

Prepartum dietary energy source fed to beef cows: II. Effects on progeny postnatal growth, glucose tolerance, and carcass composition¹

A. E. Radunz,^{*2} F. L. Fluharty,^{*3} A. E. Relling,[†] T. L. Felix,[‡] L. M. Shoup,[‡] H. N. Zerby,^{*} and S. C. Loerch^{*3}

^{*}Department of Animal Sciences, The Ohio State University, OARDC, 1680 Madison Ave., Wooster 44691; [†]National Research Council (CONICET, CCT La Plata), Departamento de Producción Animal, Facultad de Ciencias Veterinarias. Universidad Nacional de La Plata, Buenos Aires, Argentina; and [‡]Dept. of Anim. Sci., Univ. of Illinois, Urbana-Champaign, 1207 West Gregory Drive, Urbana 61801.

ABSTRACT: Mature Angus-cross beef cows ($n = 228$) were used to evaluate effects of prepartum dietary energy source on postnatal growth and carcass composition of progeny in a 2-yr study. Starting at approximately 160 d of gestation, cows were fed diets consisting of 1 of 3 primary energy sources: grass hay (HY), corn (CN), or dried corn distillers grains with solubles (DG). The CN and DG diets were limit-fed to achieve similar energy intakes as cows fed HY. Following parturition, cows were fed a common diet and managed as a single group. Calves were weaned at an average of 185 ± 6 d of age and backgrounded for 28 d. A subset of progeny ($n = 134$) was individually fed a common finishing diet until slaughter, when each calf reached 1.2 ± 0.05 cm of backfat. A glucose tolerance test (GTT) was conducted in year 2 on 4 calves/treatment after 41 and 111 d on the finishing diet (DOF). Calf birth weights were greater ($P = 0.002$) in calves from cows fed CN and DG than calves from cows fed HY, and weaning BW ($P = 0.08$) was less for calves from cows fed HY vs. CN. Receiving BW, final BW, and HCW did not differ ($P \geq 0.16$) among treatments.

No difference ($P \geq 0.28$) in ADG, morbidity, and mortality from birth to slaughter was observed among treatments. In response to a GTT, increased DOF resulted in greater ($P \leq 0.005$) fasting insulin, faster glucose disappearance rate, and greater insulin:glucose area under the curve ratio. Glucose disappearance rate was greater ($P = 0.01$) in calves from cows fed CN than in calves from cows fed HY or DG. A greater initial insulin response ($P = 0.005$) was observed in calves from cows fed CN or DG than in calves from cows fed HY. Carcass traits used to measure yield grade did not differ ($P \geq 0.19$) among treatments. Calves from dams fed CN had the lowest marbling score ($P = 0.03$) and intramuscular fat content ($P = 0.07$). These results indicate that prepartum maternal dietary energy source can alter fetal adipose tissue development and insulin sensitivity resulting in long-term effects on progeny's intramuscular fat deposition. Moreover, present findings suggest that increasing the number of days on a corn-based finishing diet increases insulin resistance in beef cattle.

Key words: beef cattle, carcass composition, fetal programming, glucose tolerance, maternal nutrition

© 2012 American Society of Animal Science. All rights reserved.

J. Anim. Sci. 2012.90:4962–4974

doi:10.2527/jas2012-5098

INTRODUCTION

Maternal nutrition during gestation plays a critical role in fetal growth and development. A disturbance

in fetal development can have long-term implications and could lead to “programming” for increased predisposition to insulin sensitivity during later postnatal life and an altered body composition (Godfrey and Barker, 2001). Overall increased adiposity or adipogenesis, especially greater amounts of intramuscular triglyceride and visceral fat, has been associated with decreased muscle cell insulin sensitivity in humans (Lewis et al., 2002). In addition, hyperglycemia, altered insulin response, and increased adiposity have been reported in progeny from ewes that experienced nutrient restriction during gestation (Gardner et al.,

¹Salaries and research support provided by state and federal funds appropriated to the Ohio Agric. Res. and Dev. Center, The Ohio State Univ.

²Current address: Univ. of Wisconsin-River Falls, Dept. of Animal and Food Science, River Falls, WI 54022.

³Corresponding author: loerch.1@osu.edu.

Received January 7, 2012

Accepted August 7, 2012

2005; Ford et al., 2007); however, limited information has been published regarding maternal nutrition and its effects on growth, insulin sensitivity, and carcass composition in cattle.

Results of previous studies investigating starch- vs. fiber-based diets fed for isocaloric intakes in late gestation have indicated greater calf birth weights in calves from dams fed a starch-based diet (Loerch, 1996; Schoonmaker et al., 2003; Radunz et al., 2010), suggesting that energy source during gestation can affect fetal growth, but long-term effects on progeny were not reported. Long-term effects on growth rate, amount of skeletal muscle tissue, and fat distribution could have far reaching implications in the beef industry, but only limited information exists on the effects of energy source in late-gestation beef cattle diets on postnatal growth and carcass composition. Therefore, our objective was to investigate the effects of maternal prepartum dietary energy source on progeny health, growth, glucose tolerance, and carcass composition of beef cattle.

MATERIALS AND METHODS

The Agricultural Animal Care and Use Committee of The Ohio State University approved the procedures used in this experiment.

Animals, Experimental Design, and Treatments

Mature multiparous Angus crossbred cows ($n = 144$ in yr 1 and $n = 84$ in yr 2) were used in a randomized complete block design (blocked by location and year) experiment to determine the effects of dietary energy source on progeny postnatal growth, glucose tolerance, and carcass composition. For yr 1, cows were fed at 3 branch locations of the Ohio Agricultural Research and Development Center: The Ohio State University campus, Columbus (OSU), the North Appalachian Experimental Watershed, Coshoc-ton (NAEW), and the Eastern Agricultural Research Station, Belle Valley (EARS); whereas for yr 2, cows were fed only at the EARS location.

Cows were synchronized for timed AI to a single sire in yr 1 and multiple sires ($n = 5$) in yr 2. Pregnancy diagnosis was conducted by transrectal ultrasonography (5-MHz linear array transducer, 500 V; Aloka, Wallingford, CT) approximately 30 d after timed AI and was confirmed by transrectal ultrasonography or hand palpation approximately 90 d after timed AI. Only cows confirmed by ultrasonography for first-service conception by timed AI were used in the trial. In yr 1, the cows were blocked by location ($n = 42$ at OSU, $n = 51$ at NAEW, and $n = 54$ at EARS) and within location were stratified by BW (606 ± 4.4 kg), BCS (5.2 ± 0.6), and cow age (4.9 ± 0.5 yr) and were assigned to 1 of 3 pens at OSU,

1 of 3 pens at NAEW, and 1 of 9 pens at EARS. In yr 2, cows were blocked by BW (620 ± 12 kg) and within block cows were stratified by sire ($n = 5$), BCS (5.2 ± 0.8), and cow age (4.1 ± 2.0 yr) and were assigned to 1 of 12 pens at EARS. Dietary treatments were assigned randomly to pens within a location. Cows were removed from the experiment for reproductive failure, failure to calve before 300 d after first AI service, twin progeny, and death. In yr 1, 3 cows were removed from hay (HY), 9 cows from corn (CN), and 8 cows from dried corn distillers grains (DG). In yr 2, 5 cows were removed from HY, 3 from CN, and 4 from DG. Reasons for removal from the trial were not associated with gestation dietary treatments ($P \geq 0.32$).

Cows were adapted to diets starting at 167 ± 9 d of gestation in yr 1 and 155 ± 8 d of gestation in yr 2. Dietary treatments were 1 of 3 dietary energy sources: 1) ad libitum grass HY (high-fiber concentration), 2) limited CN (high-starch concentration), and 3) limit-fed DG (high fiber, protein, and fat concentrations). Diets were initially formulated to meet or exceed cow nutrient requirements during late gestation ($11.08 \text{ NE}_m \text{ Mcal/d}$ and 840 g CP/d ; NRC, 2000), and intake of CN and DG diets were limited so that daily energy intakes were similar to those of cows fed HY (NRC, 2000). Late gestation diets, nutrient composition, and intake for yr 2 are shown in Tables 1 and 2. Data for yr 1 were reported by Radunz et al. (2010). Nutrient composition was similar between years, and intake varied because it was adjusted to each pen within each year so that intake was a similar percentage of cow BW. Cows fed HY were allowed ad libitum access to orchardgrass hay in round bale feeders and were provided with ad libitum access to a salt and mineral mix [29.5% trace mineralized salt, 25% dicalcium phosphate, 25% magnesium oxide, 10% limestone, 10% ground shelled corn, 0.5% ethylene diaminedihydroiodide, and 50 mg/kg Se (DM basis)]. Limit-fed CN and DG diets were hand fed in fence line bunks once daily and provided 4.6 kg of whole-shelled corn or 3.9 kg DG plus 2.2 or 2.0 kg of square-bale grass hay (respectively) and 1.0 or 0.9 kg of protein–mineral–vitamin supplement (respectively) per cow on a DM basis in yr 2 (Table 2). Intake of CP and fat was not balanced among treatments because DG had an increased concentration of CP and fat relative to CN and grass HY. The addition of protein to CN and HY diets to make them equal to DG diet would not be economically practical as a winter-feeding strategy for beef cattle.

The diet intakes were adjusted when needed every 21 d during the trial to maintain similar BW gain (based on the 2-wk BW after adaptation to diets and changes in gut fill were equilibrated) and BCS for cows fed CN or DG compared to cows fed HY. Intake adjustments also were made to compensate for energy needs in cold environmental temperatures based on BW gains during

Table 1. Late gestation diets and nutrient composition for cows in yr 2

Item	Treatment ¹		
	HY ²	CN	DG
Ingredient	----- % DM basis -----		
Grass hay	100	27.5	30.5
Whole shelled corn	–	60.0	–
DG	–	–	66.5
Ground corn	–	3.33	–
Soybean meal	–	5.83	–
Limestone	–	0.97	1.53
Dicalcium phosphate	–	0.54	–
Urea	–	0.52	–
Trace mineral salt ³	–	0.40	0.44
Animal and vegetable fat	–	0.34	0.38
Potassium chloride	–	0.26	0.29
Magnesium oxide	–	0.16	0.18
Mg and K sulfate ⁴	–	0.07	0.08
Selenium, 201 mg/g	–	0.04	0.04
Vitamin A, 30,000 IU/g	–	0.01	0.02
Vitamin D, 3,000 IU/g	–	0.01	0.02
Monensin ⁵	–	0.01	0.01
Analyzed nutrient content, %			
CP	7.73	9.70	22.44
NDF	67.4	32.8	38.8
ADF	44.5	15.6	26.6
Ether extract	2.99	4.37	6.44
Ca	0.47	0.61	0.81
P	0.19	0.26	0.57
S	0.17	0.17	0.28

¹HY = hay; CN = corn (limit-fed); DG = dried corn distillers grains with solubles (limit fed).

²Cows were provided ad libitum access to a trace-mineral salt mix [29.5% trace mineralized salt, 25% dicalcium phosphate, 25% magnesium oxide, 10% limestone, 10% ground corn, 0.5% ethylene diaminedihydroiodide, and 50 mg/kg selenium (DM basis)].

³Contained 98% NaCl, 0.35% Zn, 0.28% Mn, 0.175% Fe, 0.035% Cu, 0.007% I, and 0.007% Co.

⁴Contained 22% S, 18% K, and 11% Mg.

⁵Provided 28 mg of monensin/kg of dietary DM (Elanco, Greenfield, IN).

gestation. Cows were removed from diets 1 wk before expected calving date, fed a common diet of grass hay until parturition, and then managed on pasture as a single group within location until weaning. Additional information regarding diet composition, cow management, and cow performance is reported by Radunz et al. (2010).

Progeny Management

Treatments were applied only to the dams during late gestation, and no further treatments were applied to progeny. Data included records of 126 progeny (65 males and 61 females) in yr 1 and 73 progeny (28 males and 45 females) in yr 2 for preweaning measures. Progeny for yr 1 included 25 females and 21 males from cows fed HY, 18 females and 20 males from cows fed CN, and

Table 2. Cow nutrient intake during gestation in yr 2

Item	Treatment ¹		
	HY	CN	DG
Pens (cows)	4 (28)	4 (28)	4 (28)
DMI, kg/d	12.8	7.8	6.8
Hay	12.8	2.2	2.0
Corn	–	4.6	–
DG	–	–	3.9
Supplement, kg/d	–	1.0	0.9
NE _m intake, Mcal/d ²	14.58	14.70	13.47
CP intake, g/d	989	1,110	1,621
Crude fat intake, g/d	244	270	455

¹HY = hay; CN = corn (limit-fed); DG = dried corn distillers grains with solubles (limit-fed).

²Calculated from NRC (2000) except for DG. The DG was assumed to have 110% energy value of corn (Stock et al., 2000).

18 females and 24 males from cows fed DG. Progeny for yr 2 included 17 females and 6 males from cows fed HY, 16 females and 9 males from cows fed CN, and 12 females and 13 males from cows fed DG. Calves were weighed 24 to 72 h after parturition. At this time, progeny from 2 locations (EARS and OSU) also were measured for LM area between the 12th and 13th rib (yr 1) by ultrasonography, and a jugular blood sample was collected for IgG analysis (yr 1 and 2).

In yr 2, progeny at 93 d of age were separated from cows and withheld from feed and water for 12-h during a weigh-suckle-weigh procedure (Radunz et al., 2010). Before nursing following the 12-h separation, a jugular blood sample was collected to measure fasting insulin and glucose concentrations, and BW was measured. After calves had finished nursing, they were penned separately from dams without feed and water for 2 h, and then another jugular blood sample was collected from each calf to measure fed insulin and glucose concentrations. In yr 1, a weigh-suckle-weigh procedure (Radunz et al., 2010) was conducted at 100 d of age, and BW was measured before and after nursing on all progeny.

At approximately 60 d of age, all male progeny were castrated. Fourteen days before weaning, calves received vaccinations for infectious bovine rhinotracheitis, parainfluenza-3, *Haemophilus somnus*, *Pasteurella*, and *Clostridia* (Quadraplex, Somnugen 2P, and Dybelon, respectively; Bioceutic, St. Joseph, MO) and were treated for parasites with Ivomec Pour-On (Merial, Duluth, GA). Calves were revaccinated at weaning (184 ± 7 d of age in yr 1 and 186 ± 5 d of age in yr 2) and then backgrounded for 28 d on stockpiled grass pasture (primarily fescue) at each location. During the 28-d backgrounding period, calves were fed 2.7 kg supplement·animal⁻¹·d⁻¹ (Table 3).

In yr 1, 63 steer progeny and 18 heifers representing 7 steers and 2 heifers/treatment at each location, and in yr 2, 27 steer progeny and 27 heifer progeny were selected

Table 3. Progeny backgrounding supplement and finishing diet composition

Item	Postweaning supplement ¹	Finishing diet ²
Ingredient	----- % DM basis -----	
Cracked corn	–	45.0
DG ³	–	25.0
Corn silage	–	15.0
Ground corn	53.8	11.1
Soyhulls	22.9	–
Soybean meal	18.5	–
Limestone	2.08	2.77
Trace mineral salt ⁴	1.51	0.46
Animal and vegetable fat	–	0.50
Calcium sulfate	0.25	–
Selenium, 201 mg/g	0.73	0.05
Vitamin A, 30,000 IU/g	0.04	0.01
Vitamin D, 3,000 IU/g	0.04	0.01
Vitamin E, 44 IU/g	–	0.03
Monensin ⁵	0.05	0.02
Tylosin ⁶	–	0.05
Nutrient composition,% ⁷		
CP	17.2	13.0
Ca	0.89	0.94
P	0.36	0.58

¹Postweaning supplement was fed to progeny for 28 d after weaning. Calves were weaned at 184 ± 7 d of age in yr 1 and 186 ± 5 d of age in yr 2.

²Progeny were transported to the feedlot after the 18 d backgrounding period and were transitioned to the finishing diet.

³DG = corn dried distillers grains.

⁴Contained 98% NaCl, 0.35% Zn, 0.28% Mn, 0.175% Fe, 0.035% Cu, 0.007% I, and 0.007% Co (DM basis).

⁵Provided 28 mg of monensin/kg of dietary DM (Elanco, Greenfield, IN).

⁶Provided 10 mg of tylosin/kg of dietary DM (Elanco, Greenfield, IN).

⁷Calculated using NRC (2000) values.

randomly within treatment at weaning, backgrounded at respective locations, and transported to The Ohio Agricultural Research and Development Center Beef Unit, Wooster. Cattle were assigned randomly to individual pens for individual feeding and then placed on a finishing diet (Table 3). Initial feedlot receiving BW was determined by 2 consecutive-day weights taken on calf arrival at the feedlot. Calves were adapted over a 28-d period to the finishing diet, which included 45% cracked corn, 25% DG, 15% supplement, and 15% corn silage (DM basis). Feed intake was measured daily, and cattle were weighed every 28 d during the finishing period. On d 14 after arrival, steer calves were implanted with 20 mg of estradiol benzoate and 200 mg of progesterone (Synovex S; Ft. Dodge Animal Health, Fort Dodge, IA), and heifers calves were implanted with 200 mg testosterone propionate and 20 mg estradiol benzoate (Synovex H; Ft. Dodge Animal Health). Calves were reimplanted 98 d later with the same implants used on d 14 after arrival.

Glucose Tolerance Test

In yr 2, 12 progeny were selected randomly (2 males and 2 females/treatment) to conduct a glucose tolerance test (GTT) on d 41 and d 111 after feedlot arrival. Calves were removed from feed 24 h before the GTT and 4 h later, catheters were inserted in the jugular vein of each calf using aseptic procedures as described previously (Huntington et al., 1989). Calves were returned to their individual pens to recover overnight. Fifteen minutes before glucose infusion, calves were weighed to determine bolus size (0.25 g of glucose/kg of BW delivered in a 50% wt/vol dextrose solution). Blood samples were collected at 5 and 2 min before administration of the glucose bolus to determine fasting values of plasma glucose and insulin. Additional blood samples were collected at 5, 10, 15, 20, 30, 60, and 120 min after the glucose infusion. Before each blood sample, 4 mL of blood was collected into a syringe to clear the catheter. A new syringe was used to collect 10 mL of blood, and the collected blood was placed in a tube containing EDTA. The catheters were then flushed with sterile heparinized saline (9 g/L of NaCl) after collection of each sample. Blood samples were placed on ice for no longer than 30 min until centrifuged at $3,000 \times g$ for 20 min at 4°C. Plasma was aliquoted into four 2-mL tubes, frozen in liquid N, and stored at –80°C until analyzed for glucose and insulin.

Slaughter Procedure and Carcass Data Collection

Beginning 84 d after feedlot arrival, calves were measured for 12th rib fat thickness (BF) by ultrasonography every wk. When a calf measured 1.2 ± 0.5 cm of BF, it was slaughtered the following week at a commercial abattoir. Final BW was calculated from BW taken on 2 consecutive days before slaughter. Kidney, pelvic, and heart fat was removed and weighed on the slaughter floor before measurement of HCW. Carcasses were ribbed between the 12th and 13th rib after a 48-h chill (4°C), after which a trained university employee determined BF, LM area, and marbling score. Percentage of empty body fat (EBF) was calculated as described by Guiroy et al. (2001) in which $EBF = 17.76107 + (4.68142 \times 12\text{th rib fat thickness}) + (0.01945 \times HCW) + (0.81855 \times [\text{marbling score}/100]) - (0.06754 \times LM \text{ area})$.

Posterior to the 12th rib, a 10-cm loin section was removed from each carcass, and bones were removed. A 2.54-cm steak on the anterior end of the loin section was removed, trimmed of external fat, ground, frozen, lyophilized, and analyzed for intramuscular fat content by ether extract (Ankom Technology, Fairport, NY). In yr 1, the remainder of the boneless loin was vacuumed packaged, aged for 14 d at 4°C, and then frozen at –20°C until analyzed for tenderness by Warner-Bratzler shear force

(WBSF; AMSA, 1995). Loin sections were thawed for 24 h at 4°C before cooking. A 2.54-inch steak from the anterior end of each loin section was removed and cooked in an impingement oven (Lincoln Impinger; Food Service Products Inc., Fort Wayne, IN) set at 190°C and was removed when internal temperature reached 71°C. Steaks were then cooled to room temperature and six 1.3-cm cores were removed parallel to the muscle fibers. Then peak shear force was measured using a Texture Analyzer (TAX Texture Analyzer; Texture Technologies Corp., Scarsdale, NY) equipped with a WBSF attachment. The mean of 6 cores was used in the statistical analyses.

Blood Collection and Analyses

Jugular blood samples were collected between 24 and 72 h after parturition and placed into 3 separate Vacutainer (Becton, Dickson and Co., Franklin Lakes, NJ) collection tubes to harvest serum as described by Radunz et al. (2010). Immunoglobulin G concentration was measured in serum collected and frozen at -20°C. Jugular blood samples preweaning were collected in a similar manner as described previously for subsequent analysis of glucose and insulin.

A colorimetric assay was used to determine plasma glucose (#1070 Glucose Trinder; Standbio Laboratory, Boerne, TX) concentrations. In yr 2, plasma concentrations of insulin were measured by ELISA (Bovine Insulin ELISA assay; Mercodia, Inc., Winston Salem, NC). Concentrations of IgG in calf serum were analyzed using single radial immunodiffusion plates (VMRD, Inc., Pullman, WA). Calves were classified in 1 of 3 categories, failure of passive transfer (≤ 800 mg/dL IgG), marginal passive transfer (801 to 1599 mg/dL IgG), and adequate passive transfer (≥ 1600 mg/dL IgG), as defined by McGuire and Adams (1982).

Calculations and Statistical Analyses

The GENMOD procedure (SAS Inst. Inc., Cary, NC) was used to analyze binomial data (passive immunity, morbidity, mortality, and quality and yield grade distributions). The PROC MIXED procedure of SAS was used to analyze the remaining variables. Experimental unit was pen for cow performance data and data collected on progeny at birth. The pen variation was small compared with animal variation, and pen effects were not significant ($P \geq 0.26$); therefore, for postnatal progeny data, individual animal was used as the experimental unit. The statistical model included dam treatment group as a fixed effect. Location and year were included as random variables in all analyses. Age of calf, gender, and sire of calf were included as covariates for calf performance traits when they represented a significant ($P \leq 0.10$) source of variation.

The mean fasted (-5 and -2 min) glucose and insulin concentrations were subtracted from postglucose infusion glucose and insulin concentrations to determine values above fasted baseline values. Glucose disappearance rate was calculated by regression of natural log-transformed glucose concentrations over time from 5 to 120 min after glucose infusion. The slope of the regression model represented the fractional disappearance rate of glucose (k ; $\text{mg}\cdot\text{L}^{-1}\cdot\text{min}^{-1}$). Incremental area under the curve (AUC) for insulin ($\text{min}\cdot\text{ng}^{-1}\cdot\text{mL}^{-1}$) and glucose ($\text{min}\cdot\text{mg}^{-1}\cdot\text{dL}^{-1}$) were determined using a trapezoidal summation method (Kaneko, 1989). The first-phase insulin response was calculated as described by Soto et al. (2003) as the sum of 5- and 10-min insulin values minus the average of the fasting (-5 and -2 min) values.

Values from the GTT were analyzed using a repeated measures model that included animal and dam treatment block as random effects, maternal dietary energy source, gender, and time (minute of sampling) as fixed effects and the interaction between maternal dietary energy source, gender, and time. Five covariance structures were compared for each variable (compound symmetric, autoregressive order one, heterogeneous autoregressive order one, spatial power, and unstructured) and the covariance structure that yielded the smallest Bayesian information criterion was used for the results presented. Effects of treatment within min of GTT were generated using the SLICE function in SAS (SAS Institute Inc., Cary, NC).

RESULTS AND DISCUSSION

Cow Prepartum Measures

The prepartum diets were initially formulated to provide similar NE_m intake among treatments according to NRC (2000) for CN and HY whereas energy value used for DG was 10% greater than reported by NRC (2000). The results for cow performance in yr 1 were reported in Radunz et al. (2010). In yr 2, change in BW gain during the late-gestation feeding period did not differ among treatments ($P = 0.57$); however, BCS and ultrasound 12th rib fat thickness was greater for cows fed CN and DG than for those fed HY at d 272 of gestation ($P < 0.001$; data not shown). Similar to yr 1, no difference was detected in dystocia or gestation length ($P \geq 0.21$) among treatments. Intakes at the start of yr 2 were less than in yr 1 because average cow BW was less, such that cows in yr 2 required less energy for maintenance (NRC, 2000). Intake of DDGS was decreased during yr 2 because based on results in yr 1 and the efficiency of gain in this limit feeding scenario was greater for DG than expected. This resulted in no difference in ADG during late gestation in yr 2 whereas in yr 1, ADG was greater for cows fed DG than for those fed CN or HY. In yr 2,

cows fed HY lost BCS but had similar BW gain during late gestation, which might indicate a slightly lower energy intake. The orchardgrass hay used in yr 2 had a slightly lesser NDF and greater ADF content than in yr 1, which could have resulted in decreased digestibility and slightly lower intakes of hay. Only small differences in parturition cow performance occurred between yr 1 and yr 2, despite the fact that the dietary energy substrate provided by these 3 feedstuffs differed among treatments. For cows fed HY, energy came primarily from fiber. Energy source for cows fed CN was primarily starch, and for cows fed DG, energy came from the combination of fiber, fat, and protein.

Parturition to Weaning

Birth weights were greater ($P = 0.002$) in calves from cows fed CN and DG than in calves from cows fed HY (Table 4). These results are consistent with a similar study conducted in sheep, where birth weights tended to be greater in lambs from ewes fed primarily corn and DDGS than in lambs from ewes fed haylage during mid to late gestation (Radunz et al., 2011b). In addition, results of previous studies conducted in our laboratory indicated that calves from cows limit-fed corn had heavier birth weights than calves from cows

Table 4. Effects of parturition dam dietary energy source on progeny measurements from parturition to weaning in yr 1 and 2

Item ²	Treatment ¹			SEM	P-value
	HY	CN	DG		
Calves	89	63	67		
Parturition ³					
BW, kg	38.5 ^a	41.7 ^b	41.0 ^b	2.04	<0.001
LM area ⁴ , cm ²	12.56	13.09	12.79	0.74	0.72
LM area, cm ² /kg of BW	0.34	0.31	0.32	0.01	0.36
100 d age					
BW, kg	140.5 ^a	148.9 ^b	143.5 ^{ab}	9.11	0.02
ADG, kg	1.09	1.12	1.10	0.081	0.40
Weaning					
BW, kg	235.2 ^y	244.6 ^x	237.0 ^{xy}	15.45	0.08
ADG, kg	1.06	1.10	1.06	0.08	0.13
LM area ⁵ , cm ²	49.6	53.2	54.9	5.5	0.72
12th rib fat thickness ³ , cm	0.56	0.61	0.66	0.10	0.26

^{a,b}Row means that do not have a common superscript differ, $P < 0.05$.

^{x,y}Row means that do not have a common superscript differ, $P < 0.10$.

¹HY = hay; CN = corn (limit-fed); DG = dried corn distillers grains with solubles (limit-fed).

²Analyzed with GENMOD (SAS Inst. Inc., Cary, NC) and SEM not estimated.

³Analyzed by dam pen as experimental unit for parturition data.

⁴LM area was measured between 12th and 13th rib by ultrasonography in yr 1.

⁵Collected at weaning via ultrasonography between 12th and 13th rib in yr 1.

fed hay (Loerch, 1996) or stockpiled forage (Schoonmaker et al., 2003). Therefore, it was hypothesized cows consuming CN would have a greater maternal glucose, resulting in heavier birth weights of their progeny than with cows consuming DG or HY. Glucose supply to the fetus, which can alter fetal growth, is determined by maternal glucose concentration and placental blood flow (Bauman et al., 2002). High-starch diets, such as those based on corn, can lead to increased ruminal propionate production and greater circulating blood glucose; however, maternal circulating glucose concentrations in the present study did not differ among treatments in yr 1 (Radunz et al., 2010) or yr 2 (data not shown).

Despite the lack of differences in maternal plasma glucose concentrations, maternal plasma insulin concentrations were greater in cows (Radunz et al., 2010) and ewes (Radunz et al., 2011a) fed DG than in those fed CN or hay at 3 h after feeding. Insulin secretion can be stimulated by propionate, glucose, and AA in ruminants (Harmon, 1992). The heavier birth weights in cows fed DG than HY could be a result of greater circulating maternal amino acid supply available to the placenta and fetus, suggested by greater blood urea N (BUN) concentrations (Radunz et al., 2010) and CP intake (Radunz et al., 2010; Table 2). Cows fed DG had a greater CP intake and supply of metabolizable protein (1,656 g MP/d) than cows fed CN (923 g MP/d) or HY (860 g MP/d). Therefore, excess protein might not explain the differences in birth weight between calves from cows fed CN and HY, but it could explain the differences between calves from cows fed DG and those from cows fed HY.

Limit-feeding of high-concentrate diets has been shown to decrease maintenance requirements in growing lambs by decreasing visceral organ mass (Fluharty and McClure, 1997; Fluharty et al., 1999). Moreover, McLeod and Baldwin (2000) suggested that gut energy expenditure is more related to changes in mass relative to ME intake than to changes in viscera metabolism. Therefore, limit-feeding a high-concentrate diet to gestating cows may allow more energy to be partitioned to the fetus rather than to maintenance of maternal tissues. This decrease in maintenance requirements could partially explain greater fetal growth in calves from dams fed CN or DG. More research is warranted to determine how metabolic changes in the dam affect nutrient supply to the fetus and thereby fetal growth in ruminants.

Despite differences in birth weights, LM area and LM area per kilogram of BW as measured by ultrasound did not differ ($P \geq 0.36$) among treatments (Table 4). Heavier birth weights were assumed to be associated with greater muscle measurements, but the 2-dimensional measurement of muscle by LM area did not support this hypothesis. In agreement with our results, Micke et al. (2009) reported that fetal growth was decreased in

nutrient-restricted heifers, but distribution of tissue mass was not changed. In that study, measures were made by ultrasound during early to mid gestation. In contrast, previous studies have reported maternal or fetal nutrient restriction in sheep resulted in lighter BW and decreased LM weight in lambs (Fahey et al., 2005), decreased semitendinosus muscle weight in lambs (Greenwood et al., 2000), and decreased weights of selected leg muscles in rats (Beerman, 1983). The conflicting results among the present study and previous studies might reflect differences in species, timing of treatments, and magnitude of nutrient changes.

At 100 d of age and weaning, calves from cows fed CN had heavier ($P \leq 0.08$) BW than calves from cows fed HY, and calves from cows fed DG were intermediate. Although calves from cows fed CN had a numerically greater ADG than calves from cows fed DG, preweaning growth rate did not differ ($P \geq 0.13$) among all calves. Similar ADG might be expected because milk intake did not differ among treatments during early, mid, and late lactation measures (Radunz et al., 2010), and milk production of the dam is a major determinant in growth rate of calves preweaning (Freking and Marshall, 1992). Corrah et al. (1975) observed that a 70% restriction of energy in late gestation resulted in lighter weaning BW in calves and lower milk production in cows. Other studies have investigated modest changes in energy intake in prepartum nutrition. Small et al. (2004) and Marston et al. (1995) reported that cows supplemented with fat or energy in late gestation had no difference in offspring birth BW or weaning BW. In contrast, previous studies have reported that cows supplemented with protein in late gestation produced calves with heavier weaning BW but no difference in BW at birth (Stalker et al., 2006; Larson et al., 2009). In these studies, milk production was not measured; therefore, conclusions cannot be made about whether differences in BW were the result of differences in fetal development or dam postpartum milk production.

Although maternal dietary energy in late gestation in the present study resulted in differences in weaning BW, this was not associated with milk production or detectable changes in body composition. In the past, weaning BW has been associated with differences in body composition (Fortin et al., 1980; Guiroy et al., 2001). In the present study, however, ultrasound fat thickness ($P = 0.26$) and LM area ($P = 0.72$) at weaning did not differ among treatments regardless of differences in weaning BW.

Progeny Health

No differences ($P = 0.54$) as a result of prepartum energy source were detected in calf serum IgG concentrations (Table 5). Wittum and Perino (1995) reported

calves that did not acquire adequate passive immunity ($<1,600$ mg/dL) had a 3 times greater chance of becoming sick in the feedlot. In the present study, no differences in proportion of calves classified as having inadequate or marginal passive immunity ($P \geq 0.71$) were associated with prepartum dam energy source during gestation. Likewise, source of energy during gestation did not result ($P \geq 0.42$) in residual effects on postnatal health of progeny from birth to slaughter.

Progeny Glucose Tolerance

In yr 2, fed and fasted plasma glucose and insulin concentrations were collected on progeny during the weigh-suckle-weigh procedure (Table 6). Calves from cows fed CN had greater ($P = 0.04$) fasting glucose concentrations than calves from cows fed DG, and calves from cows fed HY were intermediate. Two hours after nursing, glucose concentrations were not affected ($P = 0.70$) by dam gestation diet. Differences between fed and fasted glucose was greatest ($P = 0.05$) for calves from cows fed DG; however, there were no differences ($P \geq 0.30$) in fasted or fed insulin concentrations among treatments. In addition, the ratio of insulin to glucose was not affected ($P \geq 0.30$) by dam prepartum dietary energy source.

Sampling at 2 h after feeding might more accurately reflect peak glucose but not peak insulin concentration; therefore, no differences among treatments were detected for insulin. Calves from cows fed CN were slightly hyperglycemic in the fasted state, but the change in glucose between fasted and fed state was less for CN than it was for other treatments. A lesser change in glucose

Table 5. Effects of prepartum dam dietary energy source on progeny health in yr 1 and 2

Item	Treatment ¹			P-value
	HY	CN	DG	
Calves	72	64	69	
Passive immunity, % ²				
Failure	23.9	16.7	21.9	0.71
Marginal	8.7	11.1	12.2	0.86
Adequate	67.4	72.2	65.8	0.82
Birth to feedlot arrival, %				
Treated	12.7	9.2	10.1	0.89
Mortality	5.6	6.4	3.0	0.62
Feedlot arrival to slaughter, %				
Treated ³	8.9	20.1	19.1	0.24
Mortality	0	0	0	–

¹HY= hay; CN = corn (limit-fed); DG = dried corn distillers grains with solubles (limit-fed).

²Failure of passive transfer (≤ 800 mg/dL), marginal passive transfer (801 to 1,599 mg/dL), and adequate passive transfer ($\geq 1,600$ mg/dL) in yr 1 collected within 24 to 72 h of parturition.

³Calves treated for respiratory disease.

Table 6. Effects of prepartum dam dietary energy source on progeny on fed and fasted plasma glucose and insulin concentration at 93 d of age in yr 2

Item	Treatment ¹			SEM	P-value
	HY	CN	DG		
Calves	23	25	24		
Glucose, mg/dL					
Fasted	102.4 ^{ab}	107.5 ^a	96.3 ^b	3.3	0.04
Fed	141.9	138.6	143.3	5.2	0.70
Difference	39.6 ^{ab}	30.9 ^b	46.7 ^a	4.9	0.05
Insulin, ng/mL					
Fasted	0.053	0.056	0.045	0.006	0.48
Fed	0.806	0.623	0.646	0.125	0.30
Difference	0.755	0.570	0.600	0.124	0.30
Insulin:glucose, ng/(mg·mL)					
Fasted	0.051	0.050	0.047	0.006	0.85
Fed	0.554	0.452	0.466	0.083	0.44

^{a,b}Row means that do not have a common superscript differ, $P < 0.05$.

¹HY= hay; CN = corn (limit-fed); DG = dried corn distillers grains with solubles (limit-fed).

concentration between the fed and fasted states, with no difference in insulin concentration, could suggest tissues were more sensitive to insulin in calves from cows fed CN. In contrast, calves from cows fed DG had the greatest change in glucose with a similar insulin response to CN, which might indicate tissues were less sensitive to insulin in cows fed DG. Milk intake and, more specifically, lactose intake did not differ ($P \geq 0.59$) among treatments (not reported); therefore, it is likely that lactose intake did not cause differences in glucose supply among treatments, and treatment differences observed were a result of carryover effects of gestation diet on fetal development.

A greater fasting glucose concentration was reported in lambs at 28 d of age when their dams were nutrient restricted during gestation, and this finding also was associated with greater insulin secretion following a glucose challenge (Ford et al., 2007). In humans, late-gestation exposure to nutrient restriction was determined to be more important than nutrient restriction during early gestation in predisposing offspring to metabolic and cardiovascular disorders of progeny in adult life (Ravelli et al., 1998). Other studies in sheep have reported that maternal nutrition during gestation can affect progeny glucose tolerance at greater than 90 d of age (Gardner et al., 2005; Husted et al., 2007). In a similar study in sheep (Radunz et al., 2011b), mid- to late-gestation dam diet affected maternal insulin secretion, which corresponded to greater insulin secretion and potential insulin resistance in response to a glucose challenge in progeny from dams fed DG vs. CN or HAY during gestation. Ford et al. (2007) observed different insulin secretion at 28 and 250 d of age in response to GTT; therefore, the differences detected at 93 d of age in the present study might not be

the same as the insulin secretion that would be observed after calves are weaned and placed on a high-concentrate diet.

After progeny had been placed on a high-concentrate finishing diet, 2 GTT were conducted in yr 2 to determine whether days on a finishing diet (DOF); 41 vs. 111 d) would result in greater differences in glucose tolerance in calves from dams fed different dietary prepartum energy sources (Table 7). Treatment and DOF means are presented for GTT calculations in Table 7; however, a gender \times treatment interaction was detected ($P < 0.05$) for fasting glucose concentration, glucose clearance rate, and initial insulin response. Fasting glucose concentrations were greater ($P \leq 0.05$) for male than for female progeny from cows fed CN, but fasting glucose concentrations did not differ between male and female progeny from cows fed HY or DG (Figure 1). Females from cows fed CN had faster glucose clearance rates than all other progeny classes (Figure 2). In addition, females from cows fed CN had the greatest ($P \leq 0.05$) initial insulin response compared with all other progeny whereas female calves from cows fed HY had the least initial insulin response (Figure 3). Insulin AUC and ratio of insulin:glucose AUC did not differ ($P \geq 0.33$) among treatments.

Fasting glucose concentrations did not differ with DOF; however, fasting insulin concentrations were greater ($P < 0.001$) at 111 vs. 41 DOF. Glucose AUC, glucose clearance rate, insulin AUC, insulin initial insulin response, and ratio of insulin AUC:glucose AUC were all greater ($P \leq 0.005$) at 111 vs. 41 DOF.

In beef cattle, systemic insulin sensitivity has not been well described with regards to the effects of high-concentrate finishing diets or management before entering the feedlot on the measures of glucose tolerance and its relationship to adipose deposition. It has been hypothesized that long-term health implications result from disturbances in fetal development, which can lead to “programming” of an increased predisposition to various disease syndromes during later postnatal life and might alter body composition (Godfrey and Barker, 2001).

Several studies in sheep and cattle have reported elevated plasma glucose and insulin concentrations when feeding high-starch vs. low-starch diets (Jenny and Polan, 1975; Evans et al., 1975); however, other studies have shown no difference in glucose concentrations but greater concentrations of insulin when high-starch vs. low-starch diets were compared (Murphy and Loerch, 1994; Schoonmaker et al., 2003). Hersom et al. (2004) reported glucose and insulin concentrations increased with days on feed of a high-starch diet from 26 to 86 d on feed of a high starch diet. Sampling time relative to feeding might have influenced the measurements in these studies, making it difficult to draw conclusions

Table 7. Main effects of parturient dam dietary energy source and days on finishing diet on progeny glucose tolerance in yr 2

Item	TRT ¹			DOF ²		SEM	P-value		
	HY	CN	DG	41	111		TRT	DOF	TRT × DOF
Calves	4	4	4	12	12				
BW, kg	610	712	634	516	788	74.3	0.58	<0.001	0.74
BF ³ , cm	0.44	0.56	0.59	0.45	0.60	0.123	0.64	0.003	0.43
Glucose									
Fasting, mg/dL	96.1	98.4	93.7	95.6	96.5	4.07	0.60	0.77	0.84
AUC ⁴ , min·mg ⁻¹ dL ⁻¹	5,299	5,103	5,589	4,762	5,901	650.0	0.84	0.002	0.08
CR ⁵ , min·mg ⁻¹ L ⁻¹	1.01 ^b	1.13 ^a	1.06 ^b	0.93	1.20	0.064	0.01	<0.001	0.38
Insulin									
Fasting, ng/mL	0.95	1.89	1.45	0.78	2.07	0.634	0.47	0.009	0.46
AUC, min·ng ⁻¹ mL ⁻¹	370.8	467.5	512.1	275.2	625.1	140.31	0.33	0.004	0.47
IR ⁶ , ng/mL	7.98 ^a	21.86 ^b	19.21 ^b	11.73	20.97	4.833	0.005	0.003	0.72
I:G ⁷ AUC, ng·mg ⁻¹ mL ⁻¹	0.07	0.09	0.09	0.06	0.11	0.028	0.85	0.005	0.58

^{a,b}Row means that do not have a common superscript differ, $P < 0.05$.

¹TRT = treatment; HY = hay; CN = corn (limit-fed); DG = dried corn distillers grains with solubles (limit-fed).

²DOF = days on finishing diet.

³BF = 12th rib fat thickness (determined via ultrasonography).

⁴AUC = absolute area under the curve above baseline.

⁵CR = clearance rate.

⁶IR = initial insulin response.

⁷I:G = ratio of insulin to glucose AUC.

relative to insulin sensitivity and high-starch diets.

Insulin sensitivity and responsiveness have been reported to decrease at heavier BW (275 vs. 490 kg) corresponding to increases in age and body fat content in the hindquarters of beef steers (Eisemann et al., 1997), indicating that insulin resistance by peripheral tissues increased with BW, age, and body fat content of beef steers. In the present study, DOF increased BW and 12th rib fat thickness at 111 vs. 41 d, which corresponded to greater insulin resistance as indicated by a greater ratio of insulin to glucose (I:G) AUC; thus, our findings support the results of Eisemann et al. (1997). In contrast, Vasconcelos et al. (2009) reported a GTT conducted at 0, 28, and 56 d of feeding a high-starch growing diet did not result in differ-

ences in glucose or insulin kinetics despite differences in BW and subcutaneous and intramuscular fat percentage (IMF) ultrasound measures at 56 d. It should be noted, however, that 56 d might not have been sufficient time to elicit a response because potentially not enough body fat accretion had occurred. In the current study, after 41 DOF, cattle had accumulated 0.45 cm of subcutaneous fat. In contrast, Vasconcelos et al. (2009) reported 0.15 to 0.34 cm of subcutaneous fat at 56 DOF and the change in subcutaneous fat accretion was less than 0.25 cm. In the present study, from 44 to 111 DOF, subcutaneous fat accretion was 0.15 cm; however, from 111 DOF to slaughter subcutaneous fat accretion was 0.6 cm. This result suggests subcutaneous fat accretion accelerates at a faster rate as

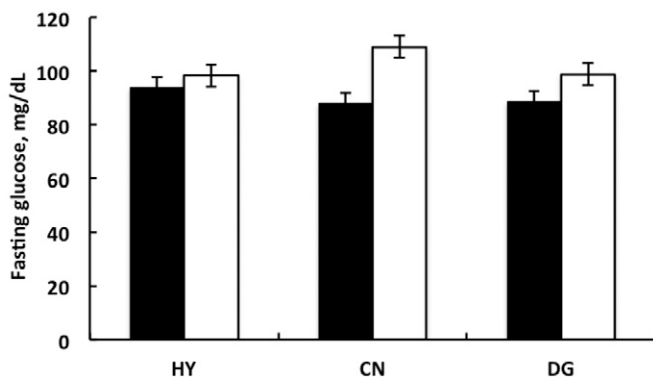


Figure 1. Mean fasting glucose concentration for females (■) and males (□) before glucose bolus infusion in year 2 at d 41 and d 111 on the finishing diet. A gender × treatment interaction was detected ($P < 0.05$), and means that do not have a common superscript differ, $P < 0.05$. HY = hay; CN = corn; DG = dried corn distillers grains.

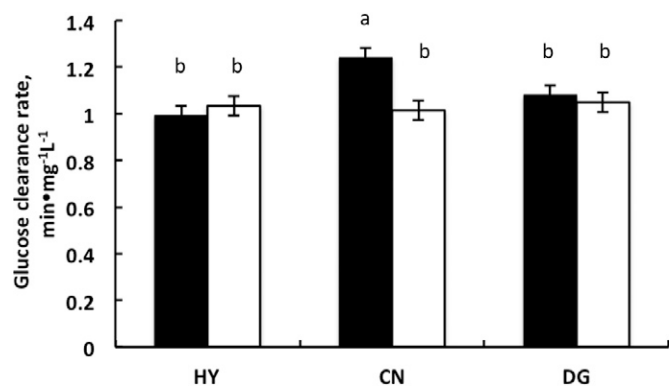


Figure 2. Mean glucose clearance rate for females (■) and males (□) after glucose bolus infusion in year 2 at d 41 and d 111 on the finishing diet. A gender × treatment interaction was detected ($P < 0.05$), and means that do not have common superscript differ, $P < 0.05$. HY = hay; CN = corn; DG = dried corn distillers grains.

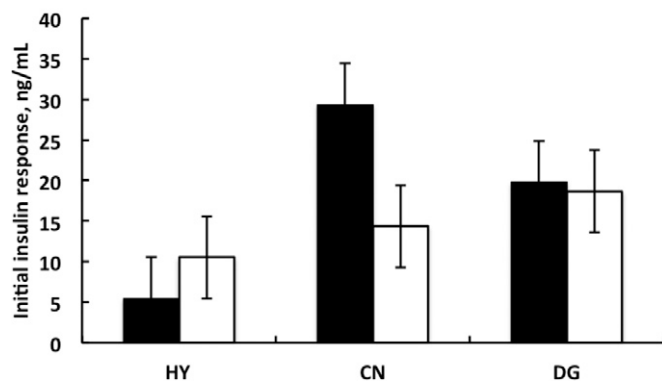


Figure 3. Mean initial insulin response for females (■) and males (□) after glucose bolus infusion in year 2 at d 41 and d 111 on the finishing diet. A gender \times treatment interaction was detected ($P < 0.05$), and means that do not have a common superscript differ, $P < 0.05$. HY = hay; CN = corn; DG = dried corn distillers grains (limit-fed).

animals become more insulin resistant with increased days on a high-starch diet. Our discovery of the effects of DOF and insulin sensitivity suggests a relationship with adipose accretion in finishing cattle.

Glucose clearance was faster for calves from cows fed CN, but this corresponded to a greater initial insulin response; therefore, the ratio of I:G AUC did not differ among treatments. This finding indicates that overall insulin sensitivity was similar among progeny. Nonetheless, the interaction of treatment \times gender indicates that post-natal glucose tolerance might elicit different responses in relationship to maternal dietary energy source relative to gender of progeny. Estrogen administration to ruminants has been associated with increased circulating insulin concentrations (Preston, 1975). No effort was made to suppress estrus in the females used for the GTT and finishing trial; therefore, these heifers could have reached puberty and might have been cycling when the GTT were conducted, potentially affecting the treatment response. Cycling status and puberty were not measured in the present study. In other growth or carcass measures, no gender \times treatment interactions were detected; however, gender of progeny was not equally represented within treatments. Therefore, there were likely insufficient animal numbers to detect differences between gender within progeny from dams fed the same maternal dietary energy source.

Finishing Phase and Carcass Composition

Feedlot receiving BW, DMI, ADG, feed efficiency, and final BW did not differ among treatments ($P \geq 0.16$; Table 8). Calves from dams fed CN and DG required fewer DOF ($P = 0.10$) to achieve a similar fat thickness compared with calves from dams fed HY. Nonetheless, overall age and lifetime ADG did not differ among treatments ($P \geq 0.28$).

Few studies regarding maternal nutrition of gestating

cows have reported feedlot performance of progeny after weaning. Heavier BW on entry to and exit from the feedlot was reported for calves from dams supplemented with protein in late gestation but DMI, ADG, and G:F were not affected by dam protein supplementation status (Stalker et al., 2006; Larson et al., 2009). Dams receiving late gestation nutrition below NRC requirements (NRC, 2000) had progeny with decreased initial BW (Nordby et al., 1987; Underwood et al., 2008). In the present study, cows were fed to meet or exceed nutrient requirements during late gestation. Mechanisms by which energy source in late gestation can affect growth rate of progeny might be minimized when energy needs of the cow are met.

At a common BF end point, HCW followed final BW and did not differ among treatments (Table 9; $P \geq 0.19$). Dressing percent was greater for progeny from cows fed HY than progeny from cows fed DG; progeny from cows fed CN were intermediate ($P = 0.04$). Before collection of HCW, KPH was removed and, when calculated as a percentage of HCW, did not differ ($P = 0.46$) among treatments. By experimental design, fat thickness did not differ among treatments ($P = 0.71$). In addition, maternal dietary energy source did not affect ($P \geq 0.45$) the carcass LM area per kilogram HCW of progeny, calculated yield grade, or distribution of yield grade. Radunz et al. (2011a) reported similar results in sheep, except a trend was observed for greater KPH content in lambs from ewes fed DDGS than lambs from ewes fed haylage.

When fed to a common BF end point, marbling scores ($P = 0.03$) were greater in carcasses from calves whose dams were fed a low-starch diet (HY and DG) vs. high-starch diet (CN), resulting in a different ($P = 0.005$) distribution of carcass grading USDA Select (0, 6.4, and 16.3% for progeny from cows fed HY, DG, and CN, respectively). The USDA quality grade distribution did not differ ($P \geq 0.32$) among treatments for USDA Low Choice, Upper 2/3 Choice, and Prime. Intramuscular fat content was greater ($P = 0.07$) in calves from dams fed HY and DG vs. CN; however, calculated percentage of EBF did not differ among treatments ($P = 0.50$). Similar to the present study, progeny from cows supplemented with protein in late gestation had increased marbling scores and a greater percentage of carcasses in the USDA Choice quality grade (Stalker et al., 2006; Larson et al., 2009); however, in those progeny, the greater marbling score resulted in an increased percentage of EBF (Larson et al., 2009). This finding is contrary to the results of the present study, in which greater marbling score did not result in greater EBF because the intramuscular fat to backfat ratio was greater in calves from dams fed HY than calves from dams fed CN, with an intermediate response for DG calves.

Maternal energy source during gestation might alter adipose tissue development, and in the present study

Table 8. Effects of prepartum dam dietary energy source on progeny feedlot performance in yr 1 and 2

Item	Treatment ¹			SEM	<i>P</i> -value
	HY	CN	DG		
Calves	45	45	45		
Receiving BW, kg	248	257	253	19.7	0.16
Final BW, kg	513	511	506	17.8	0.67
Feedlot ADG, kg/d ²	1.53	1.57	1.55	0.036	0.48
DMI, kg	8.75	8.81	8.79	0.34	0.93
G:F	0.174	0.178	0.176	0.0023	0.43
DOF ³	178.4 ^x	168.3 ^y	170.1 ^y	5.00	0.10
Age at slaughter, d	375.5	368.2	369.9	5.06	0.31
Overall ADG ⁴ , kg	1.59	1.54	1.54	0.35	0.28

^{x,y}Row means that do not have a common superscript differ, *P* < 0.10.

¹HY = hay; CN = corn (limit-fed); DG = dried corn distillers grains with solubles (limit-fed).

²Calculated from (final BW – receiving BW)/DOF.

³DOF = days on finishing diet.

⁴Measured from birth to slaughter.

increased (*P* = 0.09) intramuscular fat content per unit of backfat was observed in calves from dams fed HY than in calves from cows fed CN. Late gestation nutrient restriction was associated with greater subsequent insulin resistance in adipose but not muscle tissue and greater subsequent internal fat deposition of progeny (Gardner et al., 2005). This finding suggests that late gestation could be a critical time period for adipose tissue development. Insulin stimulates uptake of glucose and increases lipogenesis in adipocytes (Kersten, 2001). Exposing intramuscular adipose tissue from steers fed a corn-based diet to insulin resulted in a 165% increase in glucose incorporation into fatty acids compared with glucose incorporation of subcutaneous adipose tissue, indicating intramuscular adipose tissue might be more sensitive to insulin than subcutaneous adipose tissue (Rhoades et al., 2007). Because no differences were detected in insulin sensitivity in response to GTT among treatments, this could indicate that other mechanisms that influence adipose tissue development during late gestation are responsible for differences in intramuscular fat deposition of progeny.

Tenderness did not differ in steaks from calves regardless of dietary energy sources during gestation (*P* = 0.43). Underwood et al. (2008) reported that steaks were less tender from offspring whose dams were on a poor plane of nutrition in early to mid gestation than those from cows with adequate nutrition, and to our knowledge this is the only other study to report effects of maternal nutrition on tenderness of steaks from progeny. Previous studies have indicated that maternal nutrition can affect factors of muscle development, which may have implications in meat quality of progeny. Muscle fiber number (Fahey et al., 2005), muscle fiber type (Cripps et al., 2008), and muscle protein degradation factors (Du et al., 2004) can be affected by

Table 9. Effects of prepartum dam dietary energy source on progeny carcass composition and distribution of USDA yield and quality grade in yr 1 and

Item	Treatment ¹			SEM	<i>P</i> -value
	HY	CN	DG		
Calves	45	45	45		
HCW, kg	308	306	299	12.8	0.19
Dressing percent	59.8 ^a	59.5 ^{ab}	58.8 ^b	0.63	0.04
12th rib fat thickness, cm	1.20	1.23	1.24	0.054	0.71
LM area, cm ²	78.3	78.7	77.7	1.62	0.79
LM area, cm ² /kg HCW	0.429	0.434	0.435	0.1168	0.72
KPH ² , %	3.30	2.88	2.87	0.157	0.46
USDA yield grade	2.50	2.56	2.61	0.01	0.60
1.9 or less, %	4.55	2.33	6.38	–	0.63
2.0 to 2.9, %	61.4	58.1	63.8	–	0.85
3.0 to 3.9, %	31.8	39.5	27.7	–	0.48
4.0 to 4.9, %	2.3	0	2.2	–	0.45
Marbling score ³	549.2 ^a	506.3 ^b	536.4 ^{ab}	16.33	0.03
USDA quality grade					
Select, %	0 ^a	16.3 ^b	6.38 ^{ab}	–	0.005
Low choice, %	56.8	55.8	53.2	–	0.93
Upper 2/3 Choice, %	40.9	27.9	40.4	–	0.35
Prime, %	2.27	0	0	–	0.32
Intramuscular fat ⁴ , %	5.04 ^x	4.37 ^y	4.85 ^{xy}	0.30	0.07
Empty body fat ⁵ , %	28.6	28.2	28.4	0.26	0.50
IMF:BF ⁶	0.043 ^x	0.037 ^y	0.041 ^{xy}	0.0028	0.09
WBSF ⁷ , kg	3.70	3.86	3.58	0.17	0.43

^{a,b}Row means that do not have a common superscript differ, *P* < 0.05.

^{x,y}Row means that do not have a common superscript differ, *P* < 0.10.

¹HY = hay; CN = corn (limit-fed); DG = dried corn distillers grains with solubles (limit-fed).

²KPH was removed and weighed before HCW.

³Slight = 300 to 399; Small = 400 to 499; Modest = 500 to 599; Moderate = 600 to 699.

⁴Ether extract of LM at the 12th rib.

⁵Calculated as described by Guiroy et al. (2001).

⁶IMF = intramuscular fat percentage; BF = 12th rib fat thickness.

⁷WBSF = Warner-Bratzler shear force.

maternal nutrition. Because treatments were imposed during late gestation in the present study, muscle development factors affecting tenderness might not have been altered by maternal nutrition.

In summary, maternal late gestation dietary energy source seems to alter fetal growth, affecting birth weight and having long-term effects on metabolism and body composition. Feeding a diet low in starch (HY or DG) vs. one high in starch (CN) in late gestation was associated with greater intramuscular fat deposition of progeny when measured at a constant 12th rib fat thickness. Conversely, if gestational dietary energy sources imposed on cows had been fed to progeny postnatally, previous research would indicate diets high vs. low in starch fed in the finishing phase would result in greater marbling deposition. Results of our study indicated a paradox might exist such that energy composition of maternal diet could have a different effect on fetal adipose tissue development than energy com-

position of diets fed after birth. More research is needed to determine which mechanisms alter fetal growth and development in late gestation and affect resulting adipose tissue development and fat deposition during postnatal growth and development. As feed costs increase and alternative energy sources are used in gestating diets of beef cows, the resulting consequences on progeny productivity will become more important.

LITERATURE CITED

- American Meat Science Association (AMSA). 1995. Research Guidelines for Cookery, Sensory Evaluation and Instrumental Tenderness of Fresh Meat. AMSA, Chicago, IL.
- Bauman, M. U., S. Deborde, and N. P. Illsley. 2002. Placental glucose transfer and fetal growth. *Endocrine*. 19:13–22.
- Beerman, D. H. 1983. Effects of maternal dietary nutrient restriction during gestation and lactation, muscle, sex, and age on various indices of skeletal muscle growth in rat. *J. Anim. Sci.* 57:328–337.
- Corah, L. R., T. G. Dunn, and C. C. Kaltenbach. 1975. Influence of prepartum nutrition on the reproductive performance of beef females and the performance of their progeny. *J. Anim. Sci.* 41:819–824.
- Cripps, R. L., L. R. Green, J. Thompson, M. S. Martin-Gronert, M. Monk, I. M. Sheldon, M. A. Hanson, C. N. Hales, and S. E. Ozanne. 2008. The effect of maternal body condition score before and during pregnancy on glucose tolerance of adult sheep offspring. *Reprod. Sci.* 15:448–456.
- Du, M., M. J. Zhu, W. J. Means, B. W. Hess, and S. P. Ford. 2004. Effect of nutrient restriction on calpain and calpastatin content of skeletal muscle from cows and fetuses. *J. Anim. Sci.* 82:2541–2547.
- Eisemann, J. H., G. B. Huntington, and D. R. Catherman. 1997. Insulin sensitivity and responsiveness of portal-drained viscera, liver, hindquarters and whole body of beef steers weighing 275 or 490 kilograms. *J. Anim. Sci.* 75:2084–2091.
- Evans, E., J. B. Buchanan-Smith, and G. K. Macleod. 1975. Postprandial patterns of plasma glucose, insulin and volatile fatty acids in ruminants fed low- and high-roughage diets. *J. Anim. Sci.* 41:1474–1479.
- Fahey, A. J., J. M. Brameld, T. Parr, and P. J. Buttery. 2005. Ontogeny of factors associated with proliferation and differentiation of muscle in the ovine fetus. *J. Anim. Sci.* 83:2330–2338.
- Fluharty, F. L., and K. E. McClure. 1997. Effects of dietary energy intake and protein concentration on performance and visceral organ mass in lambs. *J. Anim. Sci.* 75:604–610.
- Fluharty, F. L., K. E. McClure, M. B. Solomon, D. D. Clevenger, and G. D. Lowe. 1999. Energy source and ionophore supplementation effects on lamb growth, carcass characteristics, visceral organ mass, diet digestibility, and nitrogen metabolism. *J. Anim. Sci.* 77:816–823.
- Ford, S. P., B. W. Hess, M. M. Schwoppe, 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.
- Fortin, A., J. T. Reid, A. M. Maiga, D. W. Sim, and G. H. Wellington. 1980. Effect of energy intake level and influence of breed and sex on the physical composition of carcass of cattle. *J. Anim. Sci.* 51:331–339.
- Freking, B. A., and D. M. Marshall. 1992. Interrelationships for heifer milk production and other biological traits with production efficiency to weaning. *J. Anim. Sci.* 70:646–655.
- Gardner D. S., K. Tingey, B. W. M. Van Bon, S. E. Ozanne, V. Wilson, J. Dandrea, D. H. Keisler, T. Stephenson, and M. E. Symonds. 2005. Programming of glucose-insulin metabolism in adult sheep after maternal undernutrition. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 289:R947–R954.
- Godfrey, K. M., and D. J. P. Barker. 2001. Fetal programming and adult health. *Public Health Nutr.* 4:611–624.
- Greenwood, P. L., A. S. Hunt, J. W. Hermanson, and A. W. Bell. 2000. Effects of birth weight and postnatal nutrition on neonatal sheep: II. Skeletal muscle growth and development. *J. Anim. Sci.* 78:50–61.
- Guiroy, P. J., D. G. Fox, L. O. Tedeschi, M. J. Baker, and M. D. Cravey. 2001. Predicting individual feed requirements of cattle fed in groups. *J. Anim. Sci.* 79:1983–1995.
- Harmon, D. L. 1992. Impact of nutrition on pancreatic exocrine and endocrine secretion in ruminants: A review. *J. Anim. Sci.* 70:1290–1301.
- Hersom, M. J., R. P. Wettemann, C. R. Krehbiel, G. W. Horn, and D. H. Keisler. 2004. Effect of live weight of gain of steers during winter grazing: III. Blood metabolites and hormones during feedlot finishing. *J. Anim. Sci.* 82:2059–2068.
- Huntington, G. B., C. K. Reynolds, and B. H. Stroud. 1989. Techniques for measuring blood flow in splanchnic tissues of cattle. *J. Dairy Sci.* 72:1583–1595.
- Husted, S. M., M. O. Nielsen, M. P. Tyesen, A. Kiani, D. Blache, and K. L. Ingvarntsen. 2007. Programming of intermediate metabolism in young lambs affected by late gestational maternal undernourishment. *Am. J. Physiol. Endocrinol. Metab.* 293:E548–E557.
- Jenny, B. F., and C. E. Polan. 1975. Postprandial blood glucose and insulin in cows fed high grain. *J. Dairy Sci.* 58:512–514.
- Kaneko, J. J. 1989. *Clinical Biochemistry of Domestic Animals*. 4th ed. Acad. Press, San Diego, CA.
- Kersten, S. 2001. Mechanisms of nutritional and hormonal regulation of lipogenesis. *EMBO Rep.* 2:282–286.
- 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.
- Lewis, G. F., A. Carpentier, K. Adehi, and A. Giaccca. 2002. Disordered fat storage and mobilization in the pathogenesis of insulin resistance and type 2 diabetes. *Endocrine Rev.* 23:201–229.
- Loerch, S. C. 1996. Limit-feeding corn as an alternative to hay for gestating beef cows. *J. Anim. Sci.* 74:1211–1216.
- Marston, T. T., K. S. Lusby, R. P. Wettemann, and H. T. Purvis. 1995. Effects of feeding energy or protein supplements before or after calving on performance of spring-calving cows grazing native range. *J. Anim. Sci.* 73:657–664.
- McGuire, T. C., and D. S. Adams. 1982. Failure of colostral immunoglobulin transfer to calves: Prevalence and diagnosis. *Compend. Contin. Educ. Pract. Vet.* 4:S35–S40.
- McLeod, K. R. and R. L. Baldwin, VI. 2000. Effects of diet forage:concentrate ratio and metabolizable energy intake on visceral organ growth and in vitro oxidative capacity of gut tissue in sheep. *J. Anim. Sci.* 78:760–770.
- Micke, G. C., T. M. Sullivan, R. J. Soares Magalhaes, P. J. Rolls, S. T. Norman, and V. E. A. Perry. 2009. Heifer nutrition during early- and mid-pregnancy alters fetal growth trajectory and birth weight. *Anim. Reprod. Sci.* 117(1–2):1–10. doi:10.1016/j.anireprosci.2009/03.010
- Murphy, T. A., and S. C. Loerch. 1994. Effects of restricted feeding of growing steers on performance, carcass characteristics, and composition. *J. Anim. Sci.* 72:2497–2507.
- Nordby, D. J., R. A. Field, M. L. Riley, and C. J. Kercher. 1987. Effects of maternal undernutrition during early-pregnancy on growth, muscle cellularity, fiber type and carcass composition in lambs. *J. Anim. Sci.* 64:1419–1427.

- NRC. 2000. Nutrient Requirements of Beef Cattle. 7th ed.: Update 2000. Natl. Acad. Press, Washington, DC.
- Preston, R. 1975. Biological response to estrogen additives in meat producing cattle and lambs. *J. Anim. Sci.* 41:1414–1430.
- Radunz, A. E., F. L. Fluharty, M. L. Day, H. N. Zerby, and S. C. Loerch. 2010. Prepartum dietary energy source in beef cows: I. Effects on pre- and postpartum cow performance. *J. Anim. Sci.* 88:2717–2728.
- Radunz, A. E., F. L. Fluharty, I. Susin, T. L. Felix, H. N. Zerby, and S. C. Loerch. 2011a. Winter-feeding systems for gestating sheep II. Effects on feedlot performance, glucose tolerance, and carcass composition of lamb progeny. *J. Anim. Sci.* 89:478–488.
- Radunz, A. E., F. L. Fluharty, H. N. Zerby, and S. C. Loerch. 2011b. Winter-feeding systems for gestating sheep I. Effects on pre- and postpartum ewe performance and lamb progeny preweaning performance. *J. Anim. Sci.* 89:467–477.
- Ravelli, A. C., J. H. van der Meulen, R. P. Michels, C. Osmond, D. J. Barker, C. N. Hales, and O. P. Bleker. 1998. Glucose tolerance in adults after prenatal exposure to famine. *Lancet* 351:173–177.
- Rhoades, R. D., J. E. Sawyer, K. Y. Chung, M. L., Schell, D. K. Lunt, and S. B. Smith. 2007. Effect of dietary energy source on in vitro substrate utilization and insulin sensitivity of muscle and adipose tissues of Angus and Wagyu steers. *J. Anim. Sci.* 85:1719–1726.
- Schoonmaker, J. P., M. J. Cecava, D. B. Faulkner, F. L. Fluharty, H. N. Zerby, and S. C. Loerch. 2003. Effects of source of energy and rate of growth on performance, carcass characteristics, ruminal fermentation, and serum glucose and insulin of early-weaned steers. *J. Anim. Sci.* 81:843–855.
- Small, W. T., S. I. Paisley, B. W. Hess, S. L. Lake, E. J. Scholljegerdes, T. A. Reed, E. L. Belden, and S. Bartle. 2004. Supplemental fat in limit-fed high grain prepartum diets of beef cows: Effects on cow weight gain, reproduction, and calf health, immunity, and performance. *West. Sec. Am. Soc. Anim. Sci.* 55:45–52.
- Soto, N., R. A. Bazaes, V. Pena, T. Salazar, A. Avila, G. Iniguez, K. K. Ong, D. B. Dunger, and M. V. Mericq. 2003. Insulin sensitivity and secretion are related to catch-up growth in small-for-gestational-age infants at age 1 year: Results from a prospective cohort. *J. Clin. Endocrin. Metabol.* 88:3645–3650.
- Stalker, L. A., D. C. Adams, T. J. Klopfenstein, D. M. Feuz, and R. N. Funston. 2006. Effects of pre- and post-partum nutrition on reproduction in spring calving cows and calf feedlot performance. *J. Anim. Sci.* 84:2582–2589.
- Stock, R. A., J. M. Lewis, T. J. Klopfenstein, and C. T. Milton. 2000. Review of new information on the use of wet and dry milling feed by-products in feedlot diets. *J. Anim. Sci.* 77(E-Suppl/1.23):1–12.
- Underwood, K. R., J. F. Tong, J. M. Kinzey, P. L. Price, E. E. Grings, B. W. Hess, W. J. Means, and M. Du. 2008. Gestational nutrition affects growth and adipose tissue deposition in steers. *West. Sec. Am. Soc. Anim. Sci.* 59:29–32.
- Vasconcelos, J. T., J. E. Sawyer, L. O. Tedeschi, F. T. McCollum, and L. W. Greene. 2009. Effects of different growing diets on performance, carcass characteristics, insulin sensitivity, and accretion of intramuscular and subcutaneous adipose tissue of feedlot cattle. *J. Anim. Sci.* 87:1540–1547.
- Wittum, T. E., and L. J. Perino. 1995. Passive immune status at postpartum hour 24 and long-term health and performance of calves. *Am. J. Vet. Res.* 56:1149–54.