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The effect of maternal nutritional status during mid-gestation on placental characteristics in ewes

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ABSTRACT

The aim of this study was to determine the effects of maternal nutritional status during mid-gestation on placental characteristics in ewes. Time of estrus of 3–5 years old Karayaka breed ewes was synchronized and mating was monitored to determine the day 0 of gestation. The ewes had similar body weights (47.8 ± 0.7 kg) and loin eye muscle values (thickness; 20.9 ± 1.0 mm and fat thickness; 4.7 ± 0.5 mm) at mating. The ewes were allocated into two treatment groups at day 30 of gestation; under-fed (UF; $n = 12$) and well-fed (WF; $n = 13$) groups. The ewes in UF group were fed with a diet to provide 50% of their daily requirement from day 30 to day 80 of gestation and 100% of their daily requirement during the rest of the gestation period. The ewes in WF group were fed at least 100% of their daily requirement throughout gestation. The singleton bearing ewes in the UF group had a lesser ($P < 0.05$) placental weight (354.1 compared with 378.3 g), average cotyledon weight (1.50 compared with 1.82 g) and lamb birth weight (3.8 compared with 4.2 kg) than singleton bearing ewes in the WF group. There were positive correlations between placental weight and lamb birth weight ($r = .469$; $P < 0.05$), placental weight and average cotyledon weight ($r = .695$; $P < 0.01$), average cotyledon weight and lamb birth weight ($r = .742$; $P < 0.01$) and placental efficiency and cotyledon density ($r = .853$; $P < 0.01$) for ewes in WF group. Additionally, the pattern of weight gain/loss was different ($P < 0.05$) between the two groups. Ewes in UF group lost body weight progressively from day 30 of gestation until day 80. The results of present study show that under-feeding of ewes during mid-gestation may cause an insufficient placental development and hence alter fetal development resulting in a reduced birth weight from singleton pregnancies.

1. Introduction

Maternal nutrient intake during gestation in various species affects the size and development of both the placenta and the fetus (Redmer et al., 2004). Survival of the fetus is affected especially by sufficiency of the placenta (Mellor and Stafford, 2004). Furthermore, the size and nutrient transfer capacity of the placenta play a central role in determining the prenatal growth trajectory of the fetus and resulting in long-term programming effects on birth weight, postnatal growth, viability, productivity and long-term health of the offspring (McMullen et al., 2005). Maternal nutrient restriction during gestation has been reported to cause a reduction in proliferation of placental mass, as well as impaired umbilical blood flows. A poorly developed placenta restricts nutrient and respiratory gases supply, leading to fetal hypoxia, hypoglycemia or low nutrient uptakes, asymmetric organ growth and reduced fetal growth rates (Wu et al., 2006; Ocak et al., 2009). Indeed the importance of the placental circulation is

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exemplified by the close relationships among fetal weights, placental weights and utero-placental blood flows in normal and growth restricted pregnancies (Greenwood et al., 2000; Redmer et al., 2004). Severe restrictions of substrate supply may result in maternal, placental and fetal adaptations to the altered pre-natal environment, which allows survival of the offspring, often at the expense of the normal fetal development (Quigley et al., 2008). There is increasing evidence from epidemiological and experimental studies that the programming of fetal development may be particularly sensitive to maternal nutrient status during the peri-conception period (Robinson et al., 1997; Quigley et al., 2005; Hernandez et al., 2009; Igwebuike, 2010). Thus, it is obvious that amount of maternal nutrition affecting placental vascular development will have a dramatic impact on fetal growth and development.

Attachment of fetal cotyledons to the maternal caruncles occurs between days 25 and 30 of gestation in sheep, and growth restriction during this period can limit the eventual number of placentomes that form the placenta (Igwebuike, 2010). The majority of placental growth in terms of mass and net cellular proliferation occurs during the first two-thirds of gestation in sheep (Redmer et al., 2004; Igwebuike, 2010). Also, the placenta achieves its maximum weight by day 90 of gestation and no change in tissue dry matter content occurs thereafter (Sammin et al., 2009; Igwebuike, 2010). During this period, the fetus has only 10% of its eventual birth weight by the time the placenta has reached its maximum size (Redmer et al., 2004; Sammin et al., 2009). In this context, approximately 90% of fetal growth occurs during the last third of gestation when after the complete development of the placenta in sheep (Redmer et al., 2004). The indication is that placental size and even function later in gestation may be substantially influenced at this early stage in sheep (Igwebuike, 2010).

The consequences of nutrition status in the first half of pregnancy for ruminant placental growth have been rarely studied. However, available evidence support the idea that placental growth, and by implication, fetal growth is most vulnerable to maternal nutritional status during the peri-implantation period and the first trimester of gestation when rapid placental development occurs (Wu et al., 2004). The usual mating period of ewes in most parts of the world coincides with the autumn and early winter months during which nutrient intake of pregnant ewes may be less than at other times of the year due to poor rangeland quality. Thus it can be postulated that most of sheep in most parts of the world experience malnutrition during the gestation period which may cause altered placental development resulting in lesser birth weights and poorer adult performance post weaning due to nutritional programming effects during gestation. The aim of the present study, therefore, was to determine the effects of maternal nutritional status during mid-gestation on placental characteristics in singleton bearing ewes. It is well known that litter size has a significant role in the placental size (Konyali et al., 2007; Ocak et al., 2009). The Karayaka breed sheep used in this study is a good model for assessing nutritional influences on placental characteristics because this breed is known for low prolificacy (approximately 1.1) thus the influence of litter size on placental characteristics was minimized by using this breed.

2. Materials and methods

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 ewes in Turkey (September to March). Experimental animals were of 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 and 650 m above the sea level). Time of estrus was synchronized by use of intravaginal sponges containing 30 mg flugestone acetate (Chronogest; Intervet, Turkey) for 12 days followed by an intramuscular injection of 1 ml of $PGF_{2\alpha}$ (Dinolytic; 5 mg PF2α/ml, Pharmacia, Belgium). Forty-eight hours later, the ewes were introduced to Karayaka rams (approximately one ram to every 10 ewes), and the mating was monitored to determine day 0 of gestation. The ewes had similar body weights and eye muscle values, measured by an ultrasonic linear probe at mating.

Ewes were housed in individual pens at day 55 of gestation. The mean body weights of ewes were determined at days 30, 45, 60 and 80 of gestation and at birth. Additionally, loin thickness and fat thickness values of eye muscle were determined at days 30 and 80 of gestation and at birth. The ewes were allocated into two treatment groups; under-fed (UF; $n = 12$) and well-fed (WF; $n = 13$) groups. The ewes in WF group were composed of two sub-groups; ewes offered with a diet to be fed either *ad libitum* (sub-group 1; $n = 4$; consumed 175% of the daily requirements) or 100% of their daily requirements (sub-group 2; $n = 9$) from day 30 to day 80 of gestation. These two sub-groups were combined, because there were no differences between ewes when all variables were measured. The ewes in UF group were fed with a diet to meet 50% of the daily requirements from day 30 to day 80 of gestation. During the rest of the gestation period, the ewes in both groups were fed with a diet to meet 100% of the daily requirements. The daily DM requirements of ewes throughout this study were calculated on an individual ewe body weight basis. 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). The amounts of concentrate and hay consumption were 991.3 ± 77.1 and 975.9 ± 29.1 g/day/ewe in WF group, and 200.0 ± 0.2 and 468.4 ± 8.9 g/day/ewe in UF group, respectively. Diets were given daily in two equal meals at 08:30 and 16:30. Ewes were weighed at intervals of about every 2 weeks and the quantity of diet adjusted for weight gain and for weight loss. Water and minerals were freely available throughout the study. All ewes gave birth to singletons except four ewes in WF group. These ewes were excluded from the study to avoid litter size effects on placental characteristics.

Birth weight and the sex of lambs were recorded within 12 h after lambing. Each ewe was left to deliver the placenta naturally and placentas were collected from singleton pregnancies immediately after delivery (approximately 2 h after the birth of the lamb); care was taken to ensure that any placental weights taken were of the total placenta with any fluid being removed before weighting. The numbers and weights of cotyledons were also counted, determined and recorded. Placental efficiency (defined as gram of lamb produced per gram of placenta) was calculated for each ewe. The cotyledon density was calculated as the number of cotyledons in gram placental weight.

The effect of maternal nutrition during mid-gestation on lamb birth weight, placental characteristics and other variables were investigated using a completely randomized design by using GLM procedure of Minitab (Minitab, 1998). The sex of lambs was used as a cofactor in the model to adjust the birth weight and the placental characteristics. Relationships between the placental characteristics were determined with a Pearson correlation analysis at the 95% confidence interval. The Fisher z transformation test was applied to assess the significance of the differences between correlation coefficients of two groups. Significant differences between means were tested using Tukey's multiple comparison tests and results were computed as mean ± SEM.

3. Results

The changes in maternal body weights (BW) from mating to birth in experimental ewes in WF and UF groups are presented in Fig. 1. All ewes had similar BW (47.8 ± 0.7 kg) at mating and there were no significant differences between ewes in WF (48.5 ± 0.9 kg) and UF (48.2 ± 0.7 kg) groups at day 30 of gestation. The pattern of weight gain/loss was, however, different ($P < 0.05$) between the two groups. Ewes in UF group lost weight progressively from day 30 until day 80 ($P < 0.05$) of gestation. From day 80 of gestation, following initiation of feeding of 100% of the daily requirements, ewes gained weight such that at the end of gestation the BW was not different from that of ewes in WF group (WF; 49.4 ± 0.9 kg, UF; 48.9 ± 0.7 kg).

The changes in loin thickness and fat thickness values of the loin eye muscle from mating to birth in WF and UF ewes are presented in Figs. 2 and 3, respectively. All ewes had similar loin eye (20.9 ± 1.0 mm) and fat (4.7 ± 0.5 mm) thickness values at mating. Also, there were no significant differences in loin eye and fat thickness values of eye muscle between WF (loin thickness; 21.0 ± 1.1 mm and fat thickness; 4.7 ± 0.5 mm) and UF (loin thickness; 20.9 ± 1.0 mm and fat thickness; 4.5 ± 0.7 mm) ewes at day 30 of gestation. There was a decrease ($P < 0.05$) in loin eye and fat thickness values in UF ewes at day 80 of gestation, after which there was no further change until birth. Loin eye and fat thickness values were similar throughout gestation in the WF group.

Unadjusted and adjusted means for length of gestation, lamb birth weights and placental characteristics of ewes in WF and UF groups are presented in Table 1. The sex of lambs had no effect on any variables studied. The length of gestation was not significantly different between UF and WF ewes. There was, however, a decrease in the birth weight of the lambs born from ewes in UF group compared with the lambs from ewes in WF ($P < 0.05$). Number of cotyledons, cotyledon density and placental efficiency were not significantly different between UF and WF ewes. However, there were decreases in the placental and average cotyledon weights in UF ewes compared to WF ewes ($P < 0.05$).

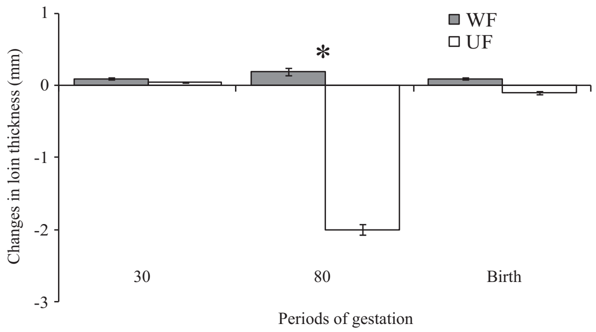

Fig. 2. The changes in loin eye thickness values from mating to day 30, 80 of gestation and birth in ewes in WF and UF groups. Asterisk indicates differences between treatment groups ($P < 0.05$). UF = under-fed group, WF = well-fed group.

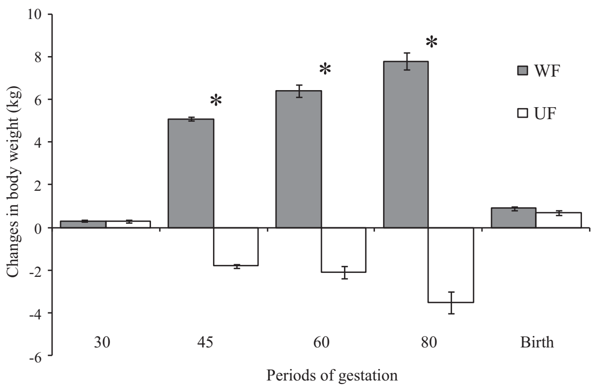

Fig. 1. The changes in maternal body weights from mating to day 30, 45, 60, 80 of gestation and birth in ewes in WF and UF groups. Asterisks indicate differences between treatment groups ($P < 0.05$). UF = under-fed group, WF = well-fed group.

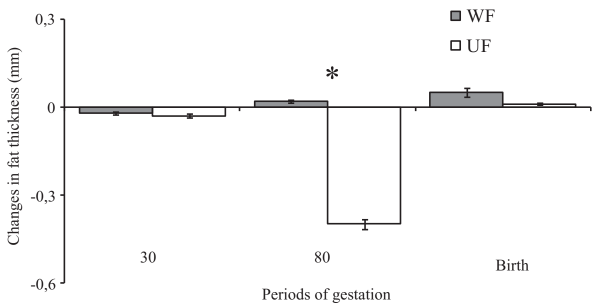

Fig. 3. The changes in fat thickness values from mating to day 30, 80 of gestation and birth in ewes in WF and UF groups. Asterisk indicates differences between treatment groups ($P < 0.05$). UF = under-fed group, WF = well-fed group.

Table 1
Unadjusted and adjusted means, according to lamb sex, for length of gestation, lamb birth weights and some placental characteristics (means ± SEM) of ewes in WF and UF groups.

Traits	Sub-group 1	Sub-group 2	Treatment groups[c]			
			WF		UF	
			Unadjusted mean	Adjusted mean	Unadjusted mean	Adjusted mean
F/M (*n*)	2/2	4/5	6/7		6/6	
LG (day)	146.7 ± 0.83	147.9 ± 0.58	147.1 ± 0.68	146.6 ± 0.83	148.9 ± 0.58	147.8 ± 0.7
BW (kg)	4.28 ± 0.039	4.21 ± 0.013	4.24 ± 0.027[a]	4.22 ± 0.033[a]	3.74 ± 0.119[b]	3.73 ± 0.141[b]
PW (g)	404.3 ± 15.4	379.8 ± 9.3	387.3 ± 10.28[a]	387.8 ± 11.94[a]	352.8 ± 13.33[b]	348.7 ± 15.54[b]
TCN (*n*)	71.28 ± 0.980	69.03 ± 0.670	69.69 ± 0.850	70.16 ± 0.982	71.75 ± 3.925	70.22 ± 4.620
ACW (g)	1.92 ± 0.497	1.90 ± 0.312	1.91 ± 0.381[a]	1.90 ± 0.051[a]	1.57 ± 0.136[b]	1.62 ± 0.176[b]
PE	11.13 ± 0.947	11.51 ± 0.803	11.35 ± 0.859	11.27 ± 0.295	10.75 ± 1.481	10.84 ± 0.455
CD	0.188 ± 0.042	0.187 ± 0.035	0.187 ± 0.038	0.188 ± 0.005	0.202 ± 0.045	0.199 ± 0.015

Means in rows with different letters (a,b) are different at $P < 0.05$.
SEM = standard error of mean, *F* = female, M = male LG = length of gestation, BW = lamb birth weight, PW = placental weight, TCN = total cotyledon number per placenta, ACW = average cotyledon weight, PE = placental efficiency, CD = cotyledon density.
[c] The ewes in WF (well-fed) group were composed of two sub-groups; ewes offered with a diet to be fed either *ad libitum* (sub-group 1; *n* = 4; consumed 175% of their daily requirement) or 100% of their daily requirements (sub-group 2; *n* = 9) from day 30 to day 80 of gestation. The ewes in UF group (under-fed; *n* = 12) were fed with a diet to meet 50% of their daily requirements from day 30 to day 80 of gestation.

Table 2
Pearson correlation coefficients (95% confidence intervals) of placental characteristics and lamb birth weight of ewes in WF groups.

Traits	PW	PE	CD	ACW	BW
CN	0.053 (−0.609, 0.715)	−0.053 (−0.715, 0.609)	0.286 (−0.349, 0.921)	−0.323 (−0.951, 0.305)	−0.059 (−0.721, 0.603)
PW		−0.868** (−1.197, 0.538)	−0.889** (−1.192, −0.585)	0.695** (0.217, 1.172)	0.469* (−0.117, 1.055)
PE			0.853** (0.506, 1.199)	−0.459 (−1.048, 0.130)	−0.077 (−0.738, 0.584)
CD				−0.799** (−1.198, −0.399)	−0.470 (−1.055, 0.115)
ACW					0.742** (0.297, 1.186)

BW = lamb birth weight; PW = placental weight; PE = placental efficiency; CN = cotyledon number; CD = cotyledon density; ACW = average cotyledon weight.
* $P < 0.05$.
** $P < 0.01$.

Table 3
Pearson correlation coefficients (95% confidence intervals) of placental characteristics and lamb birth weight of ewes in UF groups.

Traits	PW	PE	CD	ACW	BW
CN	0.032 (−0.672, 0.736)	−0.076 (−0.778, 0.626)	0.759** (0.300, 1.217)	−0.539* (−1.132, 0.054)	0.019 (−0.685, 0.723)
PW		−0.797** (−1.222, −0.371)	−0.619* (−1.172, −0.065)	0.287 (−0.387, 0.961)	0.021 (−0.683, 0.725)
PE			0.445 (−0.185, 1.075)	0.004 (−0.700, 0.708)	0.565* (−0.016, 1.146)
CD				−0.645* (−1.183, −0.106)	−0.034 (−0.738, 0.670)
ACW					0.435 (−0.199, 1.069)

BW = lamb birth weight; PW = placental weight; PE = placental efficiency; CN = cotyledon number; CD = cotyledon density; ACW = average cotyledon weight.
* $P < 0.05$.
** $P < 0.01$.

Pearson correlation coefficients of placental traits for ewes in WF and UF groups are presented in Tables 2 and 3, respectively. In both groups there were negative correlations between placental weight and placental efficiency ($r = -.868$; and $r = -.797$; $P < 0.01$), placental weight and cotyledon density ($r = -.889$; $P < 0.01$ and $r = -.619$; $P < 0.05$), and cotyledon density and average cotyledon weight ($r = -.799$; $P < 0.01$ and $r = -.645$; $P < 0.05$) for ewes WF and UF groups, respectively. There were positive correlations between placental weight and lamb birth weight ($r = .469$; $P < 0.05$), placental weight and average cotyledon weight ($r = .695$; $P < 0.01$), average cotyledon weight and lamb birth weight ($r = .742$; $P < 0.01$) and placental efficiency and cotyledon density ($r = .853$; $P < 0.01$) for ewes in WF group. As can be expected there were positive correlations between cotyledon number and cotyledon density ($r = .759$; $P < 0.01$) and negative correlations between average cotyledon weight and cotyledon number ($r = -.539$; $P < 0.05$) for ewes in UF group. There were positive correlations between placental efficiency and lamb birth weight ($r = .565$; $P < 0.05$) in the UF group. There were no significant correlation coefficients for variables in the UF and WF groups.

4. Discussion

The present study demonstrates that amount of nutrition during mid-gestation (from 30 to 80 days) influences placental weight, average cotyledon weight and birth weight in singleton bearing ewes. Additionally undernourished ewes had a lesser body weight, loin eye thickness and fat thickness value than well-fed ewes by day 80 of gestation, reflecting the nutritional treatments.

The placenta is the organ through which respiratory gases, nutrients, and wastes are exchanged between the maternal and fetal systems (Wu et al., 2006). The placenta also is the primary contributor to the intrauterine environment for growth and development of the fetus. Although the fetal genome plays an important role in growth potential *in utero*, there is evidence suggesting that the intrauterine environment is an important determinant of fetal growth (Wu et al., 2006; Igwebuike, 2010). Placental and the umbilical cord size are closely related to fetal development and growth rate (Godfrey and Barker, 2000; Wu et al., 2006; Ocak et al., 2009). Maternal nutrition, however, may impact placental development, growth and vascular bed development (angiogenesis), thereby affecting utero-placental blood flow and nutrient uptake by the fetus, all of which may play an important role in fetal growth and metabolism, as well as birth weight (Redmer et al., 2004). Experiments in sheep showed that amount of maternal nutrition in early and mid gestation can exert major effects on the growth, development and weight of the placenta and thereby alter fetal development (Clarke et al., 1998; Osgerby et al., 2002; Fahey et al., 2005; McMullen et al., 2005) as supported by the results of the present study.

Although there are differences between treatment groups in terms of birth weight, placental weight and average cotyledon weight, it is interesting that placental efficiency and cotyledon density did not differ between ewes in UF and WF groups. This may be due to similar directional changes in birth and placental weights in both groups. In fact, there were approximately 9% decreases in placental and 12% in birth weight. The results obtained from the present study show that amount of maternal nutrition between day 30 and day 80 of gestation influenced placental and average cotyledon weights, but not total cotyledon number per placenta. These observations are in agreement with the view that maternal nutrition during gestation can affect placental development and thus reduce placental weight and decrease placental size (Clarke et al., 1998; Osgerby et al., 2002; Redmer et al., 2004; Wu et al., 2006). Additionally, such an alteration in placental development may have dramatic functional consequences in fetal development. The reason for the reduced lamb birth weight in undernourished ewes might be inadequate placental growth and development. Lambs from undernourished ewes during mid-gestation may have poorer adult performance due to the genomic programming effects of nutrition during gestation (Redmer et al., 2004; Wu et al., 2006). Indeed it has been reported that the lambs from the UF group had a lesser weaning weight, altered carcass composition and muscle fiber types following fattening (Kuran et al., 2007, 2008).

Ocak et al. (2009) reported that placental weight was positively correlated with average cotyledon weight, cotyledon number and cotyledon density in sheep. Konyali et al. (2007) reported similar findings for goats. The correlations observed in the present study between placental characteristics in the well-fed group supports the view that the influence of maternal nutrition on placental characteristics results in altered birth weight. It was observed that increased placental weight as a result of amount of nutrition causes an increase in average cotyledon and lamb birth weight. There was also a positive correlation between average cotyledon and lamb birth weight in well-fed ewes. The negative correlation between placental weight and efficiency observed in the present study supports the findings of Ocak and Onder (2011) for goats.

It is interesting that the ewes in the UF group showed compensatory growth from day 80 to birth, and the nutritional influence on live weight, loin eye thickness and fat thickness was not evident between control and treatment groups by the time of birth. However differences in placental weights between ewes in UF and WF groups remained at birth representing long term effects when diets do not meet nutritional recommendations on placental growth and development. Feeding diets that do not meet nutritional recommendations during mid-gestation caused a decrease in body weight, loin eye thickness and fat thickness in the present study. This result indicates that body reserves in pregnant ewes depend on amount of nutritional intake. Osgerby et al. (2002) reported that undernourished ewes (on the 70% diet) during different periods of gestation (45, 90, 135 day of gestation) had lesser body weights and body condition scores compared to the well-fed ewes (on the 100% diet).

5. Conclusions

The results of present study showed that amount of maternal nutrition during mid-gestation impacts placental growth and development of singleton bearing ewes as indicated by placental and average cotyledon weight causing altered fetal development and hence resulting in lesser lamb birth weights which may affect adult performance of lambs. These findings may be important to develop novel nutritional strategies during critical periods of gestation which may yield preferable adult performance and meat quality.

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