The effects of protein supplementation of fall calving beef cows on pre- and postpartum plasma insulin, glucose and IGF-I, and postnatal growth and plasma insulin and IGF-I of calves¹

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ABSTRACT: Fall calving (September to October) cows ($n = 189$ calvings in 5 replications; body weight [BW] = 626 ± 6 kg, body condition score [BCS] = 4.76 ± 0.06) grazing native dormant range were used to determine the effects of protein supplementation on performance and endocrine function of cows and calves. Cows were individually fed either a control (CON; 1.82 kg/d of 38% crude protein [CP]) or restricted (RES; 0.2 kg/d of 8% CP) protein supplement from mid-November to mid-March for 6 consecutive years. During each year, cows were re-assigned dietary treatments according to calving date and BCS, and half of the CON and half of the RES cows remained on the same diets as the previous year and the other halves were assigned to the other diet. Statistical analyses were performed with the general linear model procedure utilizing a 2×2 factorial arrangement and a complete randomized design. Cows on CON diets lost less BW from November to January compared with RES cows (-25.9 ± 2.6 and -45.0 ± 2.6 kg, respectively; $P < 0.001$). Protein supplementation increased plasma concentrations of insulin of CON compared with RES cows during treatment ($P < 0.05$). Calf birth weight did not differ between prenatal supplementation of CON and RES

($P = 0.87$). A prenatal $\times$ postnatal effect was detected for BW of calves; prenatal RES and postnatal CON calves (RES-CON; 189.4 ± 4.2 , $P = 0.05$) had greater 205-d adjusted weaning weights compared with prenatal RES and postnatal RES (RES-RES) and prenatal CON and postnatal RES (CON-RES) calves (163.0 ± 4.2 and 177.8 ± 4.2 kg, respectively). There was a prenatal $\times$ postnatal effect on gain of calves from January to weaning ($P = 0.05$); RES-CON gained more than RES-RES and CON-RES calves. Adjusted yearling 365-d BW was least ($P = 0.02$) for RES-RES calves. Prenatal protein supplementation of cows decreased ($P = 0.03$) final BW of calves at harvest (23 mo). Prenatal and postnatal supplementation of cows did not influence carcass characteristics of calves ($P > 0.10$). In conclusion, increasing protein supplementation of fall calving beef cows from November to March, during breeding and early pregnancy, reduced BW loss of cows, decreased the interval from calving to pregnancy, increased plasma concentrations of insulin in December, January, and March, and increased plasma insulin-like growth factor-I in December without alteration in pregnancy rate. Reduced protein supplementation prenatally increased BW of calves at harvest.

Key words: beef calves, early gestation, fetal programming, protein supplementation

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J. Anim. Sci. 2018.96:2629–2639
doi: 10.1093/jas/sky173

¹This research was supported under project OKLA2694 and approved by the director of the Oklahoma Agricultural Experiment Station. Appreciation is expressed to C. Maxwell and C. Haviland at Willard Sparks Beef Research Center, and Klair Hartzold for assistance with this research.

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Received March 2, 2018.

Accepted May 11, 2018.

INTRODUCTION

Adequate body condition score (BCS) at calving is the most important factor that influences the postpartum anestrus interval and reproductive efficiency of a cowherd (Richards et al., 1986; Selk et al., 1988; Morrison et al., 1999). Supplemental protein for grazing cows increases input costs but may be necessary for successful pregnancy rates during times when forage quality and nutritional composition are limited (Wettemann, 1994; Horney et al., 1996; DelCurto et al., 2000). Postnatal calf supplementation of protein and energy can increase weaning weights (Stricker et al., 1979; Faulkner et al., 1994) and calf value (Dickerson, 1970).

Inadequate nutrients for the fetus during gestation may alter postnatal productivity of the offspring (Barker and Osmond, 1986; Barker et al., 1993; Ford and Long, 2012). Early gestational nutrient restriction may not influence birth weight but can have long-term consequences to calf performance (Martin et al., 2007; Long et al., 2009; Long et al., 2010c). Nutrient restriction of the fetus during early gestation decreased muscle fiber diameter and increased adipose development at slaughter (Long et al., 2012), reduced carcass quality (Stalker et al., 2006), and decreased fertility of heifers (Martin et al., 2007) compared with animals that received adequate prenatal nutrients.

Our hypothesis was that inadequate protein supplementation of fall calving cows will influence prenatal and postnatal growth of calves without affecting reproductive efficiency of the cows. The major objectives of the study were to determine the effects of protein supplementation of fall calving cows on body weight (BW), BCS, reproductive performance, prenatal and postnatal calf growth, and plasma concentrations of insulin, glucose, and insulin-like growth factor I (IGF-I) in cows and insulin and IGF-I in calves.

MATERIALS AND METHODS

All experimental procedures described were approved by the Oklahoma State University Animal Care and Use Committee (AG-09-1).

Cow Performance

Fall calving multiparous Angus cows grazing dormant native grass pasture were used to evaluate effects of protein supplementation during breeding and early gestation of the first year and the subsequent lactation the second year. Cows calved in September and October and grazed native tallgrass

prairie at the Range Cow research Center near Stillwater, OK. A total of 189 cows and calves were studied from before breeding of cows until calves were harvested at 23 mo of age.

Cows were stratified at calving by BCS and calving date, and randomly assigned to 1 of the 2 treatments and individually supplemented from mid-November to mid-March for 5 replications (REP) in different years ($n = 29$, REP 1; $n = 33$, REP 2; $n = 43$, REP 3; $n = 45$, REP 4; $n = 39$, REP 5). During lactation (mid-November to mid-March) of the subsequent year, half of the cows on CON and RES treatments were stratified by calving date and BCS, and assigned to CON and the other half were assigned to RES treatment. This resulted in a completely randomized experimental design with a 2×2 factorial arrangement with treatments of CON-prenatal and CON-lactation (CON-CON), RES-prenatal and CON-lactation (RES-CON), CON-prenatal and RES-lactation (CON-RES), and RES-prenatal and RES-lactation (RES-RES). Cows had ad libitum access to prairie grass ($\leq 6\%$ CP). Predominant forage species were little bluestem (*Andropogon scoparius*) and big bluestem (*Andropogon gerardii*). Cows on the restricted (RES) diet received 0.2 kg/d of supplement which consisted of 95% soybean hulls and 5% molasses (as-fed) which resulted in an 8% crude protein supplement. Cows on the control (CON) diet received 1.82 kg/d of supplement which consisted of 81% cottonseed meal, 11% soybean meal, and 8% wheat middlings (as-fed) which resulted in a 38% crude protein supplement. Supplements were fed 4 d/wk and CON cows received 3.2 kg and RES cow received 0.4 kg of supplement each feeding from mid-November to mid-March at 0700.

Cows were exposed to 2 fertile bulls for 60 d commencing December 1. Cows were provided mineral supplement (46.1% salt, 50.0% dicalcium phosphate, 0.4% copper sulfate, 0.5% zinc oxide, and 3.0% mineral oil) ad libitum. Prairie grass hay was provided when forage amounts were inadequate due to snow cover or forage availability. Hay was also provided when ambient temperature was less than 0 °C without precipitation or 4 °C with precipitation.

BWs and BCS (1 = emaciated and 9 = obese; Wagner et al., 1988) were obtained for cows, after 16 h without and feed and water (shrunk), 4 to 19 d before calving in August, each month during November to March, and at weaning in May. Pregnancy rates were determined at weaning via rectal palpation and the interval from calving to

conception was calculated by subtraction of 280 d from calving date the subsequent year.

Calf Growth

Protein supplementation of cows was used to alter prenatal and postnatal nutrient availability to calves. Treatment combinations for calves were CON prenatal and CON postnatal (CON-CON), RES prenatal and CON postnatal (RES-CON), CON prenatal and RES postnatal (CON-RES), and RES prenatal and RES postnatal (RES-RES). Birth weights were recorded within 24 h of birth and bull calves were castrated by applying a rubber band around the scrotum dorsal to the testes. BWs (nonshrunk) of calves were recorded in January, February, March, and at weaning in May. Weaning weights were adjusted to 205 d of age.

After weaning, each year calves were maintained as a single group and grazed native tall grass prairie until entry into the feedlot at approximately 19 mo of age. In REP 1 and 2, only steers were studied after weaning, and in REP 3, 4, and 5, both steers and heifers were studied. Calves in each REP were fed the same 38% CP supplement (1 to 2 kg/d) described for cows when the quality of the forage was inadequate to result in a daily gain of about 0.5 kg. Postweaning growth was determined by BW adjusted to yearling (365 d) weight and average daily gain (ADG) from weaning to approximately 1 yr of age.

Upon entry into the feedlot, calves were implanted as follows: REP 1 steers received Component TE-S (Elanco Animal Health, Greenfield, IN, 24-mg estradiol, 120-mg TBA) on day 0 of 141-d feeding; REP 2 steers received Revalor-S (Merck Animal Health, Madison NJ, 24-mg estradiol, 120-mg TBA) on day 0 of 115-d feeding; REP 3, steers received Component TE-IS (Elanco Animal Health, 16-mg estradiol, 80-mg TBA) on day 0 and Revalor-S on day 80 of 131-d feeding, and REP 3 heifers received Component TE-IH (Elanco Animal Health, 8-mg estradiol, 80-mg TBA) on day 0 and Component TE-H (Elanco Animal Health, 14-mg estradiol and 140-mg TBA) on day 80 of 131-d feeding; REP 4 steers received Component TE-IS on day 0 and Revalor-S on day 80 of 126 d of feeding and heifers received Component TE-IH on day 0 and Component TE-H on day 80 of 126 d of feeding; and REP 5 steers received Revalor-IS (Merck Animal Health, 16-mg estradiol and 80-mg TBA) on day 0 and Revalor-S on day 80 of 138 d of feeding, and heifers received Revalor-IH (Merck Animal Health, 8-mg estradiol,

80-mg TBA) on day 0 and Revalor-H (Merck Animal Health, 14-mg estradiol and 140-mg TBA) on day 80 of 136 d of feeding. Calves were weighed upon entry into the feedlot, every 28 d during finishing, and prior to transport to the abattoir.

Calves received a high concentrate diet, during finishing (Table 1). Calves were fed until it was estimated that adipose deposition was adequate to result in at least 65% choice carcasses with 1.25-cm back fat depth and prior to carcass weights that are penalized for excessive weight. Each year calves were harvested on a single day at a commercial abattoir in Arkansas City, KS, and carcass characteristics were determined by experienced personnel. Hot carcass weights, ribeye area, quality grade, yield grade, back fat thickness, dressing percentage, and marbling scores were obtained in all years except REP 3.

Hormone Analyses

Blood samples were collected immediately after supplement was fed. During REP 3 only, samples from cows were collected in December, January, March, and May, and calves' samples were obtained in December, January, May, and November of the subsequent year. Cow samples were from caudal veins and calves were sampled by jugular venipuncture with Monoject vacuum tubes with 15-mg EDTA (Tyco Healthcare Group, LP; Mansfield, MA). Samples (10 mL) were placed on ice and plasma was removed within 4 h by centrifugation at $1800 \times g$ for 15 min and stored at -20°C . Insulin and IGF-I were quantified in samples from calves and cows, and glucose was quantified in cows. Samples from each day were analyzed in a single assay.

Table 1. Ingredients and composition of the finishing diet

Ingredient	Dry matter basis, %
Dry-rolled corn	47.90
Ground switchgrass hay ¹	7.04
Dried distillers grains	14.75
Wet-corn gluten feed ²	14.76
Liquid supplement ³	10.43
Dry supplement, B-273 ⁴	5.12

¹Assayed to contain 1.6% crude protein and 89.5% NDF.

²Sweet Bran; Cargill, Inc., Minneapolis, MN.

³Synergy 19–14; Westway Feeds, Catoosa, OK.

⁴Formulated to contain (DM basis): 6.92% urea, 30.36% limestone, 1.03% MgO, 0.38% salt, 0.119% copper sulfate, 0.116% MnO, 0.05% selenium premix (0.6% Se), 0.618% ZnSO₄, 0.311% vitamin A (30 IU/mg), 0.085% vitamin E (500 IU/g), 0.317% Rumensin 90, 0.195% Tylan 40, 38.46% ground corn, and 21.04% wheat middlings.

Concentrations of IGF-I were quantified after acid ethanol extraction (16 h at 4 °C) using a double antibody RIA protocol (Echternkamp et al., 1990) with recombinant human IGF-I (R&D Systems, Minneapolis, MN) as the standard. Intra- and inter-assay CV for cow and calf plasma samples average 13% and 13%, respectively. Insulin was quantified by a solid-phase RIA (Bossis et al., 1999; Coat-a-Count; Siemens, Los Angeles, CA) with bovine pancreatic insulin as the standard (Sigma Chemical Co., St. Louis, MO). Intra- and inter-assay CV for cow and calf plasma samples averaged 15% and 22%, respectively.

Concentrations of glucose were quantified with Infinity Glucose Hexokinase Liquid Stable Reagent (Thermo Fisher Scientific Inc., Marietta, OH) in triplicate, at a concentration of 1:150 and plasma was maintained at 4 °C in a water bath prior to addition of reagent until incubation. Immediately following vortexing of samples and reagent, samples were incubated in a water bath at 27 °C for 10 min; after incubation samples were placed into 4 °C water until quantification. Intra- and inter-assay CV's were 7% and 5%, respectively.

Statistical Analysis

All data were analyzed as a completely randomized design with a 2 × 2 factorial arrangement. The general linear model procedure of SAS (SAS Institute Inc., Cary, NC) was used to analyze IGF-I, insulin, glucose, postpartum anestrus interval, pregnancy rate, calving date, BW and BCS for cows, and IGF-I, insulin, BW, ADG, and carcass characteristics for calves. The model for cow traits included prenatal treatment, lactational treatment, and the interaction. When applicable, date of

calving and replication were included in the model as a covariate but were removed if not significant ($P > 0.10$). The model for calf traits included prenatal treatment, lactational treatment, replication, sex, and all interactions. When appropriate, age was included into the model as a covariate but was removed if not significant ($P > 0.10$). When effects were significant, least square means were compared using least square difference (pdiff option of SAS).

RESULTS

Protein supplementation treatment the previous year, and the interaction of treatment the previous year with protein supplementation during breeding and early pregnancy, did not influence BW or BCS of cows during breeding and early gestation. Protein supplementation during breeding and early gestation did not influence ($P > 0.10$) cow BW in November, January, February, March, or August or the amount of BW lost from January to May (Table 2). Control cows lost less BW ($P < 0.001$; Table 2) from November to January, compared with RES cows. In May, BW for CON cows was greater ($P = 0.05$) compared with RES cows. Protein supplementation did not influence ($P > 0.13$) cow BCS in November, January, February, March, May, or August, or change in BCS from November to January, or change in BCS from January to May (Table 3). However, postpartum interval to pregnancy was 7 d greater ($P \leq 0.01$) in RES cows compared with CON cows (Table 3). Calving date ($P = 0.52$) and pregnancy rate ($P = 0.65$) were not influenced by protein supplementation.

Protein supplementation treatment the previous year and the interaction of treatment the previous year with protein supplementation during

Table 2. Influence of protein supplementation during breeding and early gestation (mid-November to mid-March) on body weight (BW) of fall calving cows during years 1 to 5

BW, kg	Treatment ¹		SEM	P value
	CON	RES		
Cows, No.	91	98	—	—
BW November, kg	622.8	630.5	6.3	0.39
BW change, November to January	−25.9	−45.0	2.6	<0.001
BW January, kg	598.8	586.2	6.3	0.16
BW February, kg	576.6	566.4	6.3	0.25
BW March, kg	549.8	541.0	7.1	0.38
BW change, January to May	−46.8	−48.8	2.7	0.59
BW May, kg	553.3	537.2	5.7	0.05
BW August, kg	659.9	652.8	5.9	0.40

¹Control (CON) cows were given 1.82 kg/d of a 38% crude protein supplement which consisted of 81% cottonseed meal, 11% soybean meal, and 8% wheat middlings (as-fed) and restricted (RES) cows were given 0.2 kg/d of a 8% crude protein supplement which consisted of 95% soybean hulls and 5% molasses (as-fed).

breeding and early gestation did not influence ($P > 0.10$) concentrations of insulin, glucose, and IGF-I in plasma. Concentrations of insulin in plasma of CON cows were greater ($P < 0.05$) in December, January, and March compared with RES cows. Insulin in plasma of cows at weaning (May) was not influenced by treatment ($P = 0.35$; Figure 1). Concentrations of glucose in plasma were not influenced by protein supplementation at any sampling time ($P > 0.22$; Figure 2). Concentrations of IGF-I (Figure 3) were greater in CON cows compared with RES cows in December ($P = 0.04$) but

were not influenced by supplementation in January, March, or May.

Birth weight of calves was not influenced by prenatal protein supplementation of cows ($P = 0.87$; Table 4). There was a prenatal $\times$ postnatal treatment effect ($P = 0.03$) on the BW of calves in January; RES-RES calves weighed less than calves from all other treatments (Table 4). ADG from birth to January was greater ($P < 0.01$) for calves suckling CON cows compared with RES cows and there was a tendency ($P = 0.08$) for a prenatal effect associated with RES-RES having the least ADG. Adjusted

Table 3. Influence of protein supplementation during breeding and early gestation (mid-November to mid-March), on body condition score (BCS) of fall calving cows during years 1 to 5

BCS ¹	Treatment ²		SEM	P-value
	CON	RES		
No. of cows, No.	91	98	—	—
November BCS	4.78	4.74	0.06	0.61
BCS change November to January	-0.48	-0.50	0.04	0.69
BCS January	4.36	4.33	0.06	0.73
BCS February	4.13	4.04	0.06	0.26
BCS March	3.93	3.91	0.06	0.76
BCS change January to May	-0.31	-0.37	0.05	0.42
BCS May	4.05	3.96	0.06	0.25
BCS August	5.25	5.08	0.08	0.13
Postpartum interval to pregnancy, d ³	87	94	1.90	0.01
Pregnancy rate, %	91.2	88.7	3.80	0.65
Calving date ⁴ , Julian	271	269	1.50	0.52

¹BCS: 1 = emaciated; 9 = obese (Wagner et al., 1988).

²Control (CON) cows were given 1.82 kg/d of a 38% crude protein supplement which consisted of 81% cottonseed meal, 11% soybean meal, and 8% wheat middlings (as-fed) and restricted (RES) cows were given 0.2 kg/d of a 8% crude protein supplement which consisted of 95% soybean hulls and 5% molasses (as-fed).

³Calculated by using a gestation length of 280 d to determine days of conception and the previous calving date to determine interval between calving and conception.

Figure 1. Least squares means of concentrations of insulin in plasma of fall calving cows submitted to restricted (0.2 kg/d of an 8% crude protein [CP] supplement; $n = 20$) or control (1.82 kg/d of a 38% CP supplement; $n = 19$) protein supplementation during mid-November to mid-March during year 3. ^{a,b}Within month means without a common letter differ ($P < 0.05$). Standard errors were 0.1, 0.1, 0.1, and 0.1 for December, January, March and May, respectively ($n = 43$).

Figure 2. Least squares means of glucose in plasma of fall calving cows submitted to restricted (0.2 kg/d of a 8% crude protein [CP] supplement; $n = 20$) or control (1.82 kg/d of a 38% CP supplement; $n = 19$) protein supplementation during mid-November to mid-March during year 3. Standard errors were 1, 2, 2, and 3 for December, January, March and May, respectively ($n = 43$).

Figure 3. Least squares means of insulin-like growth factor-I (IGF-I) in plasma of fall calving cows submitted to restricted (0.2 kg/d of an 8% crude protein [CP] supplement; $n = 20$) or control (1.82 kg/d of a 38% CP supplement; $n = 19$) protein supplementation during mid-November to mid-March during year 3. ^{a,b}Within month means without a common letter differ ($P < 0.05$). Standard errors were 3.0, 1.3, 0.9, and 0.7 for December, January, March and May, respectively ($n = 43$).

Table 4. Effects of prenatal¹ and postnatal² maternal protein supplementation on preweaning growth of fall born calves during years 1 to 5³

Trait	Treatment				SEM	P value		
	CON-CON ⁴	CON-RES ⁵	RES-CON	RES-RES		Prenatal	Postnatal	Prenatal×Postnatal
Birth Weight, kg	37.7		37.6		0.5	0.87	—	—
BW January, kg	127.8 ^b	125.1 ^b	129.1 ^b	115.0 ^a	2.7	0.10	< 0.01	0.03
ADG, kg/d (Birth to Jan)	0.85 ^b	0.80 ^b	0.84 ^b	0.73 ^a	0.02	0.08	< 0.01	0.12
Weaning Weight ⁶ , kg	183.8 ^{bc}	177.8 ^b	189.4 ^c	163.0 ^a	4.2	0.28	< 0.01	0.02
ADG ⁷ , kg/d (January to Weaning)	0.69 ^{bc}	0.65 ^b	0.72 ^c	0.60 ^a	0.02	0.43	< 0.01	0.03

^{a-c}Means within row without a common letter differ ($P < 0.05$).

¹Prenatal treatment during conception and the first trimester of gestation.

²Postnatal treatment during early to mid-lactation.

³Carcass characteristics were not obtained in year 3.

⁴CON-CON = prenatal control diet and postnatal control diet.

⁵CON-RES = prenatal control diet and postnatal restricted.

⁶Weaning weight was adjusted to 205 d of age.

⁷BW used for ADG calculation was BW taken at weaning.

(205 d) weaning weight was greater ($P = 0.05$) for RES-CON calves compared with CON-RES and RES-RES calves. RES-RES calves had weaning weights that were less ($P = 0.05$) than all other treatments. CON-CON and RES-CON calves had greater ($P = 0.05$) ADG from January until weaning compared with RES-RES calves (Table 4), and RES-CON calves had greater weight gain compared with CON-RES and RES-RES calves.

Prenatal $\times$ postnatal and the main effects of protein supplementation treatment of cows during prenatal growth did not influence ($P > 0.10$) insulin and IGF-I in plasma of calves before weaning. Concentrations of insulin in plasma of calves were not influenced ($P > 0.43$) by postnatal treatment (Figure 4). Concentrations of IGF-I were greater in December ($P = 0.03$) and tended to be greater in November ($P = 0.07$) in the postnatal CON calves (Figure 5) compared with postnatal RES calves.

Prenatal and postnatal protein supplementation did not affect gain of calves from weaning to 1 yr of age ($P \geq 0.26$; Table 5). Adjusted yearling (365 d) weights tended ($P = 0.10$) to be influenced by prenatal $\times$ postnatal protein supplementation and RES-RES calves weighed less ($P = 0.05$) compared with the other treatments (Table 5). There was not a prenatal $\times$ postnatal protein supplementation interaction ($P = 0.11$) on final BW. Daily gain in the feedlot was greater ($P < 0.02$) for prenatally RES calves, and final BW was greater ($P = 0.03$) for calves from prenatal RES cows (648.0 ± 7.7 kg) compared with calves from prenatal CON cows (631.2 ± 7.7 kg; Table 5). Prenatal and postnatal protein supplementation did not affect hot carcass weight ($P > 0.11$; Table 5). Dressing percentage, back fat thickness, yield grade, ribeye area, and marbling were not influenced ($P > 0.20$) by prenatal treatment, postnatal treatment, or the

Figure 4. Least squares means of insulin in plasma of calves suckling fall calving cows submitted to restricted (0.2 kg/d of an 8% crude protein [CP] supplement; $n = 20$) or control (1.82 kg/d of a 38% CP supplement; $n = 19$) protein supplementation during mid-November to mid-March of year 3. ^{a,b}Within month means without a common letter differ ($P < 0.05$). Standard errors were 0.2, 0.1, 0.1, and 0.1 before weaning in December, January, May, and in November at 13 mo of age, respectively.

Figure 5. Least squares means of insulin-like growth factor-I (IGF-I) in plasma of calves suckling fall calving cows submitted to restricted (0.2 kg/d of an 8% crude protein [CP] supplement; $n = 20$) or control (1.82 kg/d of a 38% CP supplement; $n = 19$) protein supplementation during mid-November to mid-March during year 3. ^{a,b}Within month means without a common letter differ ($P < 0.05$). Standard errors were 6.4, 2.9, 3.9, and 2.3 before weaning in December, January, May, and in November at 13 mo of age, respectively.

Table 5. Effects of prenatal¹ and postnatal² maternal protein supplementation on postweaning growth and carcass characteristics of calves fall born calves

Trait	Treatment				SEM	P value		
	CON-CON ³	CON-RES ⁴	RES-CON	RES-RES		Prenatal	Postnatal	Prenatal×Postnatal
Yearling weight ⁵ , kg	280.1 ^b	273.5 ^b	276.7 ^b	255.5 ^a	5.7	0.02	< 0.01	0.10
ADG, kg/d (weaning to 1 yr of age)	0.48	0.47	0.45	0.48	0.04	0.32	0.39	0.26
Final body weight, kg	629.0 ^a	633.5 ^a	658.1 ^b	637.8 ^{ab}	7.7	0.03	0.31	0.11
ADG, kg/d (Feedlot)	1.79 ^a	1.78 ^a	1.89 ^b	1.82 ^{ab}	0.03	0.02	0.20	0.39
Hot carcass weight, kg	377.7	377.9	392.9	380.4	5.5	0.11	0.27	0.26
DRESSing percentage, %	63.6	64.0	63.6	63.7	0.4	0.55	0.46	0.69
Ribeye area, cm ²	87.0	88.6	87.9	86.1	1.4	0.59	0.95	0.23
Yield grade	3.2	3.0	3.3	3.3	0.11	0.20	0.43	0.37
Back fat, cm	1.5	1.4	1.6	1.5	0.09	0.22	0.29	0.86
Marbling score ⁶	364	369	376	353	16.0	0.91	0.59	0.41

^{a-c}Means within row without a common letter differ ($P < 0.05$).

¹Prenatal treatment during conception and the first trimester of gestation.

²Postnatal treatment during early to mid-lactation.

³CON-CON = prenatal control diet and postnatal control diet.

⁴CON-RES = prenatal control diet and postnatal low protein diet.

⁵Yearling weight is adjusted to 365 d of age.

⁶Small = 300–399; Slight = 200–299.

interaction of prenatal × postnatal protein supplementation (Table 5).

DISCUSSION

Supplementing protein to cows grazing dormant, low-quality forages will increase dry matter intake and available energy (Fleck et al., 1988; Ovenell et al., 1991). Reduced availability of nutrients in utero may program the fetus for survival with limited nutrients in the postnatal environment, which has been termed a “thrifty phenotype” (Barker et al., 1993). Animals that are prenatally programmed to survive with limited postnatal nutrients may have increased efficiency when adequate nutrients are available after birth (Larson et al., 2009). However, reduced postnatal nutrient supply after prenatal nutrient restriction in the current experiment decreased animal growth and agrees with studies in humans (Barker et al., 1993).

Fall calving cows grazing dormant pastures are usually exposed to inadequate nutrients during early gestation if supplemental nutrients are not fed. Supplementation of lactating beef cows can influence reproductive traits (Wiltbank et al., 1962; Dunn et al., 1969; Rakestraw et al., 1986); however, milk production has a greater priority for nutrients over BW gain and endocrine functions associated with reproduction (Bauman and Currie, 1980). BCS at calving is the best indicator of reproductive performance of beef cows (Richards et al., 1986; Selk

et al., 1988; DeRouen et al., 1994). In the current experiment, BCS and BW of cows at calving were not influenced by protein supplementation the previous winter because good quality summer forages were available and cows regained BW that was lost the previous winter. The interval from parturition to pregnancy was 7 d longer in cows on RES during breeding, and overall pregnancy rate was not influenced by treatments because cows in this study were maintained with the minimal BCS that would allow onset of estrus and pregnancy to occur within a 60 d breeding season (Rakestraw et al., 1986).

The lack of effect of prenatal protein supplementation on birth weight of calves was most likely due to the stage of gestation that protein and energy were limited. The absence of an effect of nutrient deficiency during early gestation on calf birth weight has also been observed by Martin et al. (2007) and Long et al. (2009). Even without an influence of prenatal treatment on birth weight, postnatal growth of calves was influenced by prenatal nutrition. Calves that were restricted prenatally and postnatally had less BW at weaning compared with all other treatments. During the first few months after birth, the major source of nutrients for calves is milk and it is most likely that less milk was available for calves that suckling RES cows. Reynolds et al. (1978) found that milk yield of cows was highly correlated with ADG of calves. The interaction between prenatal and postnatal treatments on BW and ADG at weaning was associated

with the slightly greater weights of RES-CON compared with CON-CON calves and reduced weights of RES-RES compared with CON-RES calves. The RES-CON calves may have been predisposed to efficiently utilize nutrients due to the prenatal restriction; thus, with adequate nutrients, these calves gained more than their contemporaries. These data may then provide more evidence in support of the “thrifty phenotype” theory.

The supplementation program used in the present experiment resulted in a good model to determine whether prenatal nutrient restriction will impose long-term effects on calves. Both insulin and IGF-I are indicative of nutritional status (Rutter et al., 1989; Cicciooli et al., 2003; Lents et al., 2005). Increased concentrations of insulin and IGF-I in plasma indicate that protein supplementation increased available nutrients. Similarly, Marston et al. (1995) found that protein supplementation increased insulin in lactating cows consuming dry forage. These differences in maternal environment indicate that CON cows can provide greater concentrations of nutrients to the developing fetus, or suckling calf, due to repartitioning of nutrients toward fetal growth and milk production (Bauman and Currie, 1980). However, concentrations of glucose in plasma were not influenced by treatment. The lack of treatment effect on plasma concentrations of glucose, even with greater concentrations of insulin in CON cows, could be caused by one or more of 4 possible mechanisms: 1) increased insulin caused glucose entry into tissues; 2) excess glucose was utilized by the developing fetus and placenta; 3) excess glucose was used for lactose production in the mammary gland; and/or 4) increased dry matter intake from protein supplementation increased the amount of acetate produced which is an inefficient precursor for gluconeogenesis. The fourth possibility is not probable since concentrations of insulin in plasma were increased. Overall, these data indicate that our model created cows of differing nutritional status which influenced growth of their offspring.

Reduced BW and altered body composition occurred in humans (Ravelli et al., 1999), sheep (Ford et al., 2007; Zhu et al., 2007), and cattle (Zhu et al., 2006; Long et al., 2009; Long et al., 2010c) due to prenatal nutrient restriction. Concentrations of insulin in plasma of calves were not influenced by treatments indicating normal development of the pancreas, which agrees with Stalker et al. (2006) and Long et al. (2012). Adjusted yearling weight was influenced by prenatal $\times$ postnatal supplementation of cows, and CON-CON, RES-CON, and CON-RES calves were heavier compared with

RES-RES calves. Prenatal protein supplementation influenced final BW; RES-CON calves were heavier than CON-CON calves. Concentrate diets fed in the finishing stage of beef production increase concentrations of propionate in plasma, which could exacerbate insulin insensitivity (Ford et al., 2007; Long et al., 2010a). Severe restriction of nutrients of dams altered concentrations of glucose and insulin in plasma of adult offspring cattle (Long et al., 2010b) and sheep (Gardner et al., 2005; Ford et al., 2007). Inadequate prenatal nutrition of sheep may cause epigenetic changes postnatally resulting in a thrifty phenotype (Ford and Long, 2011). Dietary factors during prenatal development of cattle can alter postnatal expression of imprinted genes which may alter muscle growth (Wang et al., 2015). Nutrient restriction of Angus cows during early gestation increased concentrations of DNA in muscle of calves at an empty BW of 504 kg (Long et al., 2010c). Collectively, these studies indicate that prenatal protein supplementation can alter utilization of nutrient dense diets throughout the lifespan of cattle and sheep. However, more research needs to be conducted to completely elucidate the mechanisms associated with these changes in BW.

The only carcass characteristic influenced by maternal protein supplementation was a minimal increase on hot carcass weight in prenatal RES calves. Prenatal nutrient restriction decreases muscle mass in sheep (Zhu et al., 2006) and increased the area of muscle fibers in cattle (Long et al., 2010c). The robustness of these data over multiple years may explain the muted effects seen on muscle characteristics, ribeye area, dressing percentage, and hot carcass weight. Nutrient restriction also increased adiposity of carcasses by 18 wk of age (Ford et al., 2007) in sheep; however, marbling, back fat, and yield grade were not influenced by maternal protein supplementation.

In summary, protein supplementation of fall calving cows during breeding and early gestation had little or minimal influence on reproductive efficiency of cows or birth weight of calves. However, circulating concentrations of IGF-I and insulin were transiently increased by protein supplementation. This is indicative that our model created different nutritional environments for both suckling calves and developing embryos/fetuses. The restricted embryos/fetuses may have been programmed to respond to an external environment that was nutrient limited, creating a “thrifty phenotype” calf. This phenotype may explain the increased ADG and BW of prenatally RES calves when postnatal nutrition was adequate and the increased final BW

of calves that were prenatally RES. When protein intake is inadequate for fall calving cows during early gestation and although maternal BW, BCS, and reproductive function many appear adequate, postnatal growth of calves may be altered.

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