle fibre characteristics of the neonatal lambs. In the present study, lambs from ON ewes had higher numbers of Types IIA and IIB in ST muscle than those lambs from C and UN ewes, whereas there were no differences in LD muscle. Also, lambs from ON ewes had reduced diameter of Type IIB muscle fibres in ST muscle than those lambs from C and UN ewes. Additionally an increase in the number of fibres/mm^2 muscle area in lambs from ON ewes was observed in LD muscle and they had reduced diameter of Type IIA than those lambs from C and UN ewes. Daniel *et al.* (2007) reported that maternal dietary restriction (0.5 × maintenance) from Day 30 to Day 85 of gestation increased the number of Type IIB fibres in ST muscle of 17-week-old male and female lambs. Zhu *et al.* (2006) also reported that a similar increase the numbers of Type IIB fibre of LD muscle in 8-month-old lambs from ewes that had also been subjected to dietary restriction during early- and mid-gestation (from Day 28 to Day 78). Greenwood *et al.* (2000) reported that birthweight of lambs did not affect total number of muscle fibres in the ST muscle at different slaughter weight (7.5, 10, 15, and 20 kg). Similarly, Sirin *et al.* (2011) showed that lambs with different birthweight had similar muscle fibre number in mm^2 muscle area in ST muscle at 150 days of age. Although, in the present study lambs born to ewes that were fed at different levels during mid-gestation had similar birthweights, lambs from ON ewes had a higher muscle fibre number in mm^2 muscle area in ST muscle than those lambs from C and UN ewes. These changes noted in the adult offspring suggest that animals have somehow managed to compensate for

effects of maternal dietary restriction on fibre composition noted in early life.

Developmental programming is a concept that a maternal stimulus or insult at a critical period in fetal development has long-term effects on the offspring (Wu *et al.* 2006). Although some muscles weight and muscle fibre characteristics of lambs was affected by maternal nutrition level during mid-gestation, results of the present study indicate that there is no effect of maternal nutrition levels on any of the measured meat quality traits, such as drip loss, cooking loss, share force, pH and colour characteristics.

Although intramuscular fat and connective tissue protein of skeletal muscle as well as muscle fibre numbers, size and composition were influenced by maternal nutrition level during mid-gestation, DM and ash proportions in the LD and ST muscles of lambs were similar in the present study. Thus, our results with respect to lamb meat quality do not support the argument that the prenatal development of muscle fibres and adiposities has a profound impact on meat quality when the animal is slaughtered at or near adult BW (Rehfeldt *et al.* 2011), but confirm the idea that maternal nutrition during gestation does not affect meat quality parameters in sheep (Krausgrill *et al.* 1999; Tygesen *et al.* 2007). These contradictions might have been due to differences in the experimental approach followed by those authors and the system of production and animals used.

In conclusion, the results of the present study may imply that maternal nutrition levels during mid-gestation, in which skeletal muscle fibres partially begin and complete the growth and development, have important effects on growth performance, carcass composition, fibre types, muscle fibre number in mm^2 muscle area and growth (diameter) of skeletal muscle fibre of the offspring but it does not affect quality of the meat produced. Hence, these results may have implications for developing feeding strategies for the early- and mid-gestation period with a view to increase meat production from sheep.

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