

# Effects of plane of nutrition and selenium supply during gestation on ewe and neonatal offspring performance, body composition, and serum selenium<sup>1</sup>

A. M. Meyer,\* J. J. Reed,\* T. L. Neville,\* J. B. Taylor,† C. J. Hammer,\*  
L. P. Reynolds,\* D. A. Redmer,\* K. A. Vonnahme,\* and J. S. Caton\*<sup>2</sup>

\*Center for Nutrition and Pregnancy, Department of Animal Sciences, North Dakota State University, Fargo 58108; and †USDA-ARS, US Sheep Experiment Station, Dubois, ID 83423

**ABSTRACT:** To investigate the effects of nutritional plane and Se supply during gestation on ewe and offspring performance and body composition, 84 Rambouillet ewe lambs (age = 240 ± 17 d, BW = 52.1 ± 6.2 kg) were allocated to a 2 × 3 × 2 factorial arrangement of treatments. Factors included Se [adequate Se (ASe, 11.5 µg/kg of BW) or high Se (HSe, 77.0 µg/kg of BW)] initiated at breeding, nutritional plane [60% (restricted, RES), 100% (control, CON), or 140% (high, HIH) of NRC requirements] initiated at d 40 of gestation, and physiological stage at necropsy [3 to 24 h postpartum or d 20 of lactation]. Ewes were fed and housed individually in a temperature-controlled facility. At parturition, all lambs were removed and artificially reared until necropsy on d 20.6 ± 0.9 of age. Ewes assigned to the treatment at d 20 of lactation were transitioned to a common diet meeting lactation requirements and were mechanically milked. From d 95 of gestation through parturition and d 20 of lactation, ewe BW and BCS were least ( $P \leq 0.01$ ) in the RES treatment, intermediate in the CON treatment, and greatest in the HIH treatment. Ewes fed HSe had a greater ( $P \leq 0.05$ ) BCS increase than those fed ASe during mid- and late gestation. During gestation, ewes in the HIH treatment had the greatest ( $P < 0.001$ ) ADG and G:F, those in the CON treatment were intermediate, and those in the RES treatment were least, whereas ewes fed HSe had greater ( $P < 0.001$ ) ADG and G:F than those fed ASe during midgestation. Ewe backfat and LM area on d 135 of gestation were least ( $P < 0.001$ ) in the

RES treatment, intermediate in the CON treatment, and greatest in the HIH treatment, with ewes fed HSe having greater ( $P \leq 0.03$ ) backfat than those fed ASe. During the first 20 d of lactation, ewes fed the RES diet had greater ( $P < 0.09$ ) G:F than those fed the CON and HIH diets. Physiological stage had no effect on ewe omental and mesenteric fat or perirenal fat weights, although both were greater ( $P < 0.001$ ) for ewes fed the HIH diet than for those fed the RES and CON diets. At birth, lambs born to ewes in the RES group weighed less and had decreased curved crown rump lengths ( $P = 0.08$ ) compared with those born to ewes in the CON and HIH groups, and lambs from ewes in the ASe-RES treatment were lighter ( $P < 0.08$ ) than those from ewes in the HSe-RES, ASe-CON, and ASe-HIH treatments. Lambs from dams in the RES group had less ( $P < 0.05$ ) BW from d 7 to 19 and decreased ( $P < 0.07$ ) overall ADG compared with lambs from dams in the CON and HIH groups. Additionally, lambs from dams in the RES group had less ( $P \leq 0.08$ ) perirenal fat than their counterparts, and lambs from dams in the HIH group had greater ( $P = 0.01$ ) omental and mesenteric fat than lambs from dams in the RES group. Postpartum serum Se of ewes and lambs (birth and d 19) was increased ( $P < 0.001$ ) by HSe feeding during gestation. Results indicate that BW differences in pregnant ewes attributable to nutritional plane are accompanied by changes in body composition and offspring BW, both of which may be affected by Se supply.

**Key words:** developmental programming, gestation, neonate, nutritional plane, selenium, sheep

©2010 American Society of Animal Science. All rights reserved.

J. Anim. Sci. 2010. 88:1786–1800  
doi:10.2527/jas.2009-2435

<sup>1</sup>Partially supported by USDA-National Research Initiative grants 2003-35206-13621 and 2005-35206-15281, from the USDA-Cooperative State Research, Education, and Extension Service, and by National Institutes of Health grant HL 64141. The authors thank David Newman (Department of Animal Sciences, North Dakota State University) for assisting with ultrasound measurements

and employees of the Animal Nutrition and Physiology Center and Ruminant Nutrition, Physiology and Muscle Biology Laboratories (Fargo, ND) for their contributions to this project.

<sup>2</sup>Corresponding author: joel.caton@ndsu.edu

Received August 26, 2009.

Accepted January 19, 2010.

## INTRODUCTION

Gestating ruminants often have inadequate nutrient intake while grazing forages of poor quality or limited availability (Thomas and Kott, 1995; DelCurto et al., 2000). Conversely, some livestock receive excessive nutrients from grazing lush forages or from management associated with high production (Wu et al., 2006; Caldeira et al., 2007). Nutrition during gestation not only affects maternal BW gain, body condition, and reproductive performance (Wettemann et al., 2003; Hess et al., 2005), but also affects prenatal and postnatal offspring growth and development (Godfrey and Barker, 2000; Wu et al., 2006). Additionally, intake of specific nutrients, such as Se, may be suboptimal or excessive because of regional soil and feedstuff variability (Rosenfeld and Beath, 1964). Because Se has many important antioxidant and metabolic roles (Sunde, 1997), supranutritional Se may have positive effects during gestation, particularly in situations in which ewes are metabolically or nutritionally stressed. In addition, greater dietary (supranutritional) Se has increased maternal empty BW, gravid uterine weight, small intestinal weight, and fetal BW in sheep (Reed et al., 2007b).

The early lactation and neonatal periods are critical for dams and their offspring, but it is largely unknown how gestational nutrition affects these subsequent time periods. An experimental model that allows for offspring removal at birth before suckling uncouples gestational and lactational effects on both dam and offspring responses to provide a clearer evaluation of nutritional treatments during gestation. We hypothesized that changes caused by gestational nutrition would persist after parturition when ewes and their lambs were managed independently. Therefore, our objectives were to determine the effects of maternal plane of nutrition and dietary Se supply during gestation on the performance and body composition of ewes and their lambs when placed under similar but independent management systems postpartum.

## MATERIALS AND METHODS

Institutional Animal Care and Use Committees at North Dakota State University (NDSU), Fargo, and the USDA, ARS, US Sheep Experiment Station (USSES; Dubois, ID) approved animal care and use for this study.

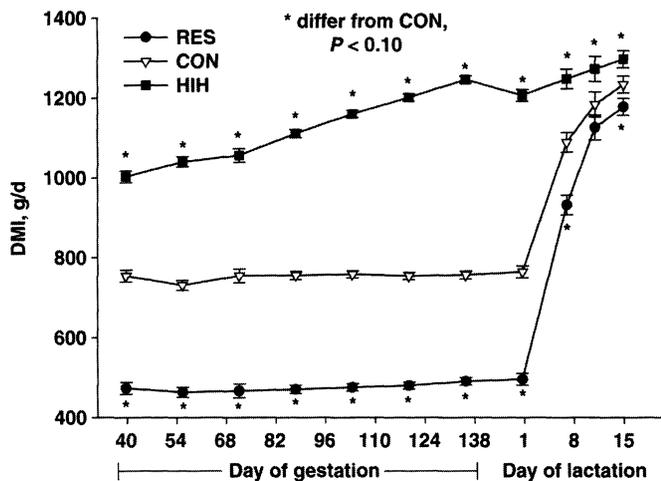
### *Animal Management and Diets*

**Gestation.** At the USSES, 178 Rambouillet ewe lambs (initial age =  $240 \pm 17$  d; initial BW =  $52.1 \pm 6.2$  kg) were synchronized for estrus and divided into 6 groups for breeding ( $n = 29$  or  $30$ /group). Ewe lambs were synchronized using intravaginal sponges (60 mg of medroxyprogesterone acetate, Veramix, Pharmacia and Upjohn, Orangeville, Ontario) and PGF<sub>2 $\alpha$</sub>  (15 mg, Lu-

talyse, Pharmacia and Upjohn, Kalamazoo, MI) over a 10-d period. On d 0, sponges were inserted; on d 7, two injections of PGF<sub>2 $\alpha$</sub>  (7.5 mg/injection) were administered approximately 4 h apart; on d 10, sponges were removed; and on d 11 to 16, ewes were exposed to rams. Marking paint was placed on the brisket of Rambouillet rams to facilitate identification of ewes that rams attempted to breed, and rams ( $n = 12$ , 2/pen) were placed in each pen of ewes for 5 d. Marked ewes were then stratified by BW and assigned randomly to 1 of 2 treatment pens. Each pen was assigned randomly to a Se treatment, either adequate Se (ASe; 3.5  $\mu$ g of Se/kg of BW per day) or high Se (HSe; 65  $\mu$ g of Se/kg of BW per day). Supranutritional amounts of dietary Se similar to those used in the HSe treatment have been shown to elicit maternal (increased empty BW and gravid uterine weight) and fetal (increased BW and visceral organ weight, and increased fetal muscle DNA concentration) responses (Reed et al., 2007b).

Selenium was provided to HSe-fed ewes in the form of Se-enriched wheat mill run, which resulted from on-site processing of wheat grown in a seleniferous region near Pierre, South Dakota, whereas the sole source of Se for ewes on the ASe treatment was the feedstuffs provided. While at USSES, ewes were fed a total mixed ration (ASe: 43% alfalfa hay, 19% dehydrated beet pulp, 18% whole corn, 8% barley straw, 6% soybean meal, and 6% condensed separator by-product; HSe: 43% alfalfa hay, 25% Se-enriched wheat mill run, 17% dehydrated beet pulp, 8% barley straw, and 6% condensed separator by-product; both 2.45 kcal of ME/kg and 10.4% MP, DM basis) during this period to achieve an ADG of 135 g/d (NRC, 1985). Pregnancy was determined 31 d after breeding via transrectal ultrasonography. Eighty-four pregnant ewes (d 36 of gestation,  $n = 42$ /treatment) were then shipped from the USSES to the Animal Nutrition and Physiology Center at NDSU (1,584 km; approximately 14.5-h transit time) for the remainder of the experiment.

At NDSU, ewes were individually housed in  $0.91 \times 1.2$  m pens in a temperature-controlled (12 to 21°C), ventilated facility for the duration of the study. Lighting within the facility was automatically timed to mimic daylight patterns. Ewes remained on their Se treatments (actual intakes: ASe, 11.5  $\mu$ g of Se/kg of BW per day; HSe, 77.0  $\mu$ g of Se/kg of BW per day), and on d 40 of gestation, ewes were assigned randomly to 1 of 3 nutritional treatments supplying 60% (restricted, RES), 100% (control, CON), or 140% (high, HIH) of NRC (1985) requirements. Within each Se  $\times$  nutritional plane treatment, one-half the ewes were assigned to be necropsied at parturition (between 3 and 24 h postpartum) or during lactation (d 20). This resulted in a completely randomized design with a  $2 \times 3 \times 2$  factorial arrangement of Se supply  $\times$  nutritional plane  $\times$  physiological stage at necropsy (ASe-RES, ASe-CON, ASe-HIH, HSe-RES, HSe-CON, HSe-HIH;  $n = 7$  for each treatment within the parturition and lactation groups).



**Figure 1.** Effects of gestational plane of nutrition on ewe DMI during gestation and the first 20 d of lactation. Nutritional planes were 60% (restricted, RES), 100% (control, CON), or 140% (high, HIH) of nutrient requirements. Least squares means  $\pm$  SEM are presented for gestation (RES, n = 26; CON, n = 28; HIH, n = 26) and lactation (RES, n = 14; CON, n = 14; HIH, n = 14).

Nutrient requirements were based on NRC (1985) recommendations for 60-kg pregnant ewe lambs during mid- to late gestation (weighted ADG of 140 g/d) according to the method of Swanson et al. (2008). Like the diets fed at USSES, the diets fed at NDSU were formulated to be similar in ME and MP and to meet or exceed other nutrient requirements (Table 1). A notable exception was the HSe treatment, for which supranutritional amounts of organically bound Se were

provided via a locally processed Se-enriched mill run. Nutritional plane for the RES and HIH treatments was achieved by proportional downward (RES) or upward (HIH) shifts in dietary intake (Figure 1), resulting in global shifts in total nutrients supplied (see below). Individual daily allotments of diets were usually totally consumed, with the appearance oforts being rare. Both Se supply and plane of nutrition treatments were terminated after parturition.

Ewes had free access to water and a trace mineralized salt block containing no additional Se (99% maximum NaCl, 96% minimum NaCl, 2,000 mg/kg of Mn, 1,000 mg/kg of Fe, 1,000 mg/kg of Mg, 500 mg/kg of S, 250 mg/kg of Cu, 100 mg/kg of Co, 80 mg/kg of Zn, and 70 mg/kg of I; Roto Salt Company, Penn Yan, NY). During gestation, diets were fed once daily at 0800 h in a complete pelleted ration (0.48-cm diameter), and 3 pellet formulations (adequate-Se pellet, high-Se pellet, and concentrated-Se pellet; Table 1) were blended to meet ME and Se amounts as dictated by the nutritional plane and Se supply treatments for each ewe. As in diets fed during early gestation, the Se source of the high-Se pellet was the Se-enriched wheat mill run described previously, and the Se source of the adequate Se pellet was feedstuffs used in the diet. Adequate-Se or high-Se pellets were fed to ewes in the ASe and HSe treatments, respectively, to meet the ME content appropriate for their plane of nutrition treatments so that feed was offered to the 60, 100, and 140% nutritional planes. The high-Se pellet was used in combination with the adequate-Se pellet as needed to meet the targeted HSe

**Table 1.** Ingredient and analyzed nutrient composition of diets fed to ewe lambs

Item	Adequate-Se pellet <sup>1</sup>	High-Se pellet <sup>2</sup>	Concentrated-Se pellet <sup>2</sup>
Ingredient, % of dietary DM			
Beet pulp, dehydrated	22.8	30.2	23.1
Alfalfa meal, dehydrated	10.0	9.1	10.0
Ground corn	13.2	—	9.9
Soybean meal	—	5.1	2.0
Limestone	1.0	1.5	1.0
Wheat middlings	53.0	6.9	53.0
Se-enriched wheat mill run	—	47.2	—
Corn starch	—	—	0.9
Selenomethionine	—	—	0.0085
Analyzed dietary composition, % of DM			
OM	92.5	93.5	92.5
CP	15.9	16.6	16.2
NDF	36.8	27.0	37.6
ADF	15.7	12.0	17.6
Starch	20.8	31.9	21.5
Ca	1.02	1.14	1.09
P	0.85	0.60	0.79
Se, mg/kg	0.67	6.13	37.1
Calculated dietary composition			
ME, <sup>3</sup> Mcal/kg	2.83	2.82	3.01

<sup>1</sup>The adequate-Se pellet was fed during gestation and lactation.

<sup>2</sup>The high-Se and concentrated-Se pellets were fed during gestation to meet the high-Se treatment at the different planes of nutrition. Selenium-enriched mill run resulted from on-site processing of wheat grown in a seleniferous region near Pierre, South Dakota. Purified selenomethionine was used in the concentrated-Se pellet.

<sup>3</sup>Estimated using values obtained from the NRC (1985).

and ME content for each ewe. When the high-Se pellet could not meet the HSe content for RES- or CON-fed ewes without exceeding the desired nutritional plane, the concentrated-Se pellet, with purified selenomethionine as its Se source, was used to augment the Se supply. Nutrient requirements were based on NRC (1985) recommendations as described by Swanson et al. (2008), and diets were individually adjusted for BW and BW gain for each 14-d interval of gestation. Feed refusals were collected daily to calculate intake (feed offered – feed refused), but ewes generally ate the feed offered daily and rarely left refusals. On d 109 of gestation, ewes were injected intramuscularly with vitamins A and D (2.0 mL/ewe; 500,000 IU of vitamin A and 75,000 IU of vitamin D<sub>3</sub>/mL; Duravet, Blue Springs, MO).

**Parturition and Lactation.** Ewes were monitored closely during lambing, and lambs were removed immediately after parturition before being allowed to suckle, for artificial rearing. A jugular blood sample was obtained for serum Se analysis from each ewe at 3 h postpartum, before stripping the udder of colostrum. The maternal blood (10 mL) was collected with Corvac serum separator vacuum tubes (Tyco Healthcare, Mansfield, MA) via jugular venipuncture and the serum harvested after centrifugation, as described below. Blood samples were placed on ice, held a minimum of 45 min, and then centrifuged at  $1,500 \times g$  for 30 min at 4°C. Supernatant was pipetted into 2-mL screw-cap vials and stored at –20°C.

Ewes assigned to necropsy on d 20 of lactation were transitioned to a diet providing 100% of NRC (1985) requirements and adequate Se for early lactation based on lambing BW, delivered by a combination of the adequate-Se pellet fed during gestation and a lactation protein pellet (50.2% CP and 2.6 Mcal of ME/kg; 70% soybean meal, 15% wheat middlings, and 15% supplement that contained 9% mineral mix, 4.5% urea, and 1.5% glycerin). A 5-d transition period was used to increase intake from the gestation to the lactation amount, and feed was delivered in 2 portions, 1 after each milking. Ewes were mechanically milked twice daily at 0500 and 1700 h until necropsy after the morning milking on d 20.

**Ewe Performance Measures and Dietary Analysis.** Consecutive 2-d BW were taken before nutritional treatment allocation (d 38 and 39 of gestation) and 1 wk before the projected lambing date (d 137 and 138 of gestation). Additional BW were taken at 14-d intervals for diet adjustment, within 24 h postpartum, and at d 20 of lactation. Ewe body condition was scored (1 to 5 scale, with 1 = emaciated, 5 = obese) by 2 trained technicians on d 45, 67, 95, 123, and 137 of gestation and by 1 technician within 24 h of parturition and on d 20 of lactation. Ultrasound measurements were taken for backfat (BF) thickness and LM area at the 12th rib, using an Aloka 500-SSV ultrasound machine (Aloka Co. Ltd., Tokyo, Japan) on d 38, 96, and 135

of gestation and at  $18.0 \pm 0.2$  d of lactation. Backfat thickness was measured at a point three-quarters the length of the LM from the backbone end, and the LM cross-section was traced to determine the LM area.

Diet samples were analyzed for DM, ash, N (methods 930.15, 942.05, and 990.02, respectively; AOAC, 1990), ADF (Ankom Technology, Fairport, NY), and NDF (Ankom Technology). Hydride-generation atomic absorption spectroscopy (5100 AAS, Perkin-Elmer Inc., Boston, MA) was used for Se analysis, as reported previously (Finley et al., 1996).

**Lamb Management.** Lambs were removed from their dams before suckling and were then towel dried and processed. Immediately after birth, lamb birth weight, curved crown rump length (CCR; the length from the crown of the head to the end of the rump, measured along the backbone), and heart girth (the distance around the rib cage directly behind the forelegs) were measured, and an initial jugular blood sample was taken for serum Se analysis. The lamb blood (10 mL) was collected with Corvac serum separator vacuum tubes via jugular venipuncture and the serum harvested after centrifugation, as described above. Lambs were then subcutaneously administered a vaccination against *Clostridium perfringens* types C and D and tetanus (Ultrabac CD, Pfizer Animal Health, New York, NY), injected intramuscularly with vitamins A and D (0.5 mL/lamb; 500,000 IU of vitamin A and 75,000 IU of vitamin D<sub>3</sub>/mL; Duravet), and had their navels clipped and dipped in a 7% iodine tincture.

Lambs were fed artificial colostrum (45% CP, 15% crude fat, 0.15% crude fiber, 10% ash, 0.40% minimum Ca, 0.90% maximum Ca, 0.30% minimum NaCl, 0.50% maximum NaCl, 1.0% minimum Na, 1.5% maximum Na, 0.40% P, 0.75 mg of Se/kg, 110,000 IU/kg of vitamin A, 22,000 IU/kg of vitamin D, 440 IU/kg of vitamin E; Acquire Colostrum Replacement, APC Inc., Ankeny, IA) within 30 min of birth and at 6 additional times by 20 h postpartum to achieve 10.64 g of IgG/kg of BW (19.1 mL of colostrum/kg of BW for the first 2 feedings and 25.5 mL of colostrum/kg of BW in subsequent feedings). This dosage of IgG was calculated to provide 50 g of IgG/4.7 kg of lamb based on previous reports using a similar product (Quigley et al., 2002).

At 24 h, lambs were transitioned to milk replacer (24% CP, 30% crude fat, 0.10% crude fiber, 6.5% ash, 25% lactose, 0.50% minimum Ca, 1.0% maximum Ca, 0.65% P, 2 mg/kg minimum Cu, 6 mg/kg maximum Cu, 0.3 mg/kg of Se, 66,000 IU/kg of vitamin A, 22,000 IU/kg of vitamin D<sub>3</sub>, 330 IU/kg of vitamin E; Super Lamb Instant Milk Replacer, Merrick's Inc., Middleton, WI) fed from a bottle until a strong suckling response was observed. Once this occurred, lambs were moved to a pen with free access to water and creep feed and were adapted to a teat bucket system for ad libitum access to milk replacer. Tails were not docked, and male lambs were left intact (not castrated) to prevent any decrease in performance caused by these procedures.

On d 19, final BW and jugular blood samples (10 mL, Corvac serum separator vacuum tubes, and processed as previously described) were obtained from all lambs before necropsy.

**Slaughter Procedures.** Ewes assigned to necropsy at parturition and lactation were slaughtered either between 3 and 24 h postpartum or after the morning milking and feeding on d 20 of lactation, respectively. Lambs were assigned randomly by treatment to necropsy between 19 and 22 d of age (average  $20.6 \pm 0.9$  d of age). Immediately before slaughter, ewes and lambs were weighed. Animals were stunned by captive bolt (Supercash Mark 2, Accles and Shelvoke Ltd., Sutton Coldfield, UK) and exsanguinated, and detailed necropsies were performed. Perirenal fat was removed from the kidneys and body wall and weighed; omental and mesenteric fat was stripped from the gastrointestinal tract, and fat from these locations was weighed together. Digesta weight was calculated by difference (total full viscera weight – visceral tissues after stripping of digesta contents). Empty BW was considered to be digesta weight subtracted from the final BW before slaughter. Ewe carcass weight was considered to be the weight of the remaining carcass with head and pelt, but without all thoracic and abdominal internal organs. In this study, carcass weight is being used as an additional measure of body composition to assess BW changes not associated with changes in thoracic and abdominal organ mass.

### Statistical Analysis

Twins ( $n = 6$ ) and their dams ( $n = 3$ ) were removed from the data set. One ewe was found to be open and was removed from the study, and another ewe was not necropsied because of dystocia-related problems. This resulted in the following ewe numbers for each treatment at each physiological stage: ASe-RES [parturition: 6 (5 at necropsy); lactation: 7], ASe-CON [parturition: 7; lactation: 7], ASe-HIH [parturition: 6; lactation: 7], HSe-RES [parturition: 6; lactation: 7], HSe-CON [parturition: 7; lactation: 7], HSe-HIH [parturition: 6; lactation: 7]. Five lambs died between birth and necropsy, although birth weight, CCR, and heart girth were included in the data set for these animals. Lamb numbers for each treatment were as follows: ASe-RES (13), ASe-CON (14), ASe-HIH [13 (12 at necropsy)], HSe-RES [13 (10 at necropsy)], HSe-CON [14 (13 at necropsy)], and HSe-HIH (13).

Data were analyzed as either a  $2 \times 3$  (ewe DMI, BW, BCS, ultrasound body composition, and all lamb variables) or  $2 \times 3 \times 2$  (ewe variables at necropsy) factorial arrangement of treatments using the GLM procedure (SAS Inst. Inc., Cary, NC). Ewe gestational Se supply (ASe vs. HSe), nutritional plane (RES vs. CON vs. HIH), and their interactions were used as fixed effects in the model for all ewe performance, ultrasound, and offspring measures. The effect of physiological stage at necropsy (parturition vs. lactation) and its interactions

with Se supply and nutritional plane were also included as fixed effects in the model for ewe necropsy variables. Lamb sex was included in the model for offspring measures where significant ( $P \leq 0.10$ ). Means were separated using LSD and were considered significant when  $P \leq 0.10$  or were considered tendencies when  $P < 0.15$ . In the absence of interactions ( $P > 0.10$ ), main effects are reported; otherwise, interactive means are discussed.

## RESULTS AND DISCUSSION

### Maternal Effects

**Ewe Feed Intake and BW.** Selenium  $\times$  nutritional plane interactions were not present ( $P > 0.10$ ) in ewe intake and BW data. According to the experimental design, DMI (Figure 1) was least ( $P < 0.001$ ) for ewes fed the RES diet, intermediate ( $P < 0.001$ ) for those fed the CON diet, and greatest ( $P < 0.001$ ) for those fed the HIH diet throughout gestation. While acclimating to their diet at NDSU from d 40 to 53 of gestation, ewes fed ASe had greater ( $P = 0.002$ ) DMI than those fed HSe (data not shown). After this, there was no effect of Se treatment or its interaction on DMI. Dry matter intake remained separated ( $P < 0.07$ ) by gestational plane of nutrition on d 1 and 15 of lactation, with DMI of ewes fed the HIH diet during gestation also being greater ( $P \leq 0.05$ ) than DMI of ewes fed the CON and RES diets on d 8 of lactation. Because ewes were fed lactation diets based on BW, continued stratification of DMI during lactation was expected.

Ewe BW (Figure 2) differed ( $P = 0.001$ ) because of nutritional plane by d 81 of gestation, when ewes fed the RES diet weighed 5.9% less ( $P = 0.04$ ;  $50.8$  vs.  $54.0 \pm 1.1$  kg) than those fed the CON diet, and those fed the HIH diet had 5.4% greater ( $P = 0.06$ ;  $56.9$  vs.  $54.0 \pm 1.1$  kg) BW than those fed the CON diet. Relative differences between nutritional treatments widened by d 137 of gestation, when RES-fed ewes had 14.4% less ( $P < 0.001$ ;  $51.6$  vs.  $60.3 \pm 1.1$  kg) BW than CON-fed ewes, and HIH-fed ewes weighed 15.8% more ( $P < 0.001$ ;  $69.8$  vs.  $60.3 \pm 1.1$  kg) than CON-fed ewes. Average daily gain and G:F (Table 2) were least ( $P < 0.001$ ) for ewes fed RES, intermediate ( $P < 0.001$ ) for those fed CON, and greatest ( $P < 0.001$ ) for those fed HIH during both mid- and late gestation (d 38 to 95 and d 96 to 137, respectively). All treatments had greater ADG and G:F during late gestation compared with midgestation, which probably resulted from the rapid fetal growth occurring during this period (Rat-tray et al., 1974; NRC, 2007).

Restricted primiparous ewes maintained BW during gestation because the increase in fetal BW offset the loss in maternal BW as pregnancy progressed. The BW gain observed in CON-fed ewes during gestation was due to fetal growth, whereas overnourished ewes gained not only fetal BW but also maternal tissue. This is illustrated by a comparison of BW of ewes immediately after parturition (d 0 of lactation; Figure 2). At parturi-

**Table 2.** Effects of gestational Se supply and plane of nutrition on ewe ADG, feed efficiency, and BCS change

Item	Se supply <sup>1</sup>			Plane of nutrition <sup>3</sup>				P-value <sup>5</sup>		
	ASe	HSe	SEM <sup>2</sup>	RES	CON	HIH	SEM <sup>4</sup>	Se	Nut	Se × Nut
ADG, g/d										
d 39 to 95 of gestation	53.7	87.0	4.1	-31.5 <sup>c</sup>	82.4 <sup>b</sup>	160.1 <sup>a</sup>	5.1	<0.001	<0.001	0.88
d 96 to 137 of gestation	115.8	128.4	5.6	16.6 <sup>c</sup>	115.4 <sup>b</sup>	234.3 <sup>a</sup>	7.0	0.12	<0.001	0.64
d 0 to 20 of lactation	148.6	111.3	28.8	187.3	121.6	81.1	35.2	0.37	0.11	0.21
G:F										
d 39 to 95 of gestation	0.04	0.09	0.01	-0.07 <sup>c</sup>	0.11 <sup>b</sup>	0.15 <sup>a</sup>	0.01	<0.001	<0.001	0.12
d 96 to 137 of gestation	0.12	0.14	0.01	0.04 <sup>c</sup>	0.15 <sup>b</sup>	0.20 <sup>a</sup>	0.01	0.19	<0.001	0.59
d 0 to 20 of lactation	0.13	0.10	0.02	0.17 <sup>a</sup>	0.10 <sup>b</sup>	0.06 <sup>b</sup>	0.03	0.34	0.03	0.23
BCS change <sup>6</sup>										
d 39 to 95 of gestation	0.13	0.26	0.04	-0.13 <sup>c</sup>	0.26 <sup>b</sup>	0.44 <sup>a</sup>	0.05	0.02	<0.001	0.73
d 95 to 137 of gestation	-0.11	-0.01	0.03	-0.42 <sup>c</sup>	-0.01 <sup>b</sup>	0.26 <sup>a</sup>	0.04	0.04	<0.001	0.84
d 0 to 20 of lactation	0.26	0.11	0.06	0.20 <sup>ab</sup>	0.05 <sup>b</sup>	0.30 <sup>a</sup>	0.07	0.07	0.06	0.73

<sup>a-c</sup>Within a row, nutritional plane means differ ( $P \leq 0.10$ ).

<sup>1</sup>Ewes fed 11.5 µg of Se/kg of BW (adequate Se, ASe) or 77.0 µg of Se/kg of BW (high Se, HSe) during gestation.

<sup>2</sup>SEM for gestation (ASe, n = 40; HSe, n = 40) and lactation (ASe, n = 21; HSe, n = 21).

<sup>3</sup>Ewes fed 60% (restricted, RES), 100% (control, CON), or 140% (high, HIH) of nutrient requirements during gestation.

<sup>4</sup>SEM for gestation (RES, n = 26; CON, n = 28; HIH, n = 26) and lactation (RES, n = 14; CON, n = 14; HIH, n = 14).

<sup>5</sup>Probabilities of difference for Se supply (Se), nutritional plane (Nut), and their interaction.

<sup>6</sup>BCS determined on a 1 to 5 scale, where 1 = emaciated and 5 = obese.

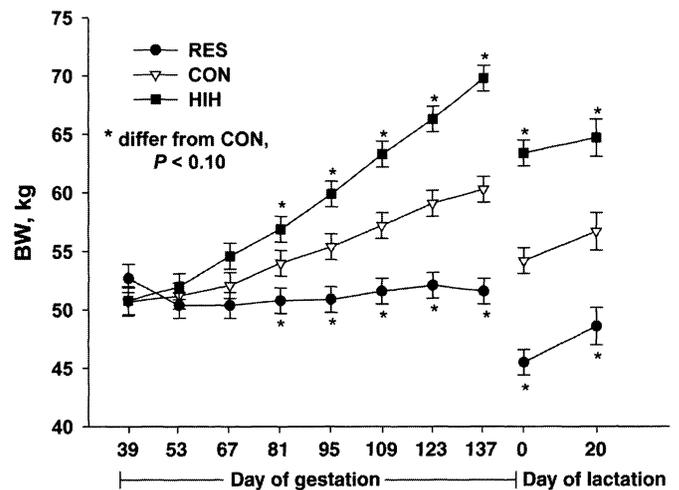
tion, CON-fed ewes had BW (54.2 kg) similar to their BW in early gestation, RES-fed ewes weighed less ( $P < 0.001$ ; 45.4 kg) than they did in early gestation, and HIH-fed ewes had greater ( $P < 0.001$ ; 63.4 kg) BW at parturition than they did in early gestation.

Although Se supply had no effect on ewe BW, Se affected ewe ADG during gestation. Ewes fed HSe had greater ( $P < 0.001$ ; Table 2) ADG than those fed ASe in midgestation and tended to have greater ( $P = 0.12$ ) ADG in late gestation. Additionally, G:F was improved ( $P < 0.001$ ) for HSe-fed ewes compared with ASe-fed ewes during midgestation. In similar studies, supranutritional Se has generally not affected ewe BW, ADG, or G:F during gestation (Caton et al., 2007b; Reed et al., 2007b; Neville et al., 2008), but similar amounts have increased empty BW (Reed et al., 2007b). Selenium supply and nutritional plane have also been shown to interact in their effects on ADG and G:F, with ewes fed high Se having greater ADG at a control plane of nutrition but poorer ADG and G:F when nutrients were restricted (Carlson et al., 2009).

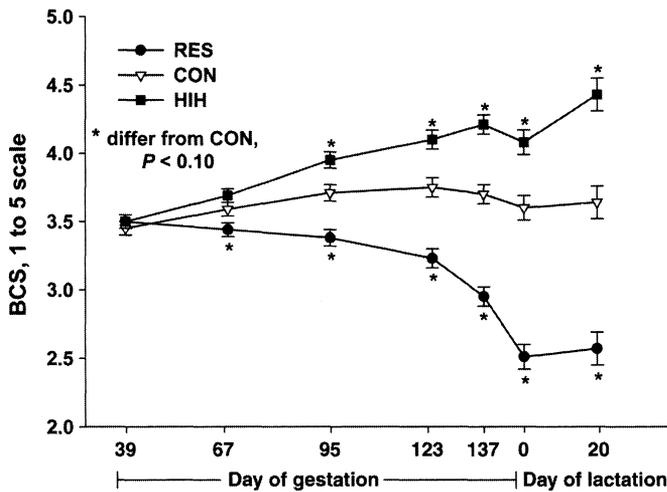
When the primiparous ewes were transitioned to a common diet providing 100% of nutrient requirements for lactation, gestational Se supply had no effect ( $P < 0.27$ ) on BW (data not shown), ADG (Table 2), or G:F (Table 2) during the first 20 d of lactation. Ewe BW remained least for the RES treatment, intermediate for the CON treatment, and greatest for the HIH treatment ( $P < 0.002$ ; 48.1, 56.7, and 64.7 ± 1.6 kg for the RES, CON, and HIH treatments, respectively) on d 20 of lactation despite previously restricted ewes tending to have greater ( $P = 0.11$ ) ADG during lactation than previously overnourished ewes. Additionally, previously restricted ewes had greater ( $P \leq 0.09$ ) G:F than ewes fed the CON or HIH diets during gestation. This increased BW gain and improved efficiency of RES-

fed ewes likely resulted from both compensatory BW gain on realimentation and decreased milk production. In this study, RES-fed ewes during gestation had decreased milk production (yield and total nutrients, data not shown) during the first 20 d of lactation (Garbel et al., 2009). A reduction in nutrients being partitioned to milk production probably allowed for increased nutrient utilization for maternal BW gain in the previously restricted ewes.

**Ewe BCS and Body Composition.** Selenium × nutritional plane interactions were not present ( $P > 0.10$ ) in ewe BCS data. On d 67 of gestation, ewes fed the RES diet had smaller ( $P < 0.05$ ) BCS than those fed the CON and HIH diets (3.44 vs. 3.59 and 3.69 ±



**Figure 2.** Effects of gestational plane of nutrition on ewe BW during gestation and the first 20 d of lactation. Nutritional planes were 60% (restricted, RES), 100% (control, CON), or 140% (high, HIH) of nutrient requirements. Least squares means ± SEM are presented for gestation (RES, n = 26; CON, n = 28; HIH, n = 26) and lactation (RES, n = 14; CON, n = 14; HIH, n = 14).



**Figure 3.** Effects of gestational plane of nutrition on ewe BCS during gestation and the first 20 d of lactation. Nutritional planes were 60% (restricted, RES), 100% (control, CON), or 140% (high, HIH) of nutrient requirements. Least squares means  $\pm$  SEM are presented for gestation (RES,  $n = 26$ ; CON,  $n = 28$ ; HIH,  $n = 26$ ) and lactation (RES,  $n = 14$ ; CON,  $n = 14$ ; HIH,  $n = 14$ ).

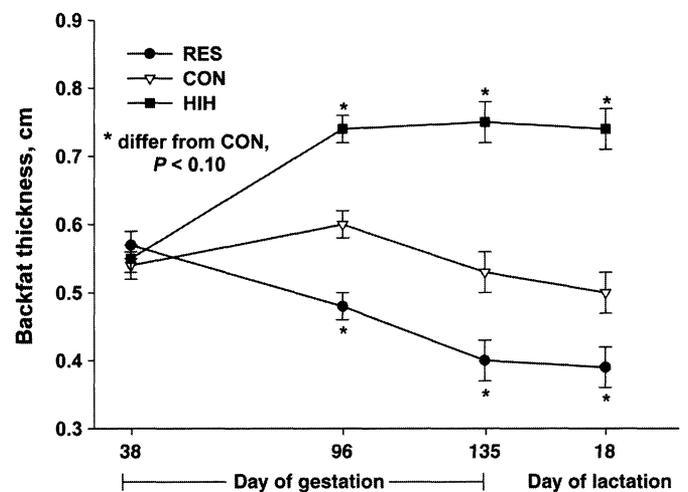
0.05; Figure 3). Ewe BCS and ultrasonic BF (Figure 4) differed because of nutritional plane by d 95 and 96, respectively, with the greatest ( $P < 0.01$ ) BCS and BF in HIH-fed ewes, intermediate ( $P < 0.01$ ) BCS and BF in CON-fed ewes, and least ( $P < 0.001$ ) BCS and BF in RES-fed ewes ( $3.38, 3.71, \text{ and } 3.95 \pm 0.06$  BCS, and  $0.48, 0.60, \text{ and } 0.74 \pm 0.02$  cm of ultrasonic BF for the RES, CON, and HIH treatments, respectively). Both BCS and BF remained stratified ( $P < 0.001$ ) by nutritional plane throughout gestation. On d 135 of gestation, RES-fed ewes had 24.5% less ( $P < 0.001$ ;  $0.40$  vs.  $0.53 \pm 0.03$  cm) BF than CON-fed ewes, and HIH-fed ewes had 41.5% greater ( $P < 0.001$ ;  $0.75$  vs.  $0.43 \pm 0.03$  cm) BF than CON-fed ewes. At parturition, RES-fed ewes had smaller ( $P < 0.001$ ;  $2.51$  vs.  $3.60 \pm 0.09$ ) BCS than CON-fed ewes, whereas HIH-fed ewes had greater BCS ( $P < 0.001$ ;  $4.08$  vs.  $3.60 \pm 0.09$ ) than CON-fed ewes. Similar to BW, CON-fed ewes at parturition maintained initial BCS and BF, compared with an increase ( $P < 0.001$ ) in BCS and BF of overnourished ewes and a decrease ( $P < 0.001$ ) in BCS and BF of RES-fed ewes. During late gestation, BCS loss (Table 2) was more dramatic for RES-fed ewes and BCS and BF gain appeared less for overnourished ewes than during midgestation. Additionally, CON-fed ewes had a slight loss of BCS and BF in late gestation compared with a gain during midgestation. This may be explained by rapid fetal growth during late gestation (Rattray et al., 1974; NRC, 2007) and the hypothesis that gestating animals have an anabolic phase of growth in early gestation followed by a catabolic phase in late gestation (Naismith and Morgan, 1976; Robinson, 1986).

When ewes were fed to meet nutritional requirements of lactation, BCS remained stratified ( $P < 0.001$ ) by nutritional plane (Figure 3) on d 20 of lactation ( $2.57, 3.64, \text{ and } 4.43 \pm 0.12$  for the RES, CON, and HIH treatments, respectively), although previously over-

nourished ewes had a greater ( $P = 0.02$ ) BCS increase than CON-fed ewes. Backfat thickness (Figure 4) also remained separated ( $P < 0.001$ ) because of the gestational plane of nutrition ( $0.39, 0.50, \text{ and } 0.74 \pm 0.03$  for the RES, CON, and HIH treatments, respectively), with no effect of previous nutritional treatments on BF change. Differences in BCS change during lactation may have been an artifact of the subjective nature of BCS because no such differences were observed in the more objective measure of ultrasonic BF thickness. Although ewe ADG during lactation did tend to be greater for previously restricted ewes, ewe gastrointestinal mass and digesta weight also increased ( $P < 0.10$ ; data not shown) in these ewes because of their increased DMI during lactation. Thus maternal BW gain of previously restricted ewes during lactation may have been due to increased visceral organ mass and digesta fill, rather than increased adiposity.

In addition to effects of nutritional plane, Se supply affected ( $P < 0.08$ ) the BCS change (Table 2) during gestation and lactation. Ewes fed the HSe diet had greater ( $P = 0.01$ ) BCS gain during midgestation, less BCS loss during late gestation, and then less ( $P = 0.07$ ) BCS gain during lactation than ASe-fed ewes. Additionally, BF thickness was greater ( $P < 0.006$ ) for ewes fed the HSe diet than for those fed the ASe diet at d 96 of gestation ( $0.65$  vs.  $0.57 \pm 0.02$  cm). The interaction of Se supply  $\times$  nutritional plane was significant ( $P < 0.05$ ) for BF thickness at d 135, when ewes fed the HSe-HIH diet had greater ( $P = 0.003$ ) BF than those fed the ASe-HIH diet ( $0.83$  vs.  $0.67 \pm 0.04$  cm), but nutritional planes were different ( $P < 0.04$ ) within each Se treatment.

There were no effects of physiological stage at necropsy or any of its interactions on ewe internal fat masses; however, there were Se  $\times$  nutritional plane interactions ( $P = 0.04$ ) for omental and mesenteric fat measure-



**Figure 4.** Effects of gestational plane of nutrition on ewe backfat thickness during gestation and the first 20 d of lactation. Nutritional planes were 60% (restricted, RES), 100% (control, CON), or 140% (high, HIH) of nutrient requirements. Least squares means  $\pm$  SEM are presented for gestation (RES,  $n = 26$ ; CON,  $n = 28$ ; HIH,  $n = 26$ ) and lactation (RES,  $n = 14$ ; CON,  $n = 14$ ; HIH,  $n = 14$ ).

ments (Table 3). Perirenal fat mass was greatest ( $P < 0.001$ ) for HIH-fed ewes, intermediate ( $P < 0.07$ ) for CON-fed ewes, and least ( $P < 0.07$ ) for RES-fed ewes. When expressed per unit of empty BW, ewes fed the HIH nutritional plane had greater ( $P \leq 0.07$ ) perirenal fat than those fed the RES and CON nutritional planes. The interaction of Se supply  $\times$  nutritional plane affected ( $P = 0.04$ ) ewe omental and mesenteric fat mass (kg and g/kg of empty BW). Regarding omental and mesenteric fat, ewes fed the RES and CON diets had less ( $P < 0.001$ ) compared with ewes fed the HIH diet within each Se treatment, but those fed the HSe-HIH diet had greater ( $P = 0.05$ ) omental and mesenteric fat than those fed the ASe-HIH diet. Per unit of empty BW, there was no effect of nutritional plane within the ASe treatment, but HIH-fed ewes had a greater ( $P < 0.004$ ) omental and mesenteric fat mass than RES- and CON-fed ewes within the HSe treatment. Additionally, ewes in the ASe-CON treatment had a greater ( $P = 0.04$ ) omental and mesenteric fat mass (g/kg of empty BW) than those in the HSe-CON treatment, whereas those in the HSe-HIH treatment had a greater ( $P = 0.06$ ) omental and mesenteric fat mass than those in the ASe-HIH treatment.

Restricted ewes likely mobilized body fat to provide energy for maintenance and fetal growth, whereas overnourished ewes increased body stores once maintenance, fetal, and maternal growth requirements were met; thus, the effects of nutritional plane were as expected. Effects of Se on BCS, BF thickness, and internal fat masses are not well understood, however. In similar studies, feeding supranutritional amounts of Se during gestation had no effect on ewe BCS (Caton et al., 2007b), omental fat (Reed et al., 2007a,b; Neville et al., 2008; Carlson et al., 2009), or perirenal fat (Reed et al., 2007a,b; Neville et al., 2008). Conversely, Carlson et al. (2009) observed ewes fed increased Se to have greater perirenal fat (g and g/kg of maternal BW). Although supranutritional Se may have increased BW gain, improved efficiency, and promoted increased adiposity in the current study, the reasons for this are unclear and merit further investigation. Additionally, it is difficult to separate the effects of Se supply and potential confounding influences of Se-enriched wheat mill run. Although the ASe and HSe diets were formulated to have similar ME concentrations, differences in fiber and starch were present (Table 1), which may have slightly altered ruminal fermentation and energy supply.

Ultrasonic LM area was not affected by Se supply, and Se  $\times$  nutritional plane interactions were not present ( $P > 0.10$ ). Longissimus muscle area (Figure 5) was less ( $P < 0.005$ ) in ewes fed the RES diet compared with those fed the CON and HIH diets by d 96 of gestation (10.8 vs. 12.2 and 12.8  $\pm$  0.3 cm<sup>2</sup>). By d 135 of gestation, ewes fed the RES diet had 21.8% less ( $P < 0.001$ ; 9.09 vs. 11.62  $\pm$  0.34 cm<sup>2</sup>) LM area than those fed the CON diet, and those fed the HIH diet had 19.8% greater ( $P < 0.001$ ; 13.92 vs. 11.62  $\pm$  0.34 cm<sup>2</sup>)

LM area than those fed the CON diet. When fed on a similar plane of nutritional during lactation, previously overnourished ewes lost LM area ( $P < 0.08$ ) compared with maintenance by CON-fed ewes and BW gain by RES-fed ewes; however, ewe LM area at d 20 of lactation remained different ( $P < 0.001$ ) because of the plane of nutrition during gestation (9.60, 11.30, and 12.93 cm<sup>2</sup> for the RES, CON, and HIH treatments, respectively).

Differences in Se supply, physiological stage at necropsy, and their interactions were not present ( $P \geq 0.15$ ) for ewe final BW, empty BW, or carcass weight at slaughter (Table 3). Ewe final BW, empty BW, and carcass weight were greatest ( $P < 0.001$ ) for HIH-fed ewes, intermediate ( $P < 0.001$ ) for CON-fed ewes, and least ( $P < 0.001$ ) for RES-fed ewes. Because empty BW and carcass weight follow the same pattern as final total BW, differences in ewe BW gain resulted from maternal tissue gain or loss in addition to digesta and internal organ weight differences. This supports the observed differences in LM area from plane of nutrition during gestation, suggesting that maternal muscle mass decreased because of feed restriction and increased because of overnourishment. Ewes in this study were primiparous yearlings, and thus were still growing during gestation and lactation (NRC, 2007). Estimated nutrient requirements provided to CON-fed ewes may not have provided an adequate nutrient supply for full expression of growth potential during late gestation and early lactation, whereas overnourished ewes appeared to have more fully expressed their growth potential, and consequently had more extensive muscle growth and increase adipose deposition. Muscle protein synthesis (protein accretion – protein degradation) must have been affected by nutrient restriction because ewes appeared to utilize skeletal muscle as a source of protein and energy for maintenance and fetal growth, resulting in a loss of muscle mass.

### Offspring Effects

**Offspring at Birth.** Gestational length (Table 4) was affected by maternal plane of nutrition ( $P = 0.002$ ), and Se supply  $\times$  nutritional plane interactions were present ( $P = 0.01$ ). Among lambs born to ASe-fed ewes, no differences in gestation length were attributable to maternal plane of nutrition. Within lambs born to ewes fed the HSe diet, RES-fed ewes had the longest gestation length ( $P < 0.06$ ), CON-fed ewes were intermediate ( $P < 0.06$ ), and HIH-fed ewes had the shortest ( $P < 0.007$ ). Additionally, lambs born to ewes in the HSe-RES treatment had a greater gestation length than those born to ewes in the ASe-RES treatment ( $P = 0.05$ ), whereas those born to ewes in the ASe-HIH treatment had a greater gestation length than those born to ewes in the HSe-HIH treatment. Overnutrition has decreased gestation length in ewes (Wallace et al., 2005; Swanson et al., 2008), but supranutritional Se did not interact with nutritional plane in previous work

**Table 3.** Effects of gestational Se supply and plane of nutrition on ewe final BW, carcass weight, and internal fat masses when necropsied after parturition or at d 20 of lactation

Item	Se supply <sup>1</sup>			Plane of nutrition <sup>3</sup>				Stage <sup>5</sup>			P-value <sup>7</sup>			
	ASe	HSe	SEM <sup>2</sup>	RES	CON	HIH	SEM <sup>4</sup>	Parturition	Lactation	SEM <sup>6</sup>	Se	Nut	Se × Nut	Stage
Final BW, kg	55.2	56.1	0.9	47.4 <sup>c</sup>	55.3 <sup>b</sup>	64.2 <sup>a</sup>	1.2	54.7	56.6	1.0	0.52	<0.001	0.74	0.15
Empty BW, <sup>8</sup> kg	46.8	47.9	0.9	39.6 <sup>c</sup>	47.1 <sup>b</sup>	55.3 <sup>a</sup>	1.1	47.9	46.8	0.9	0.44	<0.001	0.60	0.41
Carcass wt, <sup>9</sup> kg	36.4	37.5	0.7	30.6 <sup>c</sup>	36.8 <sup>b</sup>	43.5 <sup>a</sup>	0.8	37.3	36.6	0.7	0.22	<0.001	0.77	0.50
Perirenal fat, kg	0.87	0.82	0.06	0.60 <sup>c</sup>	0.78 <sup>b</sup>	1.16 <sup>a</sup>	0.07	0.90	0.79	0.06	0.57	<0.001	0.45	0.17
Perirenal fat, g/kg of empty BW <sup>8</sup>	17.6	16.1	1.0	14.7 <sup>b</sup>	16.3 <sup>b</sup>	19.5 <sup>a</sup>	1.3	17.8	15.9	1.0	0.31	0.03	0.69	0.19
Omental and mesenteric fat, kg	2.06	2.02	0.10	1.63	1.84	2.65	0.12	2.08	2.00	0.10	0.79	<0.001	0.04	0.57
ASe	—	—	—	1.74 <sup>fg</sup>	2.01 <sup>f</sup>	2.42 <sup>e</sup>	0.17	—	—	—	—	—	—	—
HSe	—	—	—	1.52 <sup>g</sup>	1.66 <sup>fg</sup>	2.88 <sup>d</sup>	0.17	—	—	—	—	—	—	—
Omental and mesenteric fat, g/kg of empty BW <sup>8</sup>	42.8	40.5	1.4	40.6	38.5	45.9	1.8	41.7	41.6	1.5	0.25	0.01	0.04	0.94
ASe	—	—	—	43.2 <sup>e</sup>	42.0 <sup>e</sup>	43.2 <sup>e</sup>	2.6	—	—	—	—	—	—	—
HSe	—	—	—	37.9 <sup>ef</sup>	35.0 <sup>f</sup>	48.5 <sup>d</sup>	2.5	—	—	—	—	—	—	—

<sup>a-c</sup>Within a row, nutritional plane means differ ( $P \leq 0.10$ ).

<sup>d-g</sup>Within a variable, interactive means differ ( $P \leq 0.10$ ).

<sup>1</sup>Ewes fed 11.5 µg of Se/kg of BW (adequate Se, ASe) or 77.0 µg of Se/kg of BW (high Se, HSe) during gestation.

<sup>2</sup>SEM for ASe (n = 39) and HSe (n = 40).

<sup>3</sup>Ewes fed 60% (restricted, RES), 100% (control, CON), or 140% (high, HIH) of nutrient requirements during gestation.

<sup>4</sup>SEM for RES (n = 25), CON (n = 28), and HIH (n = 26).

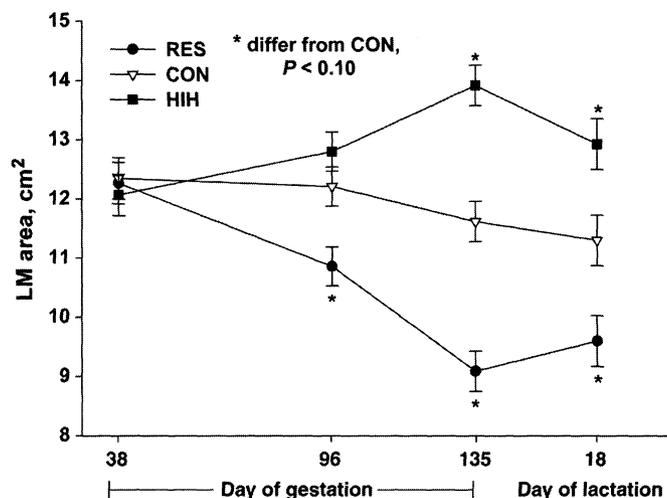
<sup>5</sup>Ewes necropsied within 24 h of parturition or on d 20 of lactation.

<sup>6</sup>SEM for the parturition group (n = 37) and the lactation group (n = 42).

<sup>7</sup>Probabilities of difference for Se supply (Se), nutritional plane (Nut), physiological stage at necropsy (Stage), and the interaction of Se and Nut; interactions with Stage were also included in the model but were not significant ( $P > 0.44$ ).

<sup>8</sup>Empty BW = final BW – digesta weight.

<sup>9</sup>Carcass wt = head, hide, and carcass weight – total internal organs.



**Figure 5.** Effects of gestational plane of nutrition on ewe LM area during gestation and the first 20 d of lactation. Nutritional planes were 60% (restricted, RES), 100% (control, CON), or 140% (high, HIH) of nutrient requirements. Least squares means  $\pm$  SEM are presented for gestation (RES, n = 26; CON, n = 28; HIH, n = 26) and lactation (RES, n = 14; CON, n = 14; HIH, n = 14).

using a similar experimental design (Swanson et al., 2008). Effects of Se in the current study may be attributable to the increased BW gain observed in ewes fed the HSe diet.

There were effects of maternal plane of nutrition ( $P = 0.08$ ) and an interaction between nutritional plane and Se supply ( $P = 0.08$ ) on lamb birth weight (Table 4). Lambs born to ewes on the ASe-RES treatment weighed less than those born to ewes on the ASe-CON ( $P = 0.06$ ), ASe-HIH ( $P = 0.009$ ), HSe-RES ( $P = 0.08$ ), and HSe-CON treatments ( $P = 0.004$ ). Overall, lambs born to ewes fed the RES diet weighed 8.1% less ( $P \leq 0.10$ ) at birth than lambs born to ewes fed the CON and HIH diets. Curved crown rump length was also reduced ( $P < 0.06$ ) in lambs born to RES-fed ewes compared with those born to CON- and HIH-fed ewes, but CCR was not affected ( $P = 0.71$ ) by maternal Se supply. Selenium  $\times$  nutritional plane interactions ( $P = 0.02$ ) for lamb heart girth measurements were present. Within lambs from ASe-fed ewes, heart girth was greater ( $P < 0.02$ ) for lambs born to HIH-fed ewes than for those born to RES-fed ewes, whereas heart girth for those born to CON-fed ewes was greater ( $P < 0.08$ ) than that for lambs born to HIH-fed dams within the HSe treatment. Additionally, of lambs born to RES-fed ewes, those born to ewes on the HSe diet had greater ( $P < 0.03$ ) heart girth than those born to ewes on the ASe diet.

In agreement with the current study, nutrient restriction of ewes during mid- and late gestation has reduced

**Table 4.** Effects of maternal Se supply and plane of nutrition during gestation on lamb gestation length, BW, growth, and internal fat mass<sup>1</sup>

Item	Se supply <sup>2</sup>			Plane of nutritional <sup>4</sup>				P-value <sup>6</sup>		
	ASe	HSe	SEM <sup>3</sup>	RES	CON	HIH	SEM <sup>5</sup>	Se	Nut	Se $\times$ Nut
Gestation length, d	148.1	148.4	0.3	149.2	148.1	147.5	0.3	0.39	0.002	0.01
ASe	—	—	—	148.5 <sup>e</sup>	147.6 <sup>ef</sup>	148.2 <sup>e</sup>	0.5			
HSe	—	—	—	149.9 <sup>d</sup>	148.6 <sup>e</sup>	146.8 <sup>f</sup>	0.5			
BW, kg										
Birth	4.5	4.6	0.1	4.3	4.7	4.6	0.1	0.36	0.08	0.08
ASe	—	—	—	4.0 <sup>e</sup>	4.6 <sup>d</sup>	4.8 <sup>d</sup>	0.2			
HSe	—	—	—	4.5 <sup>d</sup>	4.9 <sup>d</sup>	4.4 <sup>de</sup>	0.2			
d 19	9.9	10.4	0.3	9.2 <sup>b</sup>	10.6 <sup>a</sup>	10.6 <sup>a</sup>	0.4	0.31	0.03	0.59
ADG, <sup>7</sup> g/d	287	302	15	261 <sup>b</sup>	307 <sup>a</sup>	316 <sup>a</sup>	18	0.43	0.06	0.21
CCR, <sup>8</sup> cm	50.9	51.1	0.5	49.9 <sup>b</sup>	51.4 <sup>a</sup>	51.7 <sup>a</sup>	0.6	0.71	0.07	0.48
Girth, <sup>9</sup> cm	38.8	39.3	0.4	38.6	39.4	39.1	0.4	0.31	0.44	0.02
ASe	—	—	—	37.7 <sup>f</sup>	38.9 <sup>def</sup>	39.8 <sup>de</sup>	0.6			
HSe	—	—	—	39.6 <sup>de</sup>	39.9 <sup>d</sup>	38.4 <sup>ef</sup>	0.6			
Perirenal fat, <sup>10</sup> g	125	131	9	104 <sup>b</sup>	131 <sup>a</sup>	149 <sup>a</sup>	11	0.62	0.02	0.23
Perirenal fat, g/kg of empty BW <sup>11</sup>	12.4	12.6	0.7	11.5	12.1	14.0	0.9	0.81	0.11	0.11
Omental and mesenteric fat, <sup>10</sup> g	140	146	9	123 <sup>b</sup>	142 <sup>ab</sup>	163 <sup>a</sup>	12	0.61	0.05	0.55
Omental and mesenteric fat, g/kg of empty BW <sup>11</sup>	13.9	14.5	0.6	13.3	14.0	15.3	0.8	0.46	0.18	0.30

<sup>a,b</sup>Within a row, nutritional plane means differ ( $P \leq 0.10$ ).

<sup>d,f</sup>Within a variable, interactive means differ ( $P \leq 0.10$ ).

<sup>1</sup>Portions of these data previously published in Meyer et al. (2009).

<sup>2</sup>Lambs born to ewes fed 11.5  $\mu$ g of Se/kg of BW (adequate Se, ASe) or 77.0  $\mu$ g of Se/kg of BW (high Se, HSe) during gestation.

<sup>3</sup>SEM for birth (ASe, n = 40; HSe, n = 40) and d 19 (ASe, n = 40; HSe, n = 36).

<sup>4</sup>Lambs born to ewes fed 60% (restricted, RES), 100% (control, CON), or 140% (high, HIH) of nutrient requirements during gestation.

<sup>5</sup>SEM for birth (RES, n = 26; CON, n = 28; HIH, n = 26) and d 19 (RES, n = 23; CON, n = 27; HIH, n = 26).

<sup>6</sup>Probabilities of difference for Se supply (Se), nutritional plane (Nut), and their interaction.

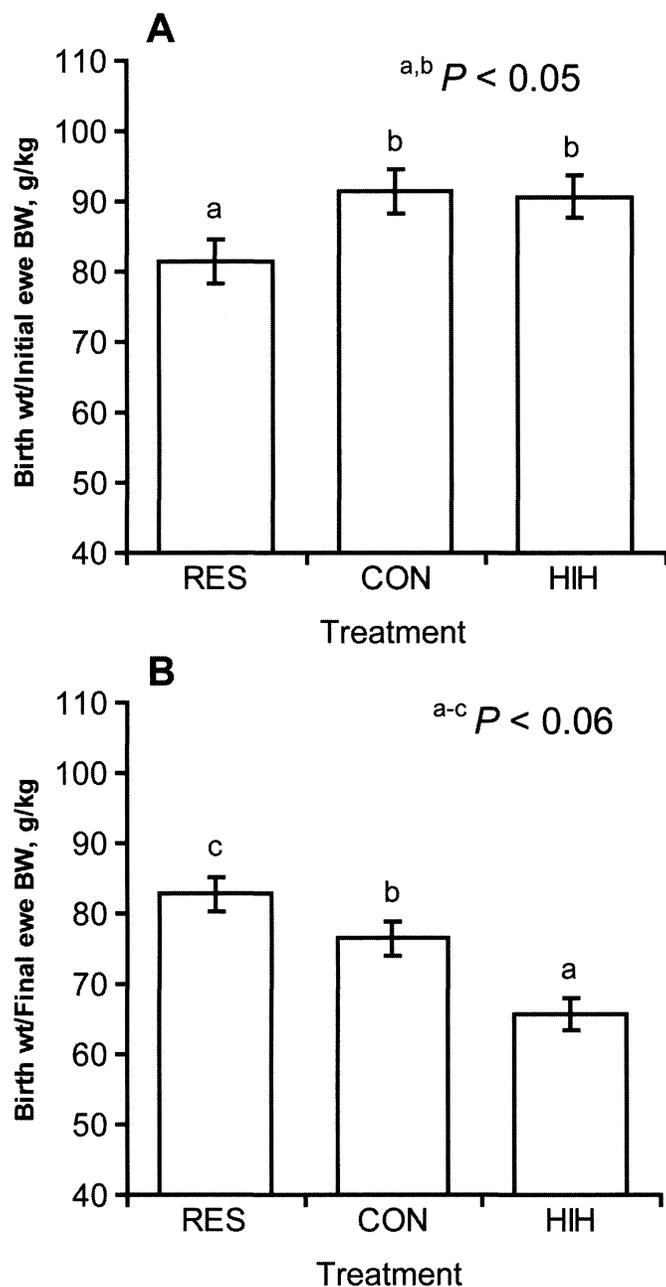
<sup>7</sup>ADG from birth to d 19 of age.

<sup>8</sup>Curved crown rump length (CCR) measured immediately after birth.

<sup>9</sup>Heart girth measured immediately after birth.

<sup>10</sup>Internal fat masses weighed after necropsy on 20.6  $\pm$  0.9 d of age.

<sup>11</sup>Empty BW = final BW - digesta weight.



**Figure 6.** Effects of maternal plane of nutrition during gestation on lamb birth weight (wt) per unit of initial (A: d 38 of gestation) and final (B: d 137 of gestation) ewe BW. Nutritional planes were 60% (restricted, RES), 100% (control, CON), or 140% (high, HIH) of nutrient requirements. Least squares means  $\pm$  SEM are presented (RES,  $n = 26$ ; CON,  $n = 28$ ; HIH,  $n = 26$ ).

fetal growth, resulting in decreased BW, CCR, and heart girth (Caton et al., 2007b; Reed et al., 2007b; Carlson et al., 2009). Greatly overnourishing ewes beyond the nutrient requirements for maintenance, growth, and pregnancy has generally also negatively affected fetal lamb growth. Wallace et al. (1999, 2000, 2001, 2004) have developed an overnourished (approximately twice maintenance) adolescent ewe research model in which fetal BW near term or offspring birth weight is reduced compared with that of lambs from control-fed ewes. Additionally, in an experimental model similar to the

current study, lambs born to overnourished primiparous ewes (140% of NRC requirements) had decreased birth weight (Swanson et al., 2008), CCR, and heart girth (Caton et al., 2007b). Although it is unclear why fetal growth was not retarded in lambs born to overnourished ewes in the current study, ADG was less for these ewes on the HIH plane of nutrition when compared with overnourished ewes (J. S. Caton, unpublished data), whose offspring were negatively affected (Caton et al., 2007b; Swanson et al., 2008). Thus, it is possible that ewes in the current study were not at a nutritional plane great enough to reduce fetal growth. Additionally, overnourished ewes that gave birth to lighter BW lambs in the previous similar study also had an approximately 3 d shorter gestation length (Swanson et al., 2008), whereas only overnourished ewes fed supranutritional Se had shorter gestation lengths in the current study.

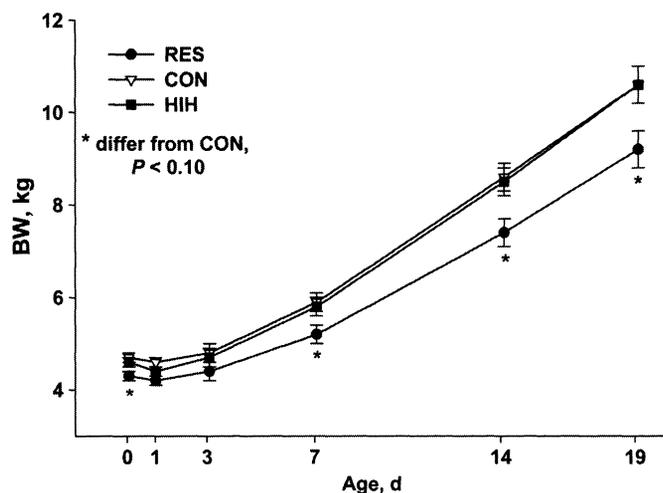
When expressed per unit of initial ewe BW (Figure 6A; d 38, initial 2-d BW before nutritional plane treatments were begun), birth weights of lambs born to ewes in the RES treatment were less ( $P < 0.05$ ) than those of lambs born to ewes in the CON and HIH treatments. This supports the concept that offspring of RES-fed ewes were less able to express their genetic potential for fetal growth when compared with CON-fed or overnourished ewes. Birth weight per unit of ewe BW near parturition (Figure 6B; d 137, final 2-d BW) was greatest ( $P < 0.06$ ) for lambs born to ewes in the RES treatment, intermediate ( $P < 0.06$ ) for those born to ewes in the CON treatment, and least ( $P < 0.002$ ) for those born to ewes in the HIH treatment. These differences suggest that RES-fed ewes conserved fetal BW gain in comparison with their decrease in maternal BW, resulting in proportionally greater fetal growth. Conversely, overnourished ewes did not have accelerated fetal growth associated with their increased maternal BW gain and actually had less proportional fetal growth.

High Se during gestation increased offspring BW and heart girth in RES-fed ewes, suggesting that Se may be able to spare offspring of some of the negative effects of intrauterine growth restriction caused by maternal undernutrition. Interestingly, supranutritional Se increased gestation length for lambs born to RES-fed ewes, which may account for observed differences because it allowed for the rapid growth in late gestation to be extended. In previous studies, lamb birth weight, CCR, and heart girth have been variably responsive to supranutritional Se. Although fetal BW and heart girth near term were increased by maternal high Se in one study (Reed et al., 2007b), supranutritional Se during gestation had no effect on offspring fetal BW or birth weight, CCR, and girth in other studies (Caton et al., 2007b; Neville et al., 2008; Carlson et al., 2009). To summarize our findings, Se fed at amounts in the current study has not reduced offspring BW or skeletal size, and, in some cases, has increased fetal growth, altered gestation length, or both.

**Offspring Growth.** Selenium  $\times$  nutritional plane interactions were not present ( $P > 0.10$ ) in lamb growth data. When lambs were separated from their dams and raised on an identical management system regardless of maternal treatment, maternal plane of nutrition during gestation continued to affect ( $P \leq 0.06$ ) lamb growth (Figure 7) through d 19 of age. Lambs born to ewes in the RES treatment tended to weigh less than those born to ewes in the CON treatment at 24 h ( $P = 0.13$ ) and those born to ewes in the CON and HIH treatments at 3 d of age ( $P = 0.14$ ). On d 7 and 14 of age, lambs from dams in the RES treatment weighed less ( $P < 0.04$ ) than those from dams in the CON and HIH treatments ( $5.2, 5.9,$  and  $5.8 \pm 0.2$  kg on d 7 of age;  $7.4, 8.6,$  and  $8.5 \pm 0.3$  kg on d 14 of age for the RES, CON, and HIH treatments, respectively). Lamb ADG (Table 4) was decreased ( $P < 0.07$ ) in lambs from dams in the RES treatment compared with those from dams in the CON and HIH treatments from birth to d 19, resulting in lambs from ewes in the RES treatment weighing 13.0% less ( $P < 0.02$ ) on d 19 of age than those from ewes in the CON and HIH treatments. In agreement with the current study, Caton et al. (2007b) recently reported that lambs born to nutrient-restricted ewes weighed less at weaning than lambs born to control-fed or overnourished dams. Although others have reported effects of maternal nutrition during gestation on postnatal growth of cattle (Stalker et al., 2006; Martin et al., 2007; Larson et al., 2009), offspring were raised by their dams in these studies, confounding effects of maternal nutrition on lactation with effects of developmental programming in utero. Because ram lambs were not castrated in the current study, growth rates may have been enhanced in intact males (Seideman et al., 1982). These results should be generally applicable to

castrated males, however, because of the early period of growth being described.

**Offspring Body Composition.** Lamb internal fat masses at slaughter on  $20.6 \pm 0.9$  d of age were affected ( $P \leq 0.05$ ) by maternal plane of nutrition during gestation, but not by Se treatment, and Se  $\times$  nutritional plane interactions ( $P \geq 0.11$ ) were not present (Table 4). Perirenal fat (g) was decreased ( $P \leq 0.08$ ) in lambs born to RES-fed ewes compared with CON- and HIH-fed ewes. When expressed per unit of empty BW, lambs born to overnourished dams tended ( $P = 0.11$ ) to have greater perirenal fat than those born to RES- and CON-fed ewes. Additionally, lambs born to ewes on a HIH nutritional plane had greater ( $P = 0.01$ ) omental and mesenteric fat (g) than lambs born to ewes on a RES nutritional plane, although there were no differences when expressed per unit of empty BW. Previous research has demonstrated that maternal nutritional plane can affect offspring adiposity and body composition. Fetal lambs near term from dams fed to gestational requirements had greater perirenal fat (g and proportionally) than those born to nutrient-restricted ewes in previous studies (Luther et al., 2007; Reed et al., 2007b). Conversely, when lambs from ewes in a similar experimental model were slaughtered at approximately 180 d of age, lambs from ewes fed high Se during gestation had increased visceral adiposity, although maternal nutritional plane had no effect (Caton et al., 2007a). Additionally, Ford et al. (2007) observed that lambs born to ewes restricted from d 28 to 78 of gestation had greater internal fat when slaughtered at 280 d of age. Results of the current study suggest that differences previously noted in fetal offspring internal fat mass caused by maternal nutritional plane persist into the neonatal stage, although previous work indicates that these differences may shift because of changes in offspring metabolism later in life.



**Figure 7.** Effects of maternal plane of nutrition during gestation on lamb BW during the first 19 d of life. Maternal nutritional planes were 60% (restricted, RES), 100% (control, CON), or 140% (high, HIH) of nutrient requirements. Least squares means  $\pm$  SEM are presented (d 0 and 1: RES,  $n = 26$ ; CON,  $n = 28$ ; HIH,  $n = 26$ ; d 3: RES,  $n = 25$ ; CON,  $n = 28$ ; HIH,  $n = 26$ ; d 7: RES,  $n = 24$ ; CON,  $n = 27$ ; HIH,  $n = 26$ ; d 14 and 19: RES,  $n = 23$ ; CON,  $n = 27$ ; HIH,  $n = 26$ ).

### Se Intake and Serum Se Concentration

**Maternal Effects.** There were Se supply  $\times$  nutritional plane interactions ( $P < 0.001$ ) for ewe Se intake during gestation and postpartum ewe serum Se concentration (Table 5). These interactions were driven primarily by magnitude differences, and not by changes in treatment ranking. Actual Se intakes were  $7.8, 11.3, 15.4, 76.5, 77.4,$  and  $77.2 \pm 1.4$   $\mu\text{g}$  of Se/kg of BW per day for ewes in the ASe-RES, ASe-CON, ASe-HIH, HSe-RES, HSe-CON, and HSe-HIH treatments, respectively. Among nutritional planes within the HSe treatment, Se intake did not differ. Within the ASe diet, HIH-fed ewes had the greatest ( $P < 0.04$ ) Se intake, CON-fed ewes were intermediate ( $P < 0.07$ ), and RES-fed ewes had the least ( $P < 0.07$ ). This discrepancy in Se intake among ASe-fed ewes resulted from 1 type of pellet being fed to all ASe-fed ewes at different intakes. Thus, ewes consuming more of the diet also consumed more Se. Intakes of Se for ASe-fed ewes were still one-fifth or less of the Se intake of HSe-fed ewes.

**Table 5.** Effects of maternal Se supply and plane of nutrition during gestation on ewe and lamb serum Se

Item	Se supply <sup>1</sup>			Plane of nutrition <sup>3</sup>				<i>P</i> -value <sup>5</sup>		
	ASe	HSe	SEM <sup>2</sup>	RES	CON	HIH	SEM <sup>4</sup>	Se	Nut	Se × Nut
Ewe serum Se, <sup>6</sup> µg/mL	0.175	0.436	0.007	0.318	0.313	0.286	0.008	<0.001	0.02	<0.001
ASe	—	—	—	0.169 <sup>c</sup>	0.173 <sup>c</sup>	0.183 <sup>c</sup>	0.012			
HSe	—	—	—	0.467 <sup>a</sup>	0.452 <sup>a</sup>	0.389 <sup>b</sup>	0.012			
Lamb serum Se, µg/mL										
Birth	0.109	0.334	0.005	0.229	0.232	0.204	0.006	<0.001	0.005	<0.001
ASe	—	—	—	0.106 <sup>c</sup>	0.107 <sup>c</sup>	0.114 <sup>c</sup>	0.009			
HSe	—	—	—	0.351 <sup>a</sup>	0.356 <sup>a</sup>	0.294 <sup>b</sup>	0.009			
d 19	0.119	0.165	0.007	0.139	0.148	0.139	0.008	<0.001	0.64	0.23

<sup>a-c</sup>Within a variable, interactive means differ ( $P \leq 0.10$ ).

<sup>1</sup>Ewes fed 11.5 µg of Se/kg of BW (adequate Se, ASe) or 77.0 µg of Se/kg of BW (high Se, HSe) during gestation.

<sup>2</sup>SEM for ewes (ASe,  $n = 39$ ; HSe,  $n = 40$ ), lambs at birth (ASe,  $n = 40$ ; HSe,  $n = 40$ ), and lambs at d 19 (ASe,  $n = 40$ ; HSe,  $n = 36$ ).

<sup>3</sup>Ewes fed 60% (restricted, RES), 100% (control, CON), or 140% (high, HIH) of nutrient requirements during gestation.

<sup>4</sup>SEM for ewes (RES,  $n = 25$ ; CON,  $n = 28$ ; HIH,  $n = 26$ ), lambs at birth (RES,  $n = 26$ ; CON,  $n = 28$ ; HIH,  $n = 26$ ), and lambs at d 19 (RES,  $n = 23$ ; CON,  $n = 27$ ; HIH,  $n = 26$ ).

<sup>5</sup>Probabilities of difference for Se supply (Se), nutritional plane (Nut), and their interaction.

<sup>6</sup>Ewe serum Se at 3 h postpartum.

Ewes fed the HSe diet at all planes of nutrition had greater ( $P < 0.001$ ) serum Se than ewes fed the ASe diet (Table 5). Within HSe, ewes fed the RES or CON diet had greater ( $P < 0.001$ ) serum Se than those fed the HIH diet. This may have resulted from a dilution effect of the plane of nutrition because ewes fed on the HIH plane of nutrition also had the greatest ( $P < 0.05$ ) blood volume at slaughter (data not shown). Thus, although Se intakes were similar for nutritional planes within the HSe treatment, the increased blood volume of overnourished ewes may have diluted serum Se. Additionally, from d 110 of gestation until parturition, the supranutritional Se supply of the HSe treatment was met for RES- and CON-fed ewes by feeding the concentrated-Se pellet containing purified selenomethionine in addition to the high-Se pellet containing Se-enriched wheat mill run. Conversely, overnourished ewes were able to meet the target supranutritional amount of Se with the Se-enriched wheat mill run pellet throughout gestation because of their elevated intake. Although most Se in grains is found as selenomethionine (Djujić et al., 2000), purified selenomethionine may be more bioavailable or more readily absorbed than Se in the enriched wheat mill run, allowing ewes fed diets containing the purified form to have greater serum Se.

**Offspring Effects.** Serum Se concentration of lambs immediately after birth (Table 5) mirrored ewe serum Se postpartum and was affected by an interaction of maternal Se supply × nutritional plane ( $P < 0.001$ ). Again, this interaction was being driven by a change in numerical magnitude, and not by differences in treatment ranking. Lambs born to ewes fed the HSe diet had more than 2 times greater ( $P < 0.001$ ) serum Se concentrations at birth than lambs born to ewes fed the ASe diet. Within the ASe treatment, maternal nutritional plane had no effect on lamb serum Se at birth, but lambs born to RES- or CON-fed ewes had greater ( $P < 0.001$ ) serum Se than HIH-fed ewes in the HSe

treatment. By d 19 of age, maternal nutritional plane or its interaction with Se supply no longer had an effect ( $P < 0.22$ ) on lamb serum Se. However, lambs born to HSe-fed ewes still had 38% greater ( $P < 0.001$ ) serum Se compared with lambs from ASe-fed dams. Because lambs in this study were fed artificial colostrum and milk replacer, differences in Se status of lambs caused by maternal nutrition were due to placental transfer, tissue accumulation, and subsequent protein turnover. Recent data from our laboratory demonstrates that supranutritional Se fed during gestation increases the caruncular and cotyledonary Se concentrations (K. A. Vonnahme, unpublished data) and that serum Se concentration can remain increased in offspring from ewes fed high Se through d 56 of life (J. S. Caton, unpublished data). Additionally, it has been hypothesized that the placenta is particularly efficient at transporting selenomethionine because the selenomethionine is treated as methionine, allowing offspring serum Se to correspond to maternal Se status (Hawkes et al., 1994; Taylor et al., 2009).

## Conclusions

In summary, ewe BW and body composition were sensitive to the plane of nutrition during gestation, and previous nutritional effects were still observed when ewes were fed to requirements during the first 20 d of lactation. Gestational Se supply also affected ewe ADG, BCS change, and adiposity, although its effects receded during lactation. Nutrient restriction during gestation reduced fetal and postnatal growth of offspring, but supranutritional Se reversed some of these changes prenatally. Results indicate that maternal nutrient restriction during gestation not only negatively affects the dam, but also has harmful consequences on offspring that occur even with the proper postnatal nutrition and

that may become more evident with advancing neonatal age.

## LITERATURE CITED

- AOAC. 1990. Official Methods of Analysis. 15th ed. Assoc. Offic. Anal. Chem., Arlington, VA.
- Caldeira, R. M., A. T. Belo, C. C. Santos, M. I. Vazques, and A. V. Portugal. 2007. The effect of long-term feed restriction and over-nutrition on body condition score, blood metabolites and hormonal profiles in ewes. *Small Rumin. Res.* 68:242-255.
- Carlson, D. B., J. J. Reed, P. P. Borowicz, J. B. Taylor, L. P. Reynolds, T. L. Neville, D. A. Redmer, K. A. Vonnahme, and J. S. Caton. 2009. Effects of dietary selenium supply and timing of nutrient restriction during gestation on maternal growth and body composition of pregnant adolescent ewes. *J. Anim. Sci.* 87:669-680.
- Caton, J. S., J. J. Reed, T. L. Neville, K. A. Vonnahme, P. P. Borowicz, J. B. Taylor, D. A. Redmer, J. S. Luther, C. J. Hammer, K. R. Carlin, and L. P. Reynolds. 2007a. Effects of maternal nutrition and selenium supply on postnatal organ mass: Evidence for developmental programming in lambs. *J. Anim. Sci.* 85(Suppl. 1):614. (Abstr.)
- Caton, J. S., K. A. Vonnahme, J. J. Reed, T. L. Neville, C. M. Efertz, C. J. Hammer, J. S. Luther, J. B. Taylor, D. A. Redmer, and L. P. Reynolds. 2007b. Effects of maternal nutrition on birth weight and postnatal nutrient metabolism in sheep. Pages 101-102 in Proc. Int. Symp. Energy Protein Metab., Vichy, France. EAAP Publ. No. 124. Wageningen Academic Publ., Wageningen, the Netherlands.
- DelCurto, T., B. W. Hess, J. E. Huston, and K. C. Olson. 2000. Optimum supplementation strategies for beef cattle consuming low-quality roughages in the western United States. *J. Anim. Sci.* 77(Suppl.):1-16.
- Djujić, I. S., O. N. Jonzanov-Stankov, M. Milovac, V. Jankovic, and V. Djermanovic. 2000. Bioavailability and possible benefits of wheat intake naturally enriched with selenium and its products. *Biol. Trace Elem. Res.* 77:273-285.
- Finley, J., L. Matthys, T. Shuler, and E. Korynta. 1996. Selenium content of foods purchased in North Dakota. *Nutr. Res.* 16:723-728.
- Ford, S. P., B. W. Hess, M. M. Schwope, M. J. Nijland, J. S. Gilbert, K. A. Vonnahme, W. J. Means, H. Han, and P. W. Nathanielsz. 2007. Maternal undernutrition during early to mid-gestation in the ewe results in altered growth, adiposity, and glucose tolerance in male offspring. *J. Anim. Sci.* 85:1285-1294.
- Garbel, L. J., A. M. Meyer, J. J. Reed, T. L. Neville, J. D. Kirsch, W. L. Keller, R. M. Weigl, J. B. Taylor, L. P. Reynolds, J. S. Luther, D. A. Redmer, J. S. Caton, and K. A. Vonnahme. 2009. Effects of nutritional plane and selenium supply during gestation on milk yield and composition in ewes. *J. Anim. Sci.* 87. (Suppl. 3):133. (Abstr.)
- Godfrey, K. M., and D. J. Barker. 2000. Fetal nutrition and adult disease. *Am. J. Clin. Nutr.* 71(Suppl.):1344S-1352S.
- Goering, H. K., and P. J. Van Soest. 1970. Forage Fiber Analysis. Apparatus, Reagents, Procedures, and Some Applications. Agric. Handbook No. 379. ARS, USDA, Washington, DC.
- Hawkes, W. C., C. C. Willhite, S. T. Omaye, D. N. Cox, and W. N. Choy. 1994. Selenium kinetics, placental transfer, and neonatal exposure in cynomolgus macaques (*Macaca fascicularis*). *Teratology* 50:148-159.
- Hess, B. W., S. L. Lake, E. J. Scholljegerdes, T. R. Weston, V. Nayigihugu, J. D. C. Molle, and G. E. Moss. 2005. Nutritional controls of beef cow reproduction. *J. Anim. Sci.* 83(E-Suppl.):E90-E106.
- Larson, D. M., J. L. Martin, D. C. Adams, and R. N. Funston. 2009. Winter grazing system and supplementation during late gestation influence performance of beef cows and steer progeny. *J. Anim. Sci.* 87:1147-1155.
- Luther, J., R. Aitken, J. Milne, M. Matsuzaki, L. Reynolds, D. Redmer, and J. Wallace. 2007. Maternal and fetal growth, body composition, endocrinology, and metabolic status in undernourished adolescent sheep. *Biol. Reprod.* 77:343-350.
- Martin, J. L., K. A. Vonnahme, D. C. Adams, G. P. Lardy, and R. N. Funston. 2007. Effects of dam nutrition on growth and reproductive performance of heifer calves. *J. Anim. Sci.* 85:841-847.
- Meyer, A. M., J. J. Reed, T. L. Neville, J. B. Taylor, D. A. Redmer, L. P. Reynolds, K. A. Vonnahme, and J. S. Caton. 2009. Effects of maternal nutritional plane and selenium supply during gestation on neonatal offspring growth and visceral organ mass. Pages 604-605 in Proc. XIth Int. Symp. Rumin. Physiol. Clermont-Ferrand, France. Wageningen Academic Publ., Wageningen, the Netherlands.
- Naismith, D. J., and B. L. G. Morgan. 1976. The biphasic nature of protein metabolism during pregnancy in the rat. *Br. J. Nutr.* 36:563-566.
- Neville, T. L., M. A. Ward, J. J. Reed, S. A. Soto-Navarro, S. L. Julius, P. P. Borowicz, J. B. Taylor, D. A. Redmer, L. P. Reynolds, and J. S. Caton. 2008. Effects of level and source of dietary selenium on maternal and fetal body weight, visceral organ mass, cellularity estimates, and jejunal vascularity in pregnant ewe lambs. *J. Anim. Sci.* 86:890-901.
- NRC. 1985. Nutrient Requirements of Sheep. 6th ed. Natl. Acad. Press, Washington, DC.
- NRC. 2007. Nutrient Requirements of Small Ruminants. Natl. Acad. Press, Washington, DC.
- Quigley, J. D., A. F. Carson, and J. Polo. 2002. Immunoglobulin derived from bovine plasma as a replacement for colostrum in newborn lambs. *Vet. Ther.* 3:262-269.
- Ratray, P. V., W. N. Garrett, N. E. East, and N. Hinman. 1974. Growth, development and composition of the ovine conceptus and mammary gland during pregnancy. *J. Anim. Sci.* 38:613-626.
- Reed, J. J., T. L. Neville, K. A. Vonnahme, P. P. Borowicz, J. B. Taylor, D. A. Redmer, J. S. Luther, C. J. Hammer, L. P. Reynolds, and J. S. Caton. 2007a. Effects of maternal nutrition and selenium supply on visceral organ mass of pregnant ewe lambs. *J. Anim. Sci.* 85(Suppl. 1):361. (Abstr.)
- Reed, J. J., M. A. Ward, K. A. Vonnahme, T. L. Neville, S. L. Julius, P. P. Borowicz, J. B. Taylor, D. A. Redmer, A. T. Grazul-Bilska, L. P. Reynolds, and J. S. Caton. 2007b. Effects of selenium supply and dietary restriction on maternal and fetal body weight, visceral organ mass, cellularity estimates, and jejunal vascularity in pregnant ewe lambs. *J. Anim. Sci.* 85:2721-2733.
- Robinson, J. J. 1986. Changes in body composition during pregnancy and lactation. *Proc. Nutr. Soc.* 45:71-80.
- Rosenfeld, M. F., and O. A. Beath. 1964. Selenium Geobotany, Biochemistry, Toxicity and Nutrition. Academic Press, New York, NY.
- Seideman, S. C., H. R. Cross, R. R. Oltjen, and B. D. Schanbacher. 1982. Utilization of the intact male for red meat production: A review. *J. Anim. Sci.* 55:826-840.
- Stalker, L. A., D. C. Adams, T. J. Klopfenstein, D. M. Feuz, and R. N. Funston. 2006. Effects of pre- and postpartum nutrition on reproduction in spring calving cows and calf feedlot performance. *J. Anim. Sci.* 84:2582-2589.
- Sunde, R. A. 1997. Selenium. Pages 493-556 in Handbook of Nutritionally Essential Mineral Elements. B. L. O'Dell and R. A. Sunde, ed. Marcel Dekker Inc., New York, NY.
- Swanson, T. J., C. J. Hammer, J. S. Luther, D. B. Carlson, J. B. Taylor, D. A. Redmer, T. L. Neville, L. P. Reynolds, J. S. Caton, and K. A. Vonnahme. 2008. Effects of gestational plane of nutrition and selenium supplementation on mammary development and colostrum quality in pregnant ewe lambs. *J. Anim. Sci.* 86:2415-2423.

- Taylor, J. B., L. P. Reynolds, D. A. Redmer, and J. S. Caton. 2009. Maternal and fetal tissue selenium loads in nulliparous ewes fed supranutritional and excessive selenium during mid- to late pregnancy. *J. Anim. Sci.* 87:1828–1834.
- Thomas, V. M., and R. W. Kott. 1995. A review of Montana winter range ewe nutrition research. *Sheep Goat Res. J.* 11:17–24.
- Wallace, J. M., R. P. Aitken, J. S. Milne, and W. W. Hay Jr. 2004. Nutritionally mediated placental growth restriction in the growing adolescent: Consequences for the fetus. *Biol. Reprod.* 71:1055–1062.
- Wallace, J. M., D. A. Bourke, and R. P. Aitken. 1999. Nutrition and fetal growth: Paradoxical effects in the overnourished adolescent sheep. *J. Reprod. Fertil.* 54(Suppl. 1):385–399.
- Wallace, J. M., D. A. Bourke, R. P. Aitken, R. M. Palmer, P. Da Silva, and M. A. Cruickshank. 2000. Relationship between nutritionally-mediated placental growth restriction and fetal growth, body composition and endocrine status during late gestation in adolescent sheep. *Placenta* 21:100–108.
- Wallace, J. M., D. A. Bourke, P. Da Silva, and R. P. Aitken. 2001. Nutrient partitioning during adolescent pregnancy. *Reproduction* 122:347–357.
- Wallace, J. M., J. S. Milne, and R. P. Aitken. 2005. The effect of overnourishing singleton-bearing adult ewes on nutrient partitioning to the gravid uterus. *Br. J. Nutr.* 94:533–539.
- Wettemann, R. P., C. A. Lents, N. H. Ciccio, F. J. White, and I. Rubio. 2003. Nutritional- and suckling-mediated anovulation in beef cows. *J. Anim. Sci.* 81(E-Suppl. 2):E48–E59.
- Wu, G., F. W. Bazer, J. M. Wallace, and T. E. Spencer. 2006. Intrauterine growth retardation: Implications for the animal sciences. *J. Anim. Sci.* 84:2316–2337.