Feeding distiller’s grains as an energy source to gestating and lactating beef heifers: Impact on female progeny growth, puberty attainment, and reproductive processes

P. J. Gunn,*2 J. P. Schoonmaker,§ R. P. Lemenager,§ and G. A. Bridges†

*Department of Animal Science, Iowa State University, Ames 50011; §Department of Animal Sciences, Purdue University, West Lafayette, IN 47907; and †North Central Research and Outreach Center, University of Minnesota, Grand Rapids 55744

ABSTRACT: This study compared postweaning growth, puberty attainment, and reproductive processes of female progeny (n = 33) born to Angus-Simmental beef heifers treated with either a control diet or a diet in which dried distiller’s grains with solubles (DDGS) were fed as an energy source during late gestation and early lactation. From 192 d of gestation through 118 ± 4 d in lactation, dams were fed either a corn silage–based control diet (CON) or corn residue with DDGS, where DDGS were supplemented as an energy source (DG). Diets were formulated to provide similar daily NEg between diets, but CP requirements were drastically exceeded in the DG treatment. Heifer progeny (n = 33) were weaned, commingled at 191 ± 4 d of age, and similarly managed for the remainder of the project. Heifer BW and blood samples for progesterone assessment to determine onset of puberty were collected weekly beginning at weaning. At 255 ± 4 d of age, a single follicular wave was mapped via ultrasonography in 10 prepubertal heifers per treatment. Prepubertal antral follicle count and ovarian size were determined at 253 ± 4 d of age. Hip height was recorded at 213, 297, and 437 ± 4 d of age. Estrous synchronization and AI was initiated at 447 ± 4 d of age. Binary data were analyzed with the GLIMMIX procedures of SAS and all other data were analyzed with the MIXED procedures of SAS. Progeny from DG-treated dams tended to be heavier (P = 0.08) than progeny from CON-treated dams from weaning until breeding. In addition, DG progeny had a greater (P < 0.01) frame score than CON throughout the developmental period. Ovarian size, antral follicle count, and follicular growth parameters did not differ between treatments. Age at puberty did not differ between CON (303 ± 10 d) and DG (320 ± 10 d) progeny; however, BW at puberty was greater (P = 0.01) for DG (326 ± 7 kg) than CON (298 ± 8 kg) progeny. Pregnancy rates to AI were greater (P = 0.05) in DG progeny (70.6%) than CON (33.3%), but overall breeding season pregnancy rate did not differ (P = 0.97). Moreover, rate of dystocia in female progeny at first parturition and grand-offspring birth BW did not differ due to treatment (P ≥ 0.74). In summary, feeding DDGS as an energy source during late gestation and early lactation to first-parity heifers resulted in female progeny with greater skeletal growth that were heavier at onset of puberty and had increased AI pregnancy rates.

Key words: beef heifer, developmental programming, dried distiller’s grains with solubles, fertility, follicular wave, puberty


INTRODUCTION

Dried distiller’s grains with solubles (DDGS) are rich in both protein and energy and may be an economical alternative to corn in ruminant diets. However, when DDGS are fed as the primary energy
source in the diets of reproducing females, the diet contains high concentrations of CP and fat. Not only may these components directly affect animal performance and reproductive processes, they may also impact subsequent progeny performance through the mechanisms associated with developmental programming (Reynolds et al., 2010). When fed at moderate or high amounts during gestation (Radunz et al., 2010; Wilson et al., 2012) or lactation (Shike et al., 2009; Shee et al., 2012; Gunn et al., 2014a,b), DDGS did not negatively impact fertility. However, few studies have investigated the impact of feeding high dietary amounts of DDGS during late gestation and early lactation on subsequent heifer progeny performance.

Previous studies have reported that altering maternal diet during gestation can affect the reproductive development of female progeny in both beef (Mossa et al., 2010; Sullivan et al., 2009; Echternkamp et al., 2012) and sheep (Da Silva et al., 2002, 2003) and ultimately impact fertility of female progeny in beef cattle (Martin et al., 2007; Cushman et al., 2014). However, reports to date have been inconsistent, and to our knowledge, none have reported on the effects of feeding DDGS during both late gestation and early lactation. Therefore, the objectives of this study were to assess postweaning growth, pubertal attainment, and fertility of female progeny from heifers fed DDGS as an energy source during the last trimester of pregnancy and early lactation. It was hypothesized that progeny of DDGS-fed heifers would not differ in postweaning growth but would have suppressed reproductive development and impaired fertility due to excess maternal dietary CP.

**MATERIALS AND METHODS**

**Animals and Diets**

All animals were handled in accordance with procedures approved by the Purdue Animal Care and Use Committee. Yearling Angus-Simmental heifers \( (n = 78) \) of similar genetic background, confirmed to have conceived on the same date in the previous breeding season and all pregnant to the same sire, were used in a randomized complete block design study to elucidate the effects of feeding DDGS as a primary energy source during late gestation and early lactation on postweaning growth and reproductive development of their female progeny. The study was conducted at the Purdue Animal Sciences Research and Education Center (ASREC) in West Lafayette, IN.

At 192 d of gestation, dams were blocked by BCS and stratified by BW within BCS and assigned to 1 of 2 drylot pens. One dietary treatment was assigned to each pen and included 1) a silage-based total mixed ration (corn silage–based control diet [CON]) or 2) corn residue with DDGS, where DDGS were supplemented as an energy source (DG). Diets were formulated to meet or exceed the dam’s nutrient requirements during late gestation and, subsequently, early lactation (NRC, 2000). All diets were formulated using individual ingredient chemical composition analysis obtained by wet chemistry methods before the start of the trial (Sure-Tech Laboratories, Indianapolis, IN). Treatments were formulated to deliver a similar amount of daily NE\(_g\) and for dam BW to be similar throughout the study. Dietary energy was formulated for heifer dams to attain a prepartum ADG of 0.45 kg and 85% of mature BW at parturition. Subsequent postpartum ADG was targeted at 0.39 kg. A more detailed description of diets and dietary formulation can be found in Gunn et al. (2014b). Due to bunk design and ration delivery, it was impossible to restrict treatment access by calves; therefore, calves may have consumed maternal diets during the neonatal period.

Dietary treatments to the dams concluded at 118 ± 4 d postpartum (DPP). Once dietary treatment concluded, all cow–calf pairs across treatments were commingled, placed on pasture, and managed as a singular group until weaning at 191 ± 4 DPP. In addition, heifer progeny were given ad libitum access to creep feed devoid of DDGS (18.2% CP and 1.39 Mcal NE\(_g\)/kg on DM basis) for 24 d immediately before weaning. Results of maternal performance, parturition, and reproductive efficiency as well as preweaning progeny performance are presented by Gunn et al. (2014b).

Heifer progeny \( (n = 15 \) for CON and \( n = 18 \) for DG) remained commingled and were managed as a singular group from weaning through their first breeding season. Immediately following weaning, heifers were placed on a high-fiber total mixed ration designed to meet or exceed the requirements of a developing heifer to reach 65% of mature BW by breeding (NRC, 2000; Table 1). Ration delivery occurred once daily at approximately 0900 h in fence line bunks and was designed to create a constant gain of 0.70 kg/d throughout the developmental phase. Intakes were adjusted as needed based on mean weekly BW measurements of the commingled group to obtain the desired ADG of the group. Individual feed ingredients were analyzed weekly for DM via forced-air oven at 60°C for 72 h to adjust intake for dietary moisture content. Composite feed samples were collected weekly and frozen at −20°C until ration delivery was terminated at AI. Subsequently, composite feed samples were subsampled and analyzed for chemical composition by wet chemistry methods (AOAC, 1990; Sure-Tech Laboratories). Following AI, heifers were returned to
the herd, placed on pasture, and similarly managed with the remainder of the ASREC yearling heifers. One heifer from the DG treatment was removed from the study due to gross reproductive tract abnormalities.

### Postweaning Growth

Between weaning and estrous synchronization, BW was measured at 7-d intervals and BCS (1 = emaciated and 9 = obese; Wagner et al., 1988) was assessed at 28-d intervals. Weight and BCS at puberty were then retrospectively ascertained based on hormonal determination of date of puberty (described below). In addition, percent of mature BW at puberty was calculated using the average mature weight of the cow herd (636 kg) obtained the previous fall. Hip height was measured at 213, 297, and 437 ± 4 d of age.

### Blood Sampling and Analyses

Blood samples were collected at 7-d intervals from weaning until initiation of estrous synchronization for determination of day of age at puberty. Samples were collected via coccygeal venipuncture in 6-mL tubes containing EDTA (BD Vacutainer; Becton, Dickinson and Co., Franklin Lakes, NJ) and immediately placed on ice. Samples were centrifuged at 1,750 × g for 25 min at 4°C and plasma was recovered, transferred to 5 mL polystyrene tubes, and frozen at −20°C until analyzed. Age at puberty was defined as 7 d before the date of a collection in which a blood sample contained >2 ng/mL of progesterone or 7 d before the first of 2 collections in which both blood samples contained >1 ng/mL of progesterone. Heifers that reached puberty before 300 d of age were considered to have experienced precocious puberty (Gaesser et al., 2006).

Progesterone concentration was determined using a commercially available RIA kit (Coat-A-Count; Siemens Medical Solutions Diagnostics, Los Angeles, CA). Across 6 assays, the average intra-assay CV was 2.4% and the interassay CV for pooled plasma samples containing 0.19 and 6.35 ng/mL of progesterone were 3.6 and 3.2%, respectively. The average sensitivity across assays was 0.25 ng/mL (95% confidence interval).

Plasma samples collected at 191, 325, and 436 ± 4 d of age were also analyzed for plasma urea nitrogen (PUN) using a commercial kit (Urea Nitrogen Procedure Number 0580; Stanbio Laboratory, Boerne, TX) as reported by Gunn et al. (2009). Samples were read in 96-well polystyrene plates (Becton, Dickinson and Co.) on an Opsys MR microplate reader (Dynex Technologies Inc., Chantilly, VA) at 530 nm. Across 3 assays, the average intra-assay CV was 3.9% and the interassay CV for a pooled serum sample containing 4.31 mg/dL of urea nitrogen was 5.4%.

### Ovarian Morphology and Reproductive Tract Development

Prepubertal antral follicle counts and ovarian length and width were measured at 253 ± 4 d of age via transrectal ultrasonography (variable megahertz linear array transducer; MicroMaxx; Sonosite, Bothell, WA). The number of antral follicles ≥3 mm in diameter was recorded for each ovary, and heifers were categorized as having a low (<16), intermediate (16 to 24), or high (>24) combined antral follicle count (Ireland et al., 2008; Cushman et al., 2009). Data were collected on each heifer and retrospectively removed from the data set if the heifer was determined to have been pubertal before ovarian measurements. Pelvic area was calculated from internal pelvic measurements taken using a Rice pelvimeter (Lane Mfg., Denver, CO) at 440 ± 4 d of age.

At 255 ± 4 DPP, a subsample of 10 prepubertal heifers from each treatment were randomly selected to undergo daily transrectal ultrasonography (variable megahertz linear array transducer; MicroMaxx; Sonosite) for a period of time sufficient to identify and characterize a single prepubertal follicular wave in its entirety. A single trained technician conducted all ovarian ultrasonography. The number, location, and diameter of all ovarian follicles ≥3 mm in diameter was recorded by
Excess maternal protein and heifer progeny

drawing sketches of both ovaries during each examination. The dominant follicle was recognized as the largest growing follicle during the follicular wave, and the secondary follicle was the second largest growing follicle identified during the wave of interest. Maximum diameter of the dominant and secondary follicle was defined as the largest diameter achieved during the follicular wave as determined by measuring the largest cross-sectional diameter using the caliper function of the ultrasound. The size at which the dominant follicle attained dominance was defined as the cross-sectional measurement taken on the first day in which the dominant follicle was at least 1 mm larger in diameter than any other growing follicle of that wave. Duration of follicle dominance was defined as the number of days from attainment of dominance until emergence of the subsequent follicular wave. Emergence of the follicular wave was determined retrospectively and defined as the day on which the dominant follicle could be traced back to be a member of a cohort of growing follicles 4 mm in diameter. Duration of the follicular wave, also referred to as wavelength, was determined to be the number of days from emergence of the follicular wave of interest until emergence of the subsequent wave. The mean number of antral follicles per day over the duration of the wave was also calculated. Daily ultrasound evaluation of individual heifer progeny was terminated once the dominant follicle of the subsequent follicular wave could be identified. One heifer from the DG treatment and 2 heifers from the CON treatment ovulated during follicular wave characterization, and therefore, their follicular data were removed from the data set and not used for statistical analysis.

**Estrous Synchronization and Breeding**

Heifers were enrolled in the 5-d Select-Synch + controlled internal drug release (CIDR) insert and timed-AI (TAI) protocol at 447 ± 4 d of age. Estrous synchronization consisted of insertion of an intravaginal progesterone insert (CIDR; Pfizer Animal Health, New York, NY) concurrent with administration of 100 μg of GnRH (Cystorelin; Merial Animal Health, Duluth, GA) at protocol initiation. Five days later, the CIDR insert was removed and heifers received 2 separate but concurrent 25 mg doses of PGF₂α (Lutalyse; Pfizer Animal Health). Heifers were visually detected for estrus, with the aid of tail paint (Tell Tail; FIL, Mount Maunganui, New Zealand), twice daily. Heifers detected in estrus within 60 h after prostaglandin administration were bred by AI based on the morning/evening rule. Seventy-two hours after CIDR insert removal, heifers not detected in estrus were TAI concurrent with GnRH administration (Cystorelin; 100 μg). Any heifer observed in estrus up to and through TAI was recorded and estrous response as well as interval from prostaglandin administration until estrus was calculated through TAI. However, any heifer not in estrus within 60 h after prostaglandin administration was classified as receiving TAI as they were not bred on the AM/PM rule. All heifers were AI by a singular technician to the same bull with all semen procured from a single collection.

Immediately following TAI, heifers were placed on pasture for the duration of the breeding season. Ten days following TAI, a fertile bull was placed with heifers for 56 d. Visual estrus detection continued twice daily throughout the breeding season and incidence of estrus was recorded. Pregnancy diagnosis was performed 34 d after TAI using transrectal ultrasonography to determine AI pregnancy rates. Final pregnancy diagnosis was conducted via transrectal ultrasound 40 d after the conclusion of the breeding season to determine breeding season pregnancy rates. In heifers that were diagnosed as pregnant to natural service, fetal age was estimated using ultrasonography and confirmed by estrus detection data.

**Parturition**

After parturition, sex of the calf was recorded, BW of the calf was measured, and a calving difficulty score (1 = no assistance, 2 = easy pull, 3 = mechanically assisted pull, 4 = abnormal presentation, and 5 = caesarian section) was assigned. Calves were monitored to ensure they nursed and received colostrum within 12 h after birth. A calf vigor score (1 = nursed on own immediately, 2 = nursed on own but slow to start, 3 = required assistance to nurse, and 4 = died shortly after birth) was assigned within 12 h after birth. In addition, cow udder score (1 = ideal, 2 = not ideal but calf nursed on own, 3 = may require intervention; cull cow with no daughters retained, and 4 = worst case; cull cow with no daughters retained) was assessed 48 h postpartum, allowing for parturition induced mammary edema to subside. Bull calves were castrated within 48 h of birth. For purposes of data analysis, dystocia was categorized on a yes/no basis. Therefore, any heifer with a calving difficulty score of greater than 1 was given a “yes” for dystocia.

**Statistical Analysis**

Differences between treatments for categorical data including ovarian antral follicle count categorization and pubertal status at 300 and 365 d of age and at estrous synchronization as well as pregnancy status were analyzed using the GLIMMIX procedure of SAS.
RESULTS

Postweaning Growth and Plasma Urea Nitrogen

Heifer progeny of DG-treated dams tended to be heavier than heifer progeny of CON-treated dams throughout the postweaning period \((P = 0.08; \text{Fig. 1})\). However, neither ADG \((P = 0.64; \text{Table 2})\) nor BCS \((P = 0.32; \text{ Fig. 2})\) differed during the postweaning period. In contrast, hip height was greater in progeny of DG-treated dams than CON-treated dams \((P = 0.007; \text{Fig. 3})\). A treatment \(\times\) day interaction was noted for circulating PUN concentrations, as heifers of DG dams had greater PUN concentrations at weaning than heifers of CON dams \((P = 0.003; \text{Fig. 4})\); however, no differences were noted \((P \geq 0.31)\) between treatments at either 325 or 436 \pm 4 d of age.

Reproductive Tract Development and Puberty

Prepubertal antral follicle count, ovarian height, and ovarian length did not differ between treatments \((P \geq 0.15; \text{Table 3})\). Moreover, the proportion of heifers classified as having low, intermediate, and high antral follicle counts did not differ due to treatment \((P \geq 0.53)\). However, ovarian length was positively related to antral follicle count \((r = 0.84, P < 0.001)\). Pelvic area at 440 \pm 4 d of age was not different due to maternal treatment \((P = 0.51)\). Body weight at puberty attainment and estimated percent of mature BW at puberty were decreased \((P = 0.02; \text{Table 2})\) in heifer progeny from CON-treated dams compared to heifer progeny from DG-treated dams. Moreover, survival analysis using the Log-Rank method determined that heifers from CON-treated dams reached puberty at a lighter BW \((P = 0.006; \text{Fig. 5a})\) than heifers of DG-treated dams. Body weight at puberty was also positively related to birth BW \((r = 0.62, P < 0.001)\) and prewean ADG \((r = 0.43, P = 0.01)\). However, age at puberty \((\text{Table 2})\) as well as survival analysis of age at puberty \((\text{Fig. 5b})\) was not affected by maternal treatment \((P \geq 0.39)\). Body condition score at puberty, proportion of heifers experiencing precocious puberty, proportion of heifers pubertal at 365 d of age, and proportion of heifers pubertal by estrous synchronization did not differ due to maternal treatment \((P \geq 0.32)\).
Excess maternal protein and heifer progeny

Ovarian Follicular Wave Characterization

For the initial analysis of prepubertal follicular wave characteristics, heifer age at follicular wave emergence (Table 4) was used as a covariate. This analysis indicated that the heifer progeny of CON-treated dams tended to have longer follicular waves ($P = 0.10$). However, follicular growth characteristics such as maximum dominant follicle and secondary follicle diameter, diameter of the dominant follicle when dominance was attained, duration of dominance, and antral follicle count did not differ ($P \geq 0.14$) in heifer progeny due to dietary treatment. Ancillary analyses of follicular data, which used days before puberty at the start of the wave as a covariate, revealed that wavelength, follicle growth, and daily antral follicle count did not differ in heifer progeny ($P \geq 0.33$) as a result of maternal treatment.

Table 2. Effect of maternal diet fed from 192 d of gestation through 118 ± 4 d in lactation on subsequent female progeny growth and puberty characteristics

<table>
<thead>
<tr>
<th>Item</th>
<th>Treatment</th>
<th>SEM 2</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>ADG, kg</td>
<td>CON</td>
<td>0.70</td>
<td>0.69</td>
</tr>
<tr>
<td>Age at puberty attainment, d</td>
<td>DG</td>
<td>0.69</td>
<td>0.02</td>
</tr>
<tr>
<td>Precocious puberty, $^3$</td>
<td>CON</td>
<td>303</td>
<td>10</td>
</tr>
<tr>
<td>% (n)</td>
<td>DG</td>
<td>315</td>
<td>3.96</td>
</tr>
<tr>
<td>Puberty by 365 d of age, % (n)</td>
<td>CON</td>
<td>87.7</td>
<td>0.10</td>
</tr>
<tr>
<td>Puberty by estrous synch. $^4$</td>
<td>DG</td>
<td>88.2</td>
<td>0.09</td>
</tr>
<tr>
<td>Weight at puberty, kg</td>
<td>CON</td>
<td>297.8</td>
<td>6.9</td>
</tr>
<tr>
<td>Percent mature wt at puberty $^5$</td>
<td>DG</td>
<td>323.6</td>
<td>16.9</td>
</tr>
<tr>
<td>BCS at puberty $^6$</td>
<td>CON</td>
<td>46.8</td>
<td>1.2</td>
</tr>
<tr>
<td></td>
<td>DG</td>
<td>50.8</td>
<td>0.02</td>
</tr>
</tbody>
</table>

1Maternal diet: CON = corn silage–based control diet; DG = corn residue with dried distillers grains supplemented as an energy source.

2Greater SEM presented ($n = 15$ for CON and $n = 17$ for DG).

3Percent of heifers in treatment reaching puberty before 300 d of age.

4Percent of heifers in treatment reaching puberty before estrous synchronization (447 ± 4 d of age).

5Estimated percent of mature weight when puberty was reached. Calculation based on 2010 mature weight of the herd at weaning (636 kg).

6Body condition score on a scale of 1 to 9 (1 = emaciated and 9 = obese; Wagner et al., 1988).

Estrous Synchronization, Breeding, and Parturition

The proportion of heifer progeny displaying estrus before TAI did not differ between treatments ($P = 0.74$; Table 5), and therefore, the proportion of heifers subjected to TAI did not differ due to maternal treat-

Figure 2. Effect of maternal treatment during the last trimester of pregnancy through 118 ± 4 d in lactation (CON = corn silage–based control diet; DG = corn residue with dried distillers grains supplemented as an energy source) on heifer progeny BCS. Body condition was graded on a scale of 1 to 9 (1 = emaciated and 9 = obese; Wagner et al., 1988). Main effects of treatment and day were $P = 0.32$ and $P < 0.001$, respectively.

Figure 3. Effect of maternal treatment during the last trimester of pregnancy through 118 ± 4 d in lactation (CON = corn silage–based control diet; DG = corn residue with dried distillers grains supplemented as an energy source) on heifer progeny hip height. Hip height score was affected by both treatment ($P = 0.007$) and day ($P < 0.001$).

Figure 4. Effect of maternal treatment during the last trimester of pregnancy through 118 ± 4 d in lactation (CON = corn silage–based control diet; DG = corn residue with dried distillers grains supplemented as an energy source) on heifer progeny plasma urea nitrogen. A treatment × day interaction ($P = 0.007$) was observed. Main effects of treatment and day were $P = 0.25$ and $P = 0.01$, respectively. Day on which plasma urea nitrogen differed between treatments ($P < 0.05$) is indicated with *.
ment \((P = 0.98)\). Of the heifers that did exhibit estrus before TAI, the interval between prostaglandin administration and estrus expression did not differ between treatments \((P = 0.26; \text{Table 5})\). Overall pregnancy rate to AI was greater in heifer progeny from DG-treated dams than heifer progeny from CON-treated dams \((P = 0.05; \text{Table 5})\). Nonetheless, overall breeding season pregnancy rate did not differ between treatments \((P = 0.97)\). In addition, maternal treatment did not affect heifer progeny first-parity gestation length, calf birth BW, calving difficulty, rate of dystocia, calf vigor, or udder structure \((P \geq 0.26; \text{data not shown})\).

### DISCUSSION

The present study was conducted to elucidate potential effects of feeding first-parity females DDGS as a primary energy source, and therefore grossly overfeeding protein, during both late gestation and early lactation, on heifer progeny postweaning growth, reproductive tract morphology, puberty attainment, and fertility. Due to previous reports of reduced antral follicle counts when dams were nutritionally suppressed during the first trimester (Mossa et al., 2010; Echternkamp et al., 2012) or overfed energy and protein during the second trimester of pregnancy (Sullivan et al., 2009), it was hypothesized that progeny of DG-fed dams would have suppressed reproductive development and impaired fertility. A greater BW at puberty in heifer progeny of DG dams when compared with progeny of CON dams partially supported our hypothesis; however, DG progeny had a similar age at puberty and improved fertility as measured by first service AI pregnancy rates.

#### Postweaning Growth and Plasma Urea Nitrogen

Heifers remained commingled throughout the developmental period and were fed a similar diet to elucidate if maternal diet could impact growth parameters. Although BW tended to differ during the postweaning period, ADG of heifer progeny during that period was not impacted by maternal treatment. These results suggest that feeding DDGS as an energy source, and thus overfeeding protein, during late gestation and early lactation does not affect heifer progeny postweaning BW rate of gain and the tendency for difference in postweaning BW is due to preweaning growth divergence between treatments. Preweaning ADG of heifer progeny in the present study was increased in the DG treatment (Gunn et al., 2014b). It is possible that preweaning ADG was greater in DG progeny due to great-
er daily DMI during the neonatal period, particularly during the 24-d preweaning creep period. However; DMI could not be quantified. The potential also exists that calves consumed some of their dam’s daily ration; however, this consumption would have been limited because their dams consumed the allotted DDGS within minutes of delivery, which limited bunk accessibility to progeny. Moreover, progeny of CON dams also had access to the CON treatment due to bunk design. Nonetheless, similar postweaning ADG between progeny of DG- and CON-treated dams is complementary to results from studies in lambs (Radunz et al., 2011)

Table 4. Effect of maternal diet fed from 192 d of gestation through 118 ± 4 d in lactation on subsequent female progeny follicular wave dynamics

<table>
<thead>
<tr>
<th>Item</th>
<th>Treatment</th>
<th>SEM²</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CON</td>
<td>DG</td>
<td></td>
</tr>
<tr>
<td>Wavelength, d</td>
<td>7.38</td>
<td>6.89</td>
<td>0.20</td>
</tr>
<tr>
<td>Dominant follicle diameter, mm</td>
<td>11.7</td>
<td>10.8</td>
<td>0.44</td>
</tr>
<tr>
<td>Secondary follicle diameter, mm</td>
<td>7.97</td>
<td>7.64</td>
<td>0.28</td>
</tr>
<tr>
<td>Size at dominance, mm</td>
<td>7.95</td>
<td>7.54</td>
<td>0.51</td>
</tr>
<tr>
<td>Duration of dominance, d</td>
<td>4.32</td>
<td>4.04</td>
<td>0.47</td>
</tr>
<tr>
<td>Total follicles</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day 1 of wave</td>
<td>22.8</td>
<td>22.0</td>
<td>2.4</td>
</tr>
<tr>
<td>Day 2 of wave</td>
<td>21.9</td>
<td>21.7</td>
<td>2.4</td>
</tr>
<tr>
<td>Day 3 of wave</td>
<td>19.6</td>
<td>21.0</td>
<td>1.8</td>
</tr>
<tr>
<td>Average of entire wave</td>
<td>21.3</td>
<td>22.2</td>
<td>1.9</td>
</tr>
</tbody>
</table>

1Days of age at wave emergence was used as a covariate in the statistical model.
2Maternal diet: CON = corn silage–based control diet; DG = corn residue with dried distillers grains supplemented as an energy source.
3Greater SEM presented (n = 8 for CON and n = 9 for DG).

Although postweaning ADG did not differ due to maternal dietary treatment, skeletal growth parameters were altered. Heifer progeny from DG-treated dams had greater hip height throughout the postweaning period. Although it is not clear why heifers born to DG dams had increased postweaning hip height, we hypothesize it may be a function of the amount of Ca and P in the maternal diet. Diets were formulated to meet NRC (2000) recommendations and deliver an acceptable Ca:P ratio; however, the inherent increase in dietary P intake associated with feeding DDGS required additional supplemental Ca in dams’ diets containing DDGS. Therefore, DG-treated dams were fed an excess of not only P but also Ca. To our knowledge, the effects of overfeeding these elements on offspring growth has not been studied in beef cattle, but Ca supplementation during pregnancy has been reported to impact bone growth in human fetuses and guinea pig offspring, as reviewed by Atkinson (2011). However, data reviewed by Atkinson (2011) largely compared adequate with inadequate amounts of maternal dietary Ca. Alternatively, increased PUFA concentrations in the milk of DG dams during the neonatal period (Gunn et al., 2011) may have increased circulating concentrations of IGF-1 (Robinson et al., 2002), promoting long bone growth during the neonatal period. Because differences in hip height remained similar throughout the developmental period, differences in skeletal growth rate were likely limited to the fetal period, the neonatal period, or a combination of both periods. Since no measurements were taken at birth in the current study to determine differential skeletal growth in utero, the period before weaning where initial differences in heifer skeletal growth occurred cannot be determined.

In addition to altered skeletal growth as a result of maternal diet, blood PUN was also impacted. However, the interaction noted for circulating PUN concentrations is not easily explained. Because it was assumed that DMI did not differ between treatments during the postweaning period, we expected similarities in PUN observed at 325 and 436 ± 4 d of age. However, the reason for which increased PUN was noted in progeny of DG-treated dams at weaning (191 ± 4 d of age) is less clear. Altered nitrogen metabolism
is a possibility; however, there was a lack of differences in PUN later in the developmental period. This suggests that nitrogen metabolism capabilities were not altered. Therefore, it is more likely that DMI of the DG progeny was greater during the 24-d preweaning creep feeding period, which would result in greater daily intake of CP on a grams per day basis and therefore greater PUN concentrations.

**Reproductive Tract Development, Follicular Waves, and Puberty**

Although the effects of maternal nutrition on male and female progeny growth have been and currently are being studied in depth, the effects of maternal nutrition on reproductive development of the female progeny are not well defined. One reproductive measurement that has been studied in more depth recently is the ovarian antral follicle count. Although the relationship between antral follicle count and fertility has not been fully established, Maurer and Echternkamp (1985) reported reduced antral follicle counts in repeat-breeder cows, and Ireland et al. (2008) reported a positive relationship between antral follicle count and fertility. Therefore, the connection has been made that increased antral follicle counts may be related to improved fertility. Previous studies (Sullivan et al., 2009; Mossa et al., 2010; Echternkamp et al., 2012) have reported that nutritional manipulation during early gestation in first-parity dams can impact ovarian antral follicle count in their female progeny. In contrast, however, Cushman et al. (2014) reported no differences in antral follicle count of heifer progeny of mature cows that were fed 75, 100, or 125% of NRC maintenance requirements during the last 2 trimesters of pregnancy. Although progeny in the current study were from first-parity dams and only prepubertal antral follicle counts were obtained, results from the current dataset is consistent with those of Cushman et al. (2014), who reported no differences in antral follicle counts obtained in progeny at 14 mo of age. Moreover, in the current study, heifer progeny from DG-treated dams were significantly heavier at birth (Gunn et al., 2014b); however, no differences were observed in antral follicle counts between treatments, and birth BW and antral follicle count were not correlated. This is in contrast to Cushman et al. (2009), who reported that antral follicle counts were positively correlated with birth BW. Collectively, these studies may suggest that the timing of nutritional alteration may be an important factor that can impact antral follicle count. Alterations during early (Mossa et al., 2010; Echternkamp et al., 2012) and mid gestation (Sullivan et al., 2009) appear to have a greater impact on progeny antral follicle count than nutritional modulation in late gestation. It should not be overlooked, however, that Da Silva et al. (2002, 2003) reported a decrease in antral follicle counts of ewe lambs resulting from dams fed a high plane of nutrition during late gestation. Therefore, individual dietary components and ratios of those constituents within the dam’s diet may also impact the physiological cues that result in alterations in progeny antral follicle count.

To our knowledge, the effects of maternal nutrition on ovarian follicular wave characteristics of subsequent progeny have not been previously conducted. Gasser et al. (2006) reported that prepubertal dominant follicle diameter and follicular wavelength increased leading up to induction of puberty. In the current study, when day of age at wave initiation was used as a covariate in the model, the CON progeny tended to have a longer wavelength than the DG progeny. Because there was no difference between treatments in day of age at the beginning of the characterization period, the tendency for a longer wavelength suggested that progeny of CON-treated dams may be advanced in reproductive maturation, thus promoting an earlier onset of puberty. Although not significant, the numerical increase in dominant follicle diameter for CON progeny supports this notion. However, it was unclear if the tendency for a difference in wavelength could be attributed directly to maternal dietary treatment or if it was an indirect effect of the number of days before puberty at wave initiation. Therefore, a secondary analysis was conducted using days before puberty as a covariate. When the secondary analysis was conducted, the tendency in wavelength difference between treatments was nullified, which indicates that maternal treatment was likely regulating puberty and not directly regulating duration of the follicular wave.

Progeny of CON-treated dams obtained puberty at a lighter BW and a numerically younger age when compared to progeny of DG-treated dams. Limited number of heifers in the current study may have limited the ability to detect statistical differences in age at puberty between treatments. Nonetheless, it is acknowledged that onset of puberty in beef cattle may be characterized by surpassing a threshold for a combination of parameters including age, BW, and BCS (Yelich et al., 1995). In addition, the data from this current study suggest that progeny of DG-treated dams had increased lean tissue growth throughout the postweaning phase, as characterized by increased hip height (skeletal growth) and numerically lower BCS. Therefore, DG progeny may have needed more time and BW to reach the needed body composition to allow puberty attainment. If so, it is feasible that maternal treatment in the current study indirectly regulated
progeny puberty attainment through an alteration in growth pattern and not directly through an alteration of the hypothalamic–pituitary–ovarian axis. Cushman et al. (2014) reported no differences in age at puberty for heifers progeny from mature cows fed differing amounts of energy during the last 2 trimesters of gestation, and Martin et al. (2007) reported that there was no difference in age at puberty of heifer progeny resulting from dams supplemented with 0.45 kg/d of a protein supplement during late gestation compared to nonsupplemented dams. However, dams in the current study were fed similar amounts of energy, with CP in the DG treatment drastically exceeding NRC requirements during the last trimester of gestation through mid lactation. As the nutritional demands of the first-parity dam are greater than those of the mature cow due to the continued growth of the first-parity dam, it is conceivable that nutritional stressors may result in a more pronounced phenotypic alteration in the progeny of those females. Given the multifaceted cascade of events that regulate attainment of puberty, how and to what extent feeding DDGS during late gestation and early lactation may alter puberty onset requires further investigation.

Breeding and Parturition

Although progeny of DG-treated dams reached puberty at a greater weight, pregnancy rates to AI were greater than in CON progeny. Although the number of observations is limited in the current study, both Martin et al. (2007) and Cushman et al. (2014) reported that heifer progeny born to dams fed a higher plane of nutrition during late pregnancy became pregnant earlier in the breeding season. However, as there were no differences between treatments in the proportion of females that were pubertal at initiation of estrous synchronization, estrous response, ovarian characteristics, and overall breeding season pregnancy rates in the current study, the underlying reason for differences in AI pregnancy rate still remains unanswered.

Birth BW, rate of dystocia, and calving difficulty were all increased at birth for DG progeny used in this study (Gunn et al., 2014b). However, there was no apparent transgenerational effect of dam nutritional treatment on grand-offspring birth parameters. This is in contrast to Blair et al. (2010), who reported increased birth BW of grand-offspring of heavy weight ewes fed ad libitum diets during late gestation, regardless of how their offspring were managed. However, in that study, the original test diets varied in daily energy consumption by the dam. This is in stark contrast to the current study that fed similar amounts of energy but differing amounts of CP during grand-dam gestation.

In summary, feeding DDGS as an energy source during late gestation and early lactation to first-parity dams did not affect postweaning BW gains in heifer progeny but did alter skeletal growth as determined by an increased hip height. Puberty attainment occurred at a greater weight in progeny of DDGS-fed dams; however, ovarian function was not altered. Although observations were limited, AI pregnancy rates were increased in heifer progeny from DG-treated dams when compared with the control. Therefore, feeding DDGS in combination with a low-quality forage source to gestating and lactating first-parity dams appears to be a viable alternative to traditional wintering rations without having a negative impact on fertility of the female offspring. Nonetheless, as data on developmental programming in female progeny is limited, further research should be directed at how maternal nutrition might regulate reproductive development of female progeny in beef cattle.

LITERATURE CITED


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