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Nutritional plane and selenium supply during gestation affect yield and nutrient composition of colostrum and milk in primiparous ewes¹

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ABSTRACT: The objectives were to investigate effects of nutritional plane and Se supply during gestation on yield and nutrient composition of colostrum and milk in first parity ewes. Rambouillet ewe lambs ($n = 84$, age = 240 ± 17 d, BW = 52.1 ± 6.2 kg) were allocated to 6 treatments in a 2×3 factorial array. Factors included Se [adequate Se (ASe, 11.5 $\mu\text{g}/\text{kg}$ of BW) or high Se (HSe, 77.0 $\mu\text{g}/\text{kg}$ of BW)] initiated at breeding, and nutritional plane [60 (RES), 100 (CON), or 140% (HIH) of requirements] initiated at d 40 of gestation. Ewes were fed individually from d 40, and lambs were removed at parturition. Colostrum was milked from all ewes at 3 h postpartum, and one-half of the ewes ($n = 42$) were transitioned to a common diet meeting lactation requirements and mechanically milked for 20 d. Colostrum yield was greater ($P = 0.02$) for HSe ewes than ASe, whereas CON had greater ($P < 0.05$) colostrum yield than RES and HIH. Colostrum Se (%) was greater ($P < 0.01$) for HSe than ASe. Colostrum from ewes fed HSe had less ($P = 0.03$) butterfat (%), but greater ($P \leq 0.05$) total butterfat, solids-not-fat, lactose, protein, milk urea N, and Se than ASe. Colostrum from HIH ewes had greater ($P \leq 0.02$) solids-not-fat (%) than RES, whereas RES had greater ($P \leq 0.04$) butterfat (%) than CON and HIH. Colostrum

from ewes fed the CON diet had greater ($P = 0.01$) total butterfat than HIH. Total solids-not-fat, lactose, and protein were greater ($P < 0.05$) in colostrum from CON than RES and HIH. Ewes fed HSe had greater ($P < 0.01$) milk yield (g/d and mL/d) than ASe, and CON and HIH had greater ($P < 0.01$) yield than RES. Milk protein (%) was greater ($P \leq 0.01$) in RES compared with CON or HIH. Ewes fed HSe had greater ($P < 0.01$) milk Se ($\mu\text{g}/\text{g}$ and mg/d) than ASe on each sampling day. Milk from CON and HIH ewes had greater ($P < 0.01$) total solids-not-fat, lactose, protein, and milk urea N than RES. Total Se was greater ($P = 0.02$) in milk from ewes fed the CON diet compared with RES. Somatic cell count and total somatic cells were greater ($P \leq 0.05$) in milk from CON than RES. A cubic effect of day ($P \geq 0.01$) was observed for milk yield (g and mL). Butterfat, solids-not-fat, lactose, milk urea N, and Se concentration responded quadratically ($P \leq 0.01$) to day. Protein (%), total butterfat, and total Se, and somatic cells (cells/mL and cells/d) decreased linearly ($P < 0.01$) with day. Results indicate that gestational nutrition affects colostrum and milk yield and nutrient content, even when lactational nutrient requirements are met.

Key words: colostrum, gestation, lactation, milk production, nutritional plane, selenium

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INTRODUCTION

Maternal environment during gestation affects the developing fetus, which may result in impaired development and potential long-term consequences (Godfrey and Barker, 2000; Wu et al., 2006; Reynolds et al., 2010) that can occur even when birth weight is unaffected (Ford et al., 2007; Martin et al., 2007; Larson et al., 2009). This concept of developmental programming often focuses on gestation, although a growing body of literature suggests that postnatal environment may also program later growth and development (Greenwood and Cafe, 2007; Patel et al., 2009). Much of the work investigating developmental programming in livestock has determined physiological or production changes in the late-term fetus or offspring reared by their dams. Despite this, few data exist characterizing the effects of gestational nutrition on milk yield and nutrient composition. Additionally, observed differences in offspring raised by their dams are clouded by possible changes in milk production that would alter postnatal nutrient intake and confound effects of fetal and postnatal environments.

Our sheep research model utilizing artificial rearing has demonstrated that many alterations caused by maternal nutrition extend past gestation (Reed et al., 2007) and into neonatal (Meyer et al., 2010b) and market-weight lambs (Neville et al., 2010a). Maternal changes in body composition (Reed et al., 2007; Carlson et al., 2009; Meyer et al., 2010b), endocrine and metabolic status (Ward et al., 2008; Lekatz et al., 2010), and colostrum yield and nutrient content (Swanson et al., 2008) have accompanied changes observed in offspring. Therefore, we hypothesized that gestational nutrition alters the subsequent milk production of the dam, even when nutrient requirements of lactation are met. Our objective was to determine the effect of nutritional plane and Se supply during gestation on ewe colostrum and milk production and nutrient content when ewes were fed a common diet during early lactation.

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

Ewes were bred and managed as described in Meyer et al. (2010b). Briefly, at the USSES, 178 Rambouillet ewe lambs (age = 240 ± 17 d; initial BW = 52.1 ± 6.2 kg) were estrus synchronized and placed with Rambouillet rams ($n = 12$, 1 ram/15 ewes) for 5 d. Serviced ewes were stratified by BW and assigned randomly to a treatment pen ($n = 2$), where they received

diets formulated to contain adequate Se (**ASe**; $3.5 \mu\text{g}$ of Se·kg of $\text{BW}^{-1}\cdot\text{d}^{-1}$) or high Se (**HSe**; $65 \mu\text{g}$ of Se·kg of $\text{BW}^{-1}\cdot\text{d}^{-1}$). Selenium was provided to HSe 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. Ewes were fed a total mixed ration (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 ultrasound, and 84 pregnant ewes (d 36 of gestation, $n = 42/\text{Se treatment}$) were 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 0.91×1.2 -m pens in a temperature-controlled (12 to 21°C), ventilated facility for the duration of the study. Lighting within the facility was timed to mimic daylight patterns for Fargo, North Dakota (latitude: 46.87°N , longitude: 96.81°W). Ewes remained on their Se treatments (actual intakes: ASe, $11.5 \mu\text{g}$ Se·kg of $\text{BW}^{-1}\cdot\text{d}^{-1}$; HSe, $77.0 \mu\text{g}$ Se·kg of $\text{BW}^{-1}\cdot\text{d}^{-1}$), and on d 40 of gestation were assigned randomly to 1 of 3 nutritional plane treatments supplying 60 (restricted; **RES**), 100 (control; **CON**), or 140% (high; **HIH**) of global nutritional requirements (NRC, 1985) except for Se. Treatment diets were fed until immediately after parturition and have been described previously in detail by Meyer et al. (2010b). Within each Se and nutritional plane treatment, one-half of the ewes were assigned to be slaughtered and necropsied after colostrum sampling (between 3 and 24 h postpartum), and the remaining ewes were mechanically milked twice daily for 20 d. This resulted in a completely randomized design with a 2×3 factorial arrangement of Se supply \times nutritional plane (ASe-RES, ASe-CON, ASe-HIH, HSe-RES, HSe-CON, HSe-HIH; $n = 14$ ewes/treatment for colostrum measures, $n = 7$ ewes/treatment for early lactation measures). Selenium treatments were based on NRC requirements (ASe), and nontoxic supranutritional amounts of Se (HSe) that have previously elicited biological response in ruminants (Soto-Navarro et al., 2004; Reed et al., 2007; Neville et al., 2008; Carlson et al., 2009).

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 (ASe pellet, HSe pellet, and concentrated Se pellet; Table 1) were blended to meet ME and Se requirements of each ewe as dictated by nutritional plane and Se supply treatments (Meyer et al., 2010b). As in diets fed during early gestation, the Se source of the HSe pellet was the previously described Se-enriched

Table 1. Ingredient composition and analyzed nutrient composition of diets fed to ewe lambs from d 37 of gestation to d 20 of lactation

Item	Adequate Se pellet ¹	High Se pellet ²	Concentrated Se pellet ²	Lactation protein pellet ³
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	70.0
Limestone	1.0	1.5	1.0	—
Wheat middlings	53.0	6.9	53.0	15.0
Se-enriched wheat mill run	—	47.2	—	—
Starch	—	—	0.91	—
Seleno-methionine	—	—	0.0085	—
Mineral mix	—	—	—	9.0
Urea	—	—	—	4.5
Glycerin	—	—	—	1.5
Analyzed dietary composition, % DM				
OM	92.5	93.5	92.5	87.0
CP	15.9	16.6	16.2	50.2
NDF	36.8	27.0	37.6	13.4
ADF	15.7	12.0	17.6	5.4
Starch	20.8	31.9	21.5	9.9
Ca	1.02	1.14	1.09	1.88
P	0.85	0.60	0.79	1.38
Se, mg/kg	0.67	6.13	37.1	4.88
Calculated dietary composition				
ME, ⁴ Mcal/kg	2.83	2.82	3.01	2.58

¹The adequate Se pellet was fed during gestation and lactation.

²The high Se and concentrated Se pellets were fed during gestation to meet the high Se treatment.

³The protein pellet was fed in addition to the adequate Se pellet during lactation to meet the protein requirement of lactating ewes.

⁴Estimated using values obtained from the NRC (1985).

wheat mill run (Meyer et al., 2010b). The Se source of the ASe pellet was feedstuffs used in the diet, and purified selenomethionine was the Se source for the concentrated Se pellet. Nutrient requirements were based on NRC (1985) recommendations for 60 kg of BW, pregnant ewe lambs during mid to late gestation (weighted ADG of 140 g/d). Diets were 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. Diet subsamples were obtained daily and analyzed for nutrient concentration as described in Meyer et al. (2010b).

Ewes were monitored closely during lambing, and lambs were removed immediately after parturition, before suckling, for artificial rearing. Both Se supply and nutritional plane treatments were terminated at parturition. Ewes that were assigned to necropsy on d 20 of lactation were transitioned to receive 100% of NRC (1985) requirements for early lactation, provided by the ASe pellet fed during gestation and a lactation protein supplement pellet (Table 1). A 5-d transition period was used to increase intake from the gestation to lactation level, and feed was delivered after each milking (2×/d).

As described in Meyer et al. (2010b), ewe DMI by nutritional plane was 487 vs. 753 vs. 1,128 ± 10 g/d during gestation and 1,079 vs. 1,169 vs. 1,273 ± 21 g/d

during lactation for RES, CON, and HIH, respectively. Ewes fed ASe and HSe consumed 794 vs. 779 ± 8 g/d and 1,185 vs. 1,161 ± 17 g/d during gestation and lactation, respectively. Specific intakes of CP, ME, NDF and starch varied depending upon dietary intake and nutrient composition (Table 1). During gestation ewes fed RES, CON, and HIH consumed approximately 77 vs. 121 vs. 180 ± 2 g/d of CP, 1.34 vs. 2.13 vs. 3.16 ± 0.03 Mcal of ME/d, 155 vs. 253 vs. 384 ± 3 g/d of NDF, and 121 vs. 184 vs. 265 ± 3 g/d of starch. Also during gestation ASe and HSe ewes consumed approximately 125 vs. 127 ± 1 g/d of CP, 2.23 vs. 2.19 ± 0.02 Mcal of ME/d, 290 vs. 238 ± 3 g/d of NDF, and 164 vs. 216 ± 2 g/d of starch. During lactation ewes fed RES, CON, and HIH consumed approximately 261 vs. 271 vs. 284 ± 4 g/d of CP, 3.40 vs. 3.67 vs. 3.99 ± 0.06 Mcal of ME/d, 403 vs. 440 vs. 485 ± 8 g/d of NDF, and 232 vs. 253 vs. 278 ± 5 g/d of starch. Also, during gestation ASe and HSe ewes consumed approximately 276 vs. 279 ± 3 g/d of CP, 3.72 vs. 3.76 ± 0.02 Mcal of ME/d, 446 vs. 440 ± 3 g/d of NDF, and 256 vs. 253 ± 2 g/d of starch.

Milking Procedures and Nutrient Analysis

Colostrum. Colostrum was obtained from ewes using methods similar to those of Swanson et al. (2008). At 3 h postpartum, ewes were injected intramuscularly

with 1 mL of oxytocin (20 IU; AgriLabs, St. Joseph, MO) to facilitate colostrum ejection, and colostrum was manually collected until the udder was empty. Colostrum was weighed, volume measurements were taken, and subsamples were collected for nutrient analysis. One sample (approximately 40 mL) was collected, treated with Broad Spectrum Microtabs II (D & F Control Systems, Dublin, CA), and refrigerated before being shipped to the Heart of America DHIA laboratory (Manhattan, KS) for analysis of butterfat, solids-not-fat, lactose, protein, milk urea N, and somatic cell count (SCC). A second colostrum sample (approximately 100 mL) was frozen for Se analysis via hydride generation atomic absorption spectroscopy (5100 AAS, Perkin-Elmer Inc., Boston, MA) using methods of Finley et al. (1996).

Early Lactation. Ewes were mechanically milked twice daily at 0500 and 1700 h until necropsy, which occurred after the morning milking on d 20. Day 1 of lactation was considered to be the day of the first morning milking of each ewe, and all ewes 4 or more hours postpartum were included in each milking.

A portable milking system (165 pulsations/min in a 50:50 ratio, 57-kPa vacuum; Coburn Co. Inc., White-water, WI, and Interpuls Inc., Ablinea, Italy) was used to mechanically milk ewes during early lactation using the following methods. Ewes were restrained during milking in a raised stanchion holding 6 ewes at a time. Each ewe was fed approximately 100 g of a corn and oat mixture after entering the stanchion. Two ewes were milked at once, and an intramuscular injection of 1 mL of oxytocin (20 IU; AgriLabs) was administered approximately 60 to 90 s before milking to facilitate milk ejection. Teat dip (Lauricare Teat Dip 1433, 3M, St. Paul, MN) was applied to each teat. After 15 s, each teat was stripped (3 times) and then towed clean. After cleaning the udder, the milking machine was applied, and each ewe was milked until ejection slowed dramatically and the udder felt loose by palpation. A small amount of residual milk was left in the udder to prevent teat damage from overmilking. After completion, teat dip was again applied to each teat, but was not towed off. The milking system was cleaned with acid and detergent washes immediately after each milking (twice daily) and with a chlorine wash immediately before each milking.

Milk from each ewe was collected in a clean, labeled container. Weight and volume were recorded at each milking, and a subsample was obtained from the 0500 h milking on d 3, 7, 14, and 20. On these days, milk from each ewe was subsampled for DHIA and laboratory analysis as described previously for colostrum.

Ewes were observed for signs of mastitis at each milking. Udders were palpated, and milk yield, SCC, and feed intake were monitored. A California Mastitis Test was also performed when mastitis was suspected. During the study, 2 ewes were treated for suspected mastitis, although SCC did not exceed 250,000 cells/mL.

Calculations

Daily totals of butterfat, protein, lactose, solids-not-fat, and Se were calculated as nutrient concentration multiplied by milk weight. Total daily milk urea N and SCC were calculated as concentration multiplied by milk volume.

Statistical Analysis

Ewes that gave birth to twins ($n = 3$) were removed from the data set. One ewe was found to be open and removed from the study, and colostrum was not obtained from another ewe due to dystocia-related problems. This resulted in the following ewe numbers for each treatment and sample type: ASe-RES (colostrum: 12, milk: 7), ASe-CON (colostrum: 14, milk: 7), ASe-HIH (colostrum: 13, milk: 7), HSe-RES (colostrum: 13, milk: 7), HSe-CON (colostrum: 14, milk: 7), and HSe-HIH (colostrum: 13, milk: 7).

All data were analyzed as a 2×3 factorial design using a general linear model (SAS Inst. Inc., Cary, NC) with ewe as the experimental unit. For colostrum variable analysis, ewe Se supply (ASe vs. HSe), nutritional plane (RES vs. CON vs. HIH), and their interaction were used as fixed effects in the model. In addition to gestational treatments, the effect of day of lactation and all interactions were included as fixed effects in the model for milk variables. Means were separated using least significant difference and considered significant when $P \leq 0.05$. In the absence of interactions ($P > 0.05$), main effects are reported; otherwise interactive means are discussed. When the effect of day was significant for milk variables, linear, quadratic, and cubic contrasts were performed.

RESULTS

Colostrum

Yield. Although there was no gestational Se supply \times nutritional plane interaction ($P > 0.83$) for colostrum weight or volume at 3 h postpartum (Table 2), main effects of both Se supply ($P = 0.02$) and nutritional plane ($P = 0.03$) were present. Colostrum weight and volume were greater ($P = 0.02$) for ewes fed the HSe diet during gestation compared with ASe. Additionally, ewes fed the CON plane of nutrition during gestation had greater ($P < 0.05$) colostrum weight and volume than RES and HIH.

Nutrient Composition. The interaction of Se supply and nutritional plane during gestation affected colostrum lactose concentration ($P = 0.04$) and Se concentration ($P < 0.001$; Table 2). Within ewes fed the HSe diet, those fed the CON or HIH plane of nutrition had greater ($P \leq 0.03$) lactose than RES, although there were no differences ($P \geq 0.10$) among ASe ewes. In addition, HSe-HIH ewes had greater ($P = 0.02$) lactose than ASe-HIH. For all nutritional planes, colos-

Table 2. Effects of Se supply and nutritional plane during gestation on ewe colostrum yield, nutrient composition, and total nutrient components

Item	Se supply ¹			Nutritional plane ³				P-value ⁵		
	ASe	HSe	SEM ²	RES	CON	HIH	SEM ⁴	Se	Nut	Se × Nut
Colostrum weight, g/d	390.5	536.6	43.4	378.4 ^a	579.3 ^b	423.9 ^a	54.1	0.02	0.03	0.88
Colostrum volume, mL/d	374.6	522.4	42.8	375.1 ^a	559.5 ^b	410.8 ^a	53.5	0.02	0.03	0.84
Nutrient composition										
Butterfat, %	13.7	12.3	0.5	14.1	12.5	12.5	0.6	0.03	0.06	0.80
Solids-not-fat, %	19.9	20.0	0.4	19.1 ^a	19.9 ^{ab}	20.9 ^b	0.4	0.96	0.03	0.48
Lactose, %	2.36	2.52	0.10	2.32	2.62	2.39	0.12	0.25	0.18	0.04
ASe	—	—	—	2.48 ^{xy}	2.51 ^{xy}	2.09 ^x	0.18			
HSe	—	—	—	2.15 ^x	2.72 ^y	2.69 ^y	0.18			
Protein, %	17.3	16.9	0.4	16.6	16.6	17.9	0.5	0.48	0.13	0.49
Milk urea N, mg/dL	6.54	6.73	0.50	5.52	6.85	7.54	0.63	0.79	0.07	0.47
Se, µg/g	0.42	2.67	0.07	1.80	1.54	1.30	0.09	<0.001	0.001	<0.001
ASe	—	—	—	0.39 ^w	0.45 ^w	0.43 ^w	0.13			
HSe	—	—	—	3.21 ^z	2.63 ^y	2.16 ^x	0.13			
Total nutrient component ⁶										
Butterfat, g/d	49.0	64.8	5.7	53.8 ^{ab}	71.1 ^b	45.7 ^a	7.0	0.05	0.03	0.81
Solids-not-fat, g/d	72.1	102.3	7.9	71.7 ^a	111.8 ^b	78.0 ^a	9.9	0.008	0.007	0.55
Lactose, g/d	9.3	14.0	1.4	8.8 ^a	15.4 ^b	10.6 ^a	1.8	0.02	0.02	0.27
Protein, g/d	61.3	85.1	6.5	61.8 ^a	92.9 ^b	65.0 ^a	8.1	0.01	0.009	0.61
Milk urea N, g/d	0.024	0.037	0.005	0.022	0.039	0.031	0.006	0.05	0.08	0.36
Se, mg/d	0.17	1.41	0.11	0.80	0.97	0.60	0.13	<0.001	0.14	0.27
Somatic cell count										
Cells/mL × 1,000	1,193	581	241	1,086	665	909	303	0.07	0.58	0.68
Cells/d × 1,000,000	404.3	269.9	95.1	473.2	267.5	270.5	117.9	0.31	0.36	0.83

^{a,b}Within an item, main effect means differ ($P \leq 0.05$).

^{w-z}Within an item, interactive means differ ($P \leq 0.05$).

¹Ewes fed 11.5 µg/kg of BW Se (ASe) or 77.0 µg/kg of BW Se (HSe) during gestation.

²SEM for $n = 39$ (ASe) or $n = 40$ (HSe).

³Ewes fed 60 (RES), 100 (CON), or 140% (HIH) of nutrient requirements during gestation.

⁴SEM for $n = 25$ (RES), $n = 28$ (CON), and $n = 26$ (HIH).

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

⁶Total nutrient components of colostrum, calculated as nutrient concentration multiplied by colostrum weight (butterfat, protein, lactose, solids-not-fat, Se) or volume (milk urea N, somatic cell count).

trum Se concentration was greater ($P < 0.001$) for ewes fed HSe than ASe during gestation. Considering only the HSe treatment, however, colostrum from RES had the greatest ($P < 0.01$) Se concentration, CON was intermediate ($P < 0.002$), and HIH had the least ($P < 0.002$) Se.

All other nutrient components (butterfat, solids-not-fat, protein, and milk urea N) were not affected ($P > 0.46$) by the interaction of Se supply and nutritional plane. Gestational Se supply affected ($P = 0.03$) colostrum butterfat concentration (Table 2) at 3 h postpartum, where ewes fed the ASe diet during gestation had a greater butterfat concentration than HSe.

Nutritional plane during gestation affected ($P = 0.03$) concentration of solids-not-fat and tended to affect ($P \leq 0.07$) butterfat and milk urea N concentration of colostrum (Table 2). Ewes fed the HIH diet had greater concentration of solids-not-fat ($P = 0.009$) and milk urea N ($P = 0.02$) than RES, whereas RES ewes had greater ($P \leq 0.04$) butterfat concentration than CON and HIH. Colostrum protein concentration was not affected ($P > 0.12$) by nutritional plane or Se supply during gestation.

Total Nutrient Components. When expressed as total nutrients in colostrum, the interaction of Se supply and nutritional plane had no effect ($P > 0.26$) on any colostrum component (Table 2). The main effect of Se supply during gestation affected ($P \leq 0.05$) all components, however. Total colostrum butterfat, solids-not-fat, lactose, protein, milk urea N, and Se were greater ($P \leq 0.05$) for ewes fed HSe compared with ASe.

Nutritional plane during gestation affected ($P \leq 0.03$) total colostrum butterfat, solids-not-fat, lactose, and protein and tended to affect ($P = 0.08$) milk urea N (Table 2). Ewes fed the CON plane of nutrition had greater ($P = 0.01$) butterfat compared with HIH. In addition, total solids-not-fat, lactose, and protein were greater ($P < 0.05$) in colostrum from ewes fed the CON plane of nutrition compared with RES and HIH. Total milk urea N tended to be greater ($P = 0.07$) in CON than RES.

Somatic Cells. Nutritional plane and its interaction with Se supply did not affect ($P > 0.57$) colostrum SCC or total somatic cells (Table 2). Gestational Se supply tended to affect ($P = 0.07$) SCC (cells/mL ×

Table 3. Effects of Se supply and nutritional plane during gestation on ewe milk yield, nutrient composition, and total nutrient components

Item	Se supply ¹			Nutritional plane ³				P-value ⁵		
	ASe	HSe	SEM ²	RES	CON	HIH	SEM ⁴	Se	Nut	Se × Nut
Milk weight, g/d	848.1	935.6	16.8	749.2 ^a	960.8 ^b	965.5 ^b	20.6	<0.001	<0.001	0.20
Milk volume, mL/d	831.2	919.7	16.6	736.5 ^a	943.6 ^b	946.3 ^b	20.3	<0.001	<0.001	0.17
Nutrient composition										
Butterfat, %	5.92	5.60	0.14	6.60	5.66	5.02	0.18	0.12	<0.001	0.02
ASe	—	—	—	6.40 ^{yz}	5.85 ^{xy}	5.50 ^x	0.25			
HSe	—	—	—	6.80 ^z	5.47 ^x	4.53 ^w	0.25			
Solids-not-fat, %	11.4	11.3	0.1	11.5	11.3	11.2	0.1	0.10	0.17	0.40
Lactose, %	5.18	5.14	0.03	5.10	5.20	5.18	0.04	0.32	0.13	0.58
Protein, %	5.24	5.14	0.05	5.38 ^b	5.11 ^a	5.09 ^a	0.06	0.13	<0.001	0.45
Milk urea N, mg/dL	25.0	24.0	0.5	22.0	25.3	26.1	0.7	0.22	<0.001	0.006
ASe	—	—	—	20.7 ^w	26.7 ^{yz}	27.5 ^z	1.0			
HSe	—	—	—	23.4 ^x	24.0 ^x	24.7 ^{xy}	1.0			
Se, µg/g	0.19	0.40	0.01	0.32	0.32	0.26	0.01	<0.001	<0.001	0.03
ASe	—	—	—	0.20 ^x	0.20 ^x	0.18 ^x	0.02			
HSe	—	—	—	0.45 ^z	0.43 ^z	0.33 ^y	0.02			
Total nutrient component ⁶										
Butterfat, g/d	51.4	51.6	2.5	48.0	55.7	50.9	3.0	0.95	0.19	0.10
Solids-not-fat, g/d	99.4	106.7	4.4	85.9 ^a	109.9 ^b	113.2 ^b	5.4	0.24	<0.001	0.67
Lactose, g/d	45.2	49.0	2.1	38.4 ^a	50.6 ^b	52.3 ^b	2.6	0.21	<0.001	0.71
Protein, g/d	45.5	48.4	2.0	40.1 ^a	49.7 ^b	51.0 ^b	2.4	0.30	0.003	0.61
Milk urea N, g/d	0.20	0.23	0.01	0.17 ^a	0.24 ^b	0.24 ^b	0.01	0.07	<0.001	0.30
Se, mg/d	0.17	0.37	0.02	0.24 ^a	0.31 ^b	0.26 ^{ab}	0.02	<0.001	0.05	0.64
Somatic cell count										
Cells/mL × 1,000	94.2	88.5	16.1	62.5 ^a	133.1 ^b	78.5 ^{ab}	19.8	0.80	0.03	0.74
Cells/d × 1,000,000	80.3	87.0	20.7	44.1 ^a	135.0 ^b	71.9 ^{ab}	25.2	0.82	0.04	0.94

^{a,b}Within an item, main effect means differ ($P \leq 0.05$).

^{w-z}Within an item, interactive means differ ($P \leq 0.05$).

¹Ewes fed 11.5 µg/kg of BW Se (ASe) or 77.0 µg/kg of BW Se (HSe) during gestation.

²SEM for $n = 21$ /treatment.

³Ewes fed 60 (RES), 100 (CON), or 140% (HIH) of nutrient requirements during gestation.

⁴SEM for $n = 14$ /treatment.

⁵Probabilities of difference for Se supply (Se), nutritional plane (Nut), and their interaction. Day of lactation and its interactions ($P \geq 0.06$ for all variables except for Se) were also included in the model.

⁶Total daily nutrient components of milk, calculated as nutrient concentration multiplied by milk weight (butterfat, protein, lactose, solids-not-fat, Se) or volume (milk urea N, somatic cell count).

1,000), where ewes fed HSe had less than ASe. Total colostrum somatic cells were unaffected ($P > 0.30$) by nutritional plane and Se supply during gestation.

Milk

Yield. The interaction of gestational Se supply and nutritional plane had no effect ($P > 0.17$) on milk yield (Table 3) during the first 20 d of lactation. Milk yield and volume were influenced by day of lactation (Figure 1A); however, day of lactation did not interact ($P \geq 0.06$) with gestational treatment to affect milk weight or volume, so only main effects are presented. Similar to colostrum yield, ewes fed HSe during gestation continued to have greater ($P < 0.001$) milk weight and volume than ASe during the 20-d milking period. Milk production of ewes fed the HIH plane of nutrition increased on d 2 (Figure 1B); therefore, ewes fed both CON and HIH diets during gestation had greater ($P < 0.001$) subsequent milk weight and volume than RES during the first 20 d of lactation.

Nutrient Composition. Day of lactation did not interact with gestational Se supply or nutritional plane ($P > 0.06$) to affect milk concentrations of butterfat, solids-not-fat, lactose, protein, and milk urea N. However, butterfat and milk urea N concentrations in milk were affected ($P \leq 0.02$) by the interaction of Se supply and nutritional plane (Table 3). Within ewes fed the ASe diet during gestation, RES had greater ($P = 0.01$) butterfat than HIH. Among ewes in the HSe treatment, milk from ewes fed RES had the greatest ($P < 0.001$) butterfat, CON was intermediate ($P \leq 0.008$), and HIH had the least ($P \leq 0.008$). Additionally, within ewes fed the HIH plane of nutrition, ASe had greater ($P = 0.006$) butterfat concentration than HSe. Although there were no differences ($P > 0.32$) in milk urea N due to nutritional plane among HSe ewes, within ewes in the ASe treatment, CON and HIH had greater ($P < 0.001$) milk urea N than RES. Within the RES nutritional plane, ewes fed HSe had greater ($P = 0.05$) milk urea N than ASe, whereas ASe was greater ($P < 0.02$) than HSe among CON and HIH planes of nutrition.

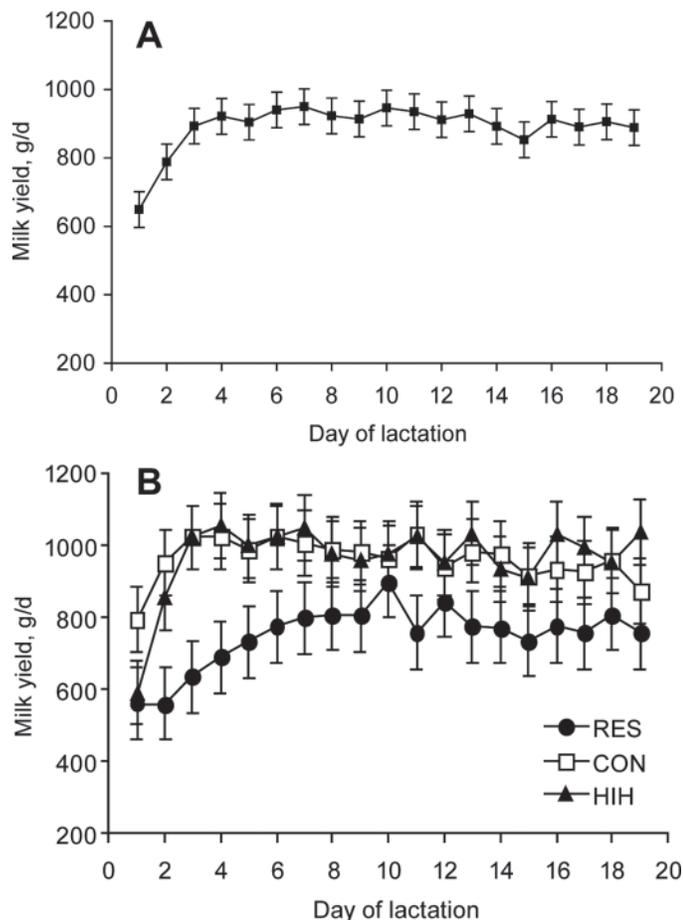


Figure 1. Effect of day of lactation (panel A) and gestational nutritional plane \times day of lactation (panel B) on ewe milk yield during the first 19 d of lactation. Nutritional planes were 60 (restricted, RES), 100 (control, CON), or 140% (high, HIH) of nutrient requirements. Least squares means \pm SEM are presented for each day of lactation (A; $n = 42$) and nutritional plane (B; $n = 14$ per treatment). Day of lactation affected (day $P = 0.02$; linear $P = 0.04$, quadratic $P < 0.001$, cubic $P = 0.003$) milk production (panel A). There was a main effect of gestational nutritional plane (nutritional plane $P < 0.001$, nutritional plane \times day $P > 0.99$) on milk production (panel B).

Milk Se concentration was also affected by the interactions of Se supply \times nutritional plane during gestation ($P = 0.03$; Table 3) and Se supply \times day of lactation ($P < 0.001$; Figure 2A). Ewes fed HSe had greater ($P < 0.001$) milk Se than ASe for all nutritional planes, and within ASe ewes there was no difference ($P > 0.46$) in Se concentration. Among ewes fed HSe, however, RES and CON had greater ($P < 0.001$) milk Se concentration compared with HIH. Ewes fed HSe during gestation had greater ($P < 0.001$) milk Se on each day, but the milk Se concentration of HSe ewes decreased from d 3 to 7 ($P < 0.001$) and 7 to 14 ($P < 0.001$).

A main effect of nutritional plane during gestation was observed ($P < 0.001$) for milk protein concentration (Table 3), where protein was greater ($P \leq 0.001$) in ewes fed the RES plane of nutrition compared with CON or HIH. There were no effects ($P \geq 0.10$) of either gestational treatment on milk concentration of solids-not-fat or lactose.

Total Nutrient Components. Selenium supply and nutritional plane did not interact with day of lactation to affect ($P > 0.40$) any total milk nutrient component except Se during the first 20 d of lactation (Table 3). Total milk Se was affected ($P = 0.005$) by the interaction of Se supply during gestation and day of lactation (Figure 2B). Similar to milk Se concentration, total Se was greater ($P \leq 0.04$) in milk from HSe-fed ewes than ASe at each day of lactation. However, total milk Se decreased ($P = 0.002$) in HSe ewes from d 7 to 14.

Gestational Se supply tended to affect ($P = 0.07$) total milk urea N (Table 3), where ewes fed HSe had greater N than ASe. Total solids-not-fat, lactose, protein, milk urea N, and Se were affected ($P \leq 0.05$) by nutritional plane during gestation (Table 3). Milk from ewes fed the CON and HIH planes of nutrition during gestation had greater ($P < 0.006$) total solids-not-fat, lactose, protein, and milk urea N than RES. Total Se was greater ($P = 0.02$) in milk from ewes fed the CON diet compared with RES. There was no effect ($P > 0.18$) of either gestational treatment on total milk butterfat during the first 20 d of lactation.

Somatic Cells. There was no interaction ($P > 0.15$) of day of lactation with gestational treatment for milk somatic cells. Both SCC (cells/mL \times 1,000) and total somatic cells were greater ($P \leq 0.05$) in milk from CON-fed ewes than RES.

Day of Lactation. Milk yield, expressed as both weight (g/d; $P = 0.02$) and volume (mL/d; $P = 0.02$), was affected by day of lactation. A cubic effect of day was observed for both milk weight ($P = 0.003$; Figure 1A) and volume ($P = 0.004$; data not shown). Milk yield (g/d) increased from d 1 to 3 ($P = 0.001$), after which no differences were observed.

Day of lactation affected ($P \leq 0.05$) milk concentration (%) of all components measured (Table 4). Butterfat, solids-not-fat, lactose, milk urea N, and Se concentration responded quadratically ($P \leq 0.006$) to day, whereas protein decreased linearly ($P < 0.001$) with advancing day.

There was no effect of day ($P > 0.26$) on total milk content of solids-not-fat, lactose, or protein. Total butterfat and Se were affected ($P < 0.006$) and milk urea N tended ($P = 0.09$) to be influenced by day of lactation. A linear decrease ($P < 0.001$) was observed for total butterfat and Se, whereas milk urea N responded quadratically ($P = 0.03$).

Both SCC (cells/mL \times 1,000) and total daily somatic cells tended ($P \leq 0.08$) to be affected by day of lactation, where both decreased linearly ($P \leq 0.04$) with advancing day.

DISCUSSION

Data from this study demonstrate the profound effects that gestational nutrition can have on the subsequent lactation of the dam, even when she is fed to

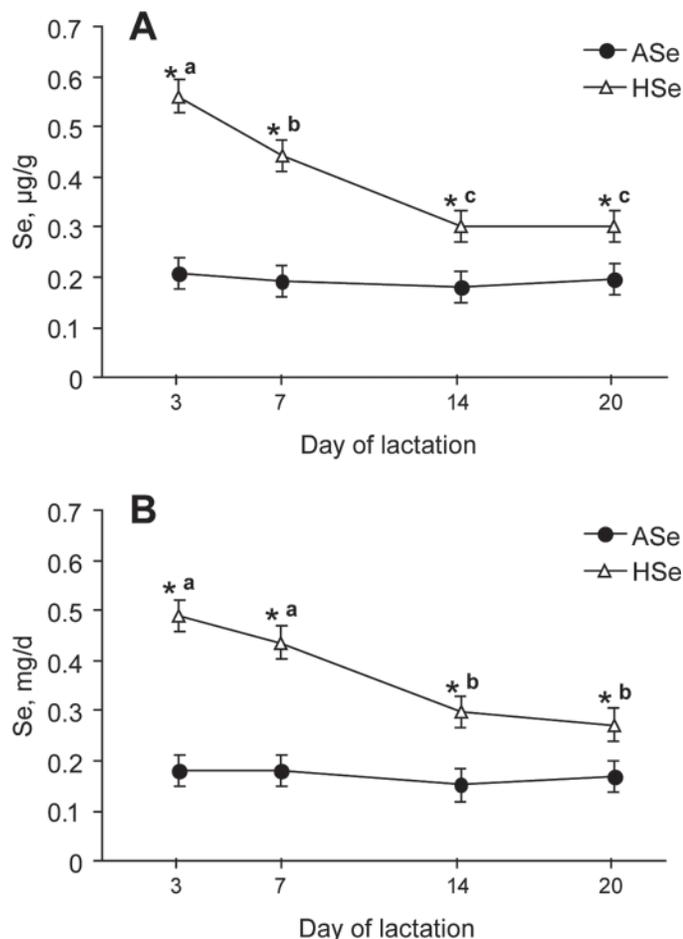


Figure 2. Effect of gestational Se supply \times day of lactation on ewe milk Se concentration (panel A) and total milk Se (panel B) during the first 19 d of lactation. The Se supply provided during gestation was adequate Se (11.5 $\mu\text{g}/\text{kg}$ of BW, ASe) or high Se (77 $\mu\text{g}/\text{kg}$ of BW, HSe). Least squares means \pm SEM are presented for each Se supply treatment ($n = 21$ per treatment). Selenium supply during gestation interacted with day of lactation to affect milk Se concentration ($\mu\text{g}/\text{g}$; panel A; Se $P < 0.001$, day $P < 0.001$, Se \times day $P < 0.001$) and total milk Se (mg/d; panel B; Se $P < 0.001$, day $P < 0.001$, Se \times day $P < 0.005$). In both panels, * denotes treatments that differ on that day. The letters a, b, and c denote differences within the HSe treatment across days.

meet nutrient requirements postpartum. To the authors' knowledge, lactational data presented here, in combination with ewe and neonatal offspring performance previously published (Meyer et al., 2010b) and forthcoming additional data, provide the first example of a comprehensive study of developmental programming in which dams and their offspring were managed independently during their respective early lactation and neonatal periods. This study provides an example of not only developmental programming of offspring by maternal gestational nutrition, but also of alteration of milk production by maternal nutrition during pregnancy.

Colostrum and Milk Production

Primiparous ewe colostrum and milk production were both affected by nutritional plane and Se supply during

gestation in this study, even though all ewes received a common diet during lactation. In this study, ewes fed both restricted and high nutritional planes during gestation had reduced colostrum yield compared with ewes fed to meet NRC requirements. This has been observed previously both in our model (Swanson et al., 2008) as well as others (Mellor and Murray, 1985; Mellor et al., 1987; Wallace et al., 2001; Bancharo et al., 2006; Tygesen et al., 2008). In the current study, milk yield of ewes fed a high plane of nutrition quickly increased and was similar to control ewes by d 2 of lactation. However, milk production of ewes restricted during gestation did not reach control amounts during the first 20 d of lactation, even as all ewes received a similar diet meeting nutrient requirements for lactation. Colostrum begins to accumulate in the mammary gland during the last few days of gestation in ewes (Mellor, 1987) and has been reduced in nutrient-restricted ewes (Mellor and Murray, 1985). Although both a restricted and high nutritional plane reduced colostrum accumulation in the current study, ewes that were fed a high nutritional plane during gestation were able to increase milk synthesis postpartum, unlike restricted ewes.

Three major factors were likely altered by gestational nutrition, which affected milk production even when ewes received adequate nutrition postpartum: 1) nutrient partitioning changes during gestation altered lactational nutrient use; 2) prepartum mammary gland development, blood flow, or both was affected; and 3) endocrine profiles during both gestation and lactation were altered, affecting both nutrient utilization and mammary gland growth and function.

Although increased dietary nutrients were available postpartum for milk production in this study, ewes that were nutrient restricted in gestation likely partitioned these nutrients to rebuild muscle and organ mass during lactation. Because primiparous ewes in this study were still growing, ewes that had been restricted exhibited more compensatory skeletal growth postpartum. To illustrate this, gestationally nutrient-restricted ewes tended to have increased ADG and had improved G:F when realimented during early lactation, even though their BW and BCS remained less compared with ewes fed a control or high plane of nutrition (Meyer et al., 2010b). In addition, visceral organ mass of ewes that were nutrient restricted in gestation increased during the postpartum realimentation period (Meyer et al., 2009), which probably diverted nutrients from milk production.

Mammary gland growth and development during gestation is crucial for a successful subsequent lactation. Although mammary gland growth is slow in early gestation, this becomes exponential in late pregnancy (Anderson et al., 1985). Mammary gland growth of ewes has been impaired within 3 d of nutrient restriction during late gestation (Mellor and Murray, 1985). This model resulted in decreased gland mass at parturition (Mellor and Murray, 1985), even when ewes were realimented during the last 5 d of pregnancy (Mellor et

Table 4. Effect of day of lactation on milk nutrient composition and total nutrient components

Item	Day of lactation				SEM ¹	P-value ²	Day of lactation, ³ P =		
	3	7	14	20			Linear	Q	Cubic
Nutrient composition									
Butterfat, %	6.93	5.71	5.17	5.22	0.20	<0.001	<0.001	<0.001	0.29
Solids-not-fat, %	11.1	11.6	11.4	11.2	0.1	0.007	0.84	0.002	0.10
Lactose, %	4.83	5.20	5.33	5.28	0.04	<0.001	<0.001	<0.001	0.09
Protein, %	5.35	5.36	5.10	4.95	0.07	<0.001	<0.001	0.55	0.31
MUN, ⁴ mg/dL	23.2	25.5	25.7	23.6	0.8	0.05	0.84	0.006	0.67
Se, µg/g	0.38	0.32	0.24	0.25	0.02	<0.001	<0.001	0.004	0.69
Total nutrient component ⁵									
Butterfat, g/d	60.7	54.2	45.4	45.8	3.5	0.005	<0.001	0.19	0.78
Solids-not-fat, g/d	99.9	110.7	101.9	99.7	6.3	0.57	0.63	0.39	0.30
Lactose, g/d	43.7	50.1	47.7	47.0	3.0	0.50	0.66	0.28	0.31
Protein, g/d	47.7	51.1	45.2	43.7	2.8	0.27	0.12	0.55	0.29
MUN, g/d	0.20	0.24	0.22	0.20	0.01	0.09	0.36	0.03	0.34
Se, mg/d	0.34	0.31	0.22	0.22	0.02	<0.001	<0.001	0.32	0.35
Somatic cell count									
Cells/mL × 1,000	145.7	78.6	72.0	69.2	23.0	0.06	0.03	0.15	0.35
Cells/d × 1,000,000	148.8	71.0	57.3	57.5	29.2	0.08	0.04	0.16	0.45

¹SEM for n = 21/treatment.

²Probability of difference for day of lactation. Effects of Se supply, nutritional plane, and their interactions were also included in the model.

³Q = quadratic.

⁴MUN = milk urea N.

⁵Total daily nutrient components of milk, calculated as nutrient concentration multiplied by milk weight (butterfat, protein, lactose, solids-not-fat, Se) or volume (MUN, somatic cell count).

al., 1987). Anderson (1975) reported that 98% of ovine mammary gland growth after breeding occurs during gestation, with only 2% occurring during lactation. Thus, gestational nutrition has the ability to greatly affect mammary gland growth and development.

In a similar model to the current study, mammary gland capillary surface density, a measure of capillary surface area of the tissue, was greater for control than restricted ewes within the ASe treatment (Jorgenson et al., 2010). Additionally, mRNA expression of angiogenic factors has been altered by nutrient restriction and form of supranutritional Se during gestation (Neville et al., 2010b). Because blood flow to the mammary gland is one of the major determinants of nutrient availability for milk synthesis (Anderson et al., 1985), impaired angiogenesis of the tissue caused by gestational nutrition has the potential to negatively affect subsequent milk production.

Mammary gland development during gestation and subsequent milk production in ewes are influenced by many hormones, including GH, placental lactogen, progesterone, estradiol, prolactin, and cortisol (Anderson et al., 1985; Mellor, 1987; Park and Jacobson, 1993). In this research model, nutritional plane during gestation has affected ewe endocrine profiles. Nutrient-restricted ewes had decreased IGF-I (Ward et al., 2008), progesterone (Vonnahme et al., 2007; Lekatz et al., 2010), and thyroid hormones (Ward et al., 2008; Lekatz et al., 2010), whereas ewes fed a high nutritional plane had decreased estradiol and progesterone but increased prolactin (Camacho et al., 2010) and cortisol (Vonnahme et al., 2007) during gestation. These alterations in hor-

mones likely interact to play a role during the crucial mammary growth and development of gestation (Mellor et al., 1987; Banchero et al., 2006). Additionally, postpartum alterations in metabolic hormones would affect nutrient utilization by the ewe during both gestation and lactation. For example, ewes that were fed a high plane of nutrition during gestation continued to have increased thyroid hormones postpartum in this study (Meyer et al., 2010a).

In this study, supranutritional Se increased colostrum and milk yield of primiparous ewes. Selenium supplementation at a similar level but with an alternate form than in the current study previously had no effect on colostrum yield (Swanson et al., 2008), although exogenous Se and vitamin E treatments during late gestation in other studies have increased colostrum and later milk yield in dairy heifers (Moeini et al., 2009) and cows (Lacetera et al., 1996). Ewes fed the HSe diet in the current study had greater ADG and BCS during gestation (Meyer et al., 2010b); thus greater energy reserves may have contributed to increased milk production of these ewes. Reasons for performance differences due to Se supply are unclear, and 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, which may have slightly altered ruminal fermentation and energy supply.

Additionally, in a similar study, supranutritional gestational Se increased mammary gland vascularity immediately after parturition (Jorgenson et al., 2010).

Thus, increased blood flow and nutrient delivery to the mammary gland may have resulted in increased milk yield.

Although effects of nutrient intake during prepubertal heifer development and the dry or transition periods have been greatly studied in dairy cattle, less is known about the specific effects of gestational nutrient intake on milk production, especially in beef cattle or sheep. In previous studies, energy balance (Lake et al., 2005) and source of dietary energy during mid and late gestation (Radunz et al., 2010) of multiparous beef cows or nutrient restriction of primiparous heifers during late gestation (Corah et al., 1975) did not affect subsequent milk yield. Conversely, when multiparous beef cows were restricted for the last 100 d of gestation, realimentation for 30 d prepartum increased milk production compared with continued restriction (Corah et al., 1975). Multiparous beef cows grazing corn residue had greater milk yield than those grazing winter range in another study, which followed BW and BCS (Larson et al., 2009). In addition, multiparous ewes nutrient restricted during late gestation had decreased milk production, as determined using the deuterium dilution technique on their suckling lambs (Tygesen et al., 2008). Early gestation effects have not been researched heavily, but milk yield was reduced in heifers that were overnourished during early gestation in one study (Sullivan et al., 2009). Although these varied data sets exist, offspring remained on the dams in all of the cited work, and therefore suckling behavior may have influenced milk production.

Colostrum and Milk Nutrient Composition

Colostrum and milk composition and total components were altered by both nutritional plane and Se supply in this study. Although differences were observed in concentration of some colostrum and milk nutrients, gestational nutrition effects on total nutrients appear to have been driven more by yield than nutrient composition. Butterfat and protein concentration of milk was greater for ewes that were nutrient restricted during gestation, but generally colostrum and milk were not more carbohydrate dense even though weight and volume were decreased. Milk butterfat depression with increasing nutritional plane was observed, as expected. As reported in previous work (Wallace et al., 2001; Banchemo et al., 2006; Swanson et al., 2008), ewes fed a control plane of nutrition had greater total colostrum butterfat, solids-not-fat, lactose, and protein than ewes fed either a restricted or high plane of nutrition. Few similar studies have investigated gestational nutrition effects on milk quality. In these there was no effect of energy source during mid and late gestation on milk fat, CP, or lactose content in beef cows (Radunz et al., 2010), whereas beef cows calving at a BCS of 6 produced milk with a greater percentage of protein than those at a BCS of 4 (Lake et al., 2005).

Colostrum Se was increased with supranutritional dietary Se, similar to previous reports (Abdelrahman and Kincaid, 1995; Rowntree et al., 2004; Hefnawy et al., 2008; Swanson et al., 2008; Moeini et al., 2009). Additionally, Se remained increased in milk throughout the first 20 d of lactation, despite a decrease in both concentration of and total Se in milk. Because organic forms of Se (Se-enriched wheat mill run and selenomethionine) were fed in this study, selenomethionine would have been used similarly to methionine in body protein synthesis during gestation (Waschulewski and Sunde, 1988; Butler et al., 1989), providing a source of circulating Se during protein turnover in early lactation (Taylor et al., 2009). Moreover, organic forms of Se, such as selenomethionine, are more efficiently incorporated into milk protein because they do not have to first be converted to an organic form (Pappas et al., 2008). Plasma and milk Se concentrations have been reported as highly correlated in ewes (Hefnawy et al., 2008), and colostrum Se mirrors ewe serum Se at 3 h postpartum in the current study (Meyer et al., 2010b). Differences in colostrum and milk Se from ewes of differing nutritional planes within the HSe treatment also follow serum Se and may have been caused by dilution of maternal blood volume or differences in bioavailability, absorption, or incorporation into protein of Se sources (Meyer et al., 2010b). Increased milk Se caused by supranutritional maternal Se during gestation could serve as a means to increase neonatal lamb Se intake, especially in Se-deficient areas or in extensive range conditions where supplementation of lambs is not feasible.

Mammary gland health, as assessed by SCC, was affected by both gestational Se and nutritional plane. In agreement with previous work (Weiss et al., 1990; Morgante et al., 1999), increased maternal Se decreased colostrum SCC. Later in lactation, gestational Se supply had no effect on SCC, whereas ewes that were restricted during gestation had fewer somatic cells than controls. Although concentration was also reduced in restricted ewes, this may have been a function of mammary gland work load.

Day of Lactation

In this study, the peak milk yield of primiparous Rambouillet ewes was reached by d 3 of lactation and remained increased for the remainder of the 20-d milking period. Previous work has demonstrated peak lactation for ewes to be between 1 and 2 wk (Mellor, 1987) or 21 and 30 d (Cardellino and Benson, 2002). Methodology for determining milk production and ewe breed, age, and offspring number differ among studies and affect milk yield (Wohlt et al., 1984; Ramsey et al., 1998; Cardellino and Benson, 2002); thus comparisons between studies should be made with caution. In the current study, day of lactation affected concentration of all milk nutrients analyzed, where butterfat decreased

and lactose increased during early lactation. This is in agreement with limited previous work in ewes (Wohlt et al., 1984; Ramsey et al., 1998).

Potential Impacts of Milk Production

In addition to observed differences in lactational performance of ewes, lamb growth, health, body composition, and endocrine status were altered by gestational nutrition in this study (Meyer et al., 2010b; Camacho et al., 2011; C. J. Hammer, unpublished data). Birth weight and ADG were reduced in lambs born to nutrient-restricted ewes, even when lambs were offered an ad libitum milk replacer diet (Meyer et al., 2010b). Milk production by the ewe and intake by the lamb are highly and positively correlated to lamb ADG (Burriss and Baugus, 1955; Torres-Hernandez and Hohenboken, 1980; Wohlt et al., 1984; Snowden and Glimp, 1991). Although not all concentrations of nutrients were affected by gestational nutritional plane, totals for all nutrients measured except for butterfat were reduced in milk from ewes that were nutrient restricted during gestation. Neonatal lambs rely upon colostrum and early milk as a rapid energy and protein source, especially when exposed to cold stress (Nowak and Poindron, 2006). Increased colostrum intake generally increases rate and amount of IgG absorption up to a maximal amount in calves (Stott et al., 1979a,b). Additionally, total colostral IgG was reduced in ewes that were restricted or fed a high nutritional plane during gestation in a similar study (Swanson et al., 2008). Thus, if lambs had been maintained on their dams postpartum in a normal production setting, greater neonatal morbidity and mortality would likely have been observed in addition to a further reduction of growth.

Additionally, recent research has yielded the lactocrine hypothesis, stating that specific factors in colostrum and milk, such as relaxin, program development of the uterus in pigs (Bartol et al., 2008). Thus growth factors, hormones, and other compounds in colostrum and milk not measured in the present study may be altered due to gestational nutrition and may continue to affect development of important tissues such as the female reproductive tract in offspring, which may contribute to later differences in reproductive performance (Martin et al., 2007).

Inadequate nutrient intake is common for gestating beef cows and ewes while grazing forages of poor quality or limited availability (Thomas and Kott, 1995; Del-Curto et al., 2000). Many production systems strive for parturition to coincide with seasonal peaks of forage growth, however, allowing cows and ewes to receive poor gestational nutrition but adequate nutrition during lactation. The reduction in milk yield of restricted ewes observed in this study suggests that milk production may be decreased by grazing ruminants under this type of management. Thus, although reduced milk production has negative consequences for the offspring, it may be positive for the dam. Decreased milk production

would decrease the nutrient demands of early lactation and allow the dam to replenish body stores when nutrient intake during early lactation is high (Wettemann et al., 2003; Hess et al., 2005). This could facilitate earlier return to estrus and improved conception rates, as lactation and rebreeding occur simultaneously, and may be more dramatic in first-parity heifers that are also growing during this period and are more likely to have long postpartum anestrus periods (Short et al., 1990).

Conclusions

Results of this study indicate that ramifications of gestational nutrition on postnatal nutrient supply to the offspring must be considered in developmental programming research models. Studies in which offspring birth weight is unaffected by maternal nutrition or management during gestation, but postnatal growth or development is affected, may be influenced by altered milk production and thus early postnatal programming.

In conclusion, colostrum and milk production were affected by both nutritional plane and Se supply during mid and late gestation, even when ewes were managed similarly postpartum. Both nutrient restriction and excess during gestation decreased colostrum production in this study, whereas only nutrient restriction reduced milk yield during early lactation. Additionally, supra-nutritional Se fed during gestation increased both colostrum and milk yield. Results indicate that maternal nutrient restriction during gestation not only negatively affects offspring prenatal growth and development, but also decreases lactational potential of the dam, which may further impair offspring development postnatally. Further research is necessary to determine if gestational nutrition of primiparous ewes affects lactation potential during subsequent parities.

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