KEY WORDS: beef cattle, fetal programming, nutrition, supplementation

INTRODUCTION

Many factors influence livestock nutrient requirements, including age, breed, season, and physiological function (NRC, 2000). Matching nutrient requirements with nutrient availability has been considered a key factor in optimizing production efficiency. Production cycle characteristics later in life. The concept of fetal programming is that maternal stimuli during critical periods of fetal development have long-term implications for offspring. Depending on timing, magnitude, and duration of nutrient limitation or supplementation, it is possible that early measures in life, such as calf birth BW, may be unaffected, whereas measures later in life, such as weaning BW, carcass characteristics, and reproductive traits, may be influenced. This body of research provides compelling evidence of a fetal programming response to maternal nutrition in beef cattle. Future competitiveness of the US beef industry will continue to be dependent on the use of high-forage diets to meet the majority of nutrient requirements. Consequences of nutrient restriction or supplementation must be considered not only on individual animal performance but also the developing fetus and its subsequent performance throughout life.


2 Corresponding author: rfunston2@unl.edu

Received August 8, 2011.

Accepted October 16, 2011.
tal development. Possible scenarios include 1) breeding of young dams resulting in competition for nutrients that are being partitioned toward maternal needs or those of the rapidly growing fetus; 2) increased incidences of multiple fetuses or large litters; 3) selection for increased milk production, which competes for nutrients with increasing energy demand from fetal and placental growth during late gestation; and 4) breeding of livestock during environmental conditions that result in poor pasture conditions during pregnancy (Wu et al., 2006; Reynolds et al., 2010). Studies have reported instances of compromised maternal nutrition during gestation resulting in increased neonatal mortality, intestinal and respiratory dysfunction, metabolic disorders, decreased postnatal growth rates, and reduced meat quality (Wu et al., 2006). Recent research also confirms that proper management of cow nutrition during gestation can improve progeny performance and health.

HEIFER PROGENY PERFORMANCE

Data from 2 Nebraska studies evaluating effects of late-gestation protein supplementation on heifer progeny performance are reported in Table 1. Martin et al. (2007) conducted a study with cows grazing dormant Sandhills range during late gestation. One group received a 42% CP (on a DM basis) cube offered 3 times weekly at the equivalent of 0.45 kg/d, whereas another group received no supplement. Heifer calf birth BW from supplemented and nonsupplemented dams was not different; however, heifer progeny from supplemented cows had greater 205-d adjusted weaning BW, prebreeding BW, BW at pregnancy diagnosis, and improved pregnancy rates compared with heifers from nonsupplemented dams. Martin et al. (2007) also reported that DMI, ADG, and residual feed intake between heifer progeny from supplemented and nonsupplemented dams was not different.

Funston et al. (2010b), using the same cow herd, offered a distillers-based supplement (28% CP, DM basis) 3 times weekly at the equivalent of 0.45 kg/d, or no supplement during late gestation as cows grazed either dormant Sandhills range or corn crop residue. Calf weaning BW was greater ($P = 0.04$) for heifers from protein-supplemented dams, whereas Martin et al. (2007) reported a trend for increased weaning BW for heifers from protein-supplemented dams. Funston et al. (2010b) also reported a decreased age at puberty for heifers from protein-supplemented cows and a trend for greater pregnancy rates when compared with heifers from nonsupplemented dams, possibly related to decreased age at puberty. Similarly, Corah et al. (1975) reported that heifers born to primiparous heifers fed 100% of their dietary energy requirement during the last 90 d of gestation were pubertal 19 d earlier than heifers born to primiparous heifers fed 65% of their dietary energy requirement.

Funston et al. (2010b) reported no differences in heifer BW at prebreeding and no differences in calf birth BW, calf production, or second calf rebreeding when comparing heifer progeny from supplemented and nonsupplemented cows. Martin et al. (2007) reported a 28% increase in the proportion of heifers calving in the first 21 d of the calving season from protein-supplemented dams compared with heifers from nonsupplemented dams.

A long-term research project at the USDA-ARS Fort Keogh Livestock and Range Research Laboratory in Miles City, Montana, has also identified differences in performance of heifer progeny from cows provided 2 levels of harvested feed inputs during winter grazing (last 4 to 5 mo of pregnancy; Roberts et al., 2009a). Beginning in the fall of 2001, cows in a stable composite population (1/2 Red Angus, 1/4 Charolais, 1/4 Tarentaise) were randomly assigned to be fed levels of harvested feed from December to March of each year that were expected to be marginal (MARG) or adequate (ADEQ), based on average quality and availability of winter forage and on NRC requirements. Each group of cows was managed on separate pastures during the winter to allow differential feeding. For the majority of the winters in this study, pasture forage was readily available for grazing and the only additional harvested feed provided was alfalfa cubes or hay, depending on year, as a supplemental source of protein. This supplement was fed either daily or every other day to achieve approximately 1.8 kg/d for each ADEQ cow and approximately 1.1 kg/d for each MARG cow. When access to pasture forage was

### Table 1. Effect of maternal protein supplementation on heifer progeny performance

<table>
<thead>
<tr>
<th>Item</th>
<th>Martin et al. (2007)</th>
<th>Funston et al. (2010b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weaning BW, kg</td>
<td>207</td>
<td>212</td>
</tr>
<tr>
<td>Adjusted 205-d wt, kg</td>
<td>218&lt;sup&gt;a&lt;/sup&gt;</td>
<td>226&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>DMI, kg/d</td>
<td>6.50</td>
<td>6.75</td>
</tr>
<tr>
<td>ADG, kg/d</td>
<td>0.41</td>
<td>0.40</td>
</tr>
<tr>
<td>Residual feed intake, kg</td>
<td>−0.12</td>
<td>0.07</td>
</tr>
<tr>
<td>Age at puberty, d</td>
<td>334</td>
<td>339</td>
</tr>
<tr>
<td>Pregnant, %</td>
<td>80&lt;sup&gt;a&lt;/sup&gt;</td>
<td>93&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a,b</sup>Means within a study with different superscripts differ ($P \leq 0.05$).

<sup>NS</sup> = dams did not receive protein supplement while grazing dormant Sandhills range during the last third of gestation; SUP = dams were supplemented 3 times per week with the equivalent of 0.45 kg/d of 42% CP cube (DM basis) while grazing dormant Sandhills range during the last third of gestation.

<sup>2</sup:NS = dams did not receive protein supplement while grazing dormant Sandhills range or corn residue during the last third of gestation; SUP = dams were supplemented 3 times per week with the equivalent of 0.45 kg/d of a 28% CP cube (DM basis) while grazing dormant Sandhills range or corn residue during the last third of gestation.
provided the MARG level of supplemental feed during late pregnancy had greater BW at 5 yr of age than cows from ADEQ dams. Measures of BCS at 5 yr of age were least for winter, and restricted heifers were provided MARG levels. Performance of heifers through first breeding indicate differences in growth, carcass, and reproductive performance due to postweaning heifer development treatment (Roberts et al., 2007, 2009b), but not nutritional treatment of their dams (data not reported). However, measures taken later in life were influenced by dam treatment and interaction of dam treatment and progeny treatment (Table 2), providing evidence that fetal programming can influence response to nutrient environment later in life. Regardless of their own feeding treatment, cows born from mothers who were provided the MARG level of supplemental feed during late pregnancy had greater BW at 5 yr of age than cows from ADEQ dams. Measures of BCS at 5 yr of age were least for restricted cows from ADEQ dams compared with the other cow × dam classifications. Restricted cows from ADEQ dams also appear to have reduced retention rates to 5 yr of age than other cow × dam classifications when culled for reproductive failure (Roberts et al., 2009a). Restricted cows from MARG-supplemented dams produced calves that had lighter birth and weaning BW than their contemporary herd mates born from ADEQ-supplemented dams. Circulating concentrations of IGF-I in a subset of these cows sampled before and after first calving and before re-breeding revealed an interaction of individual and dam nutrional treatments (Roberts et al., 2010). Concentrations of IGF-I were less in restricted cows from ADEQ dams than the other groups. Because this growth factor has been shown previously to be indicative of capacity for resumption of estrus after calving (Roberts et al., 1997), it is interesting to speculate a possible association with capacity for maintaining BW and reproductive function over time (Table 2).

### STEER PROGENY PERFORMANCE

In addition to altering growth and production of replacement females, variations in dietary protein and energy during pregnancy may also alter growth and carcass traits of steers reared for slaughter. Greenwood et al. (2009) reported that steers from cows nutritionally restricted during gestation had reduced live BW and carcass weight at 30 mo of age compared with steers from adequately fed cows. Both Larson et al. (2009) and Greenwood et al. (2009) reported a retail yield on a carcass-weight basis was greater in steers from cows subjected to nutrient restriction during pregnancy, indicating that an increased propensity for carcass fatness was not a consequence of nutritional restriction in utero. Underwood et al. (2010) reported that steers from cows that had grazed improved pasture from d 120 to 180 of gestation had greater BW gains, final BW, and HCW than steers from cows that had grazed native range during the same period of pregnancy, even though cows and steers were managed together for all other periods in life (Table 3). Furthermore, steers from cows that grazed improved pasture during gestation had increased backfat and tended to have improved marbling scores compared with steers from cows grazing native range.

To determine the effect dietary energy source had on progeny calf performance, Radunz (2009) offered cows 1 of 3 diets during gestation beginning on approximately d 209 until 1 wk before predicted calving date: hay (fiber), corn (starch), or distillers grains with solubles (fiber plus fat). Corn and distillers grains diets were limited fed to ensure isocaloric intake among all 3 treatments. Results indicated that there was reduced birth BW for calves from dams fed grass hay when compared with calves from the other 2 groups (Table 3), with an increase in calf BW reported through weaning when comparing calves from corn-fed dams with hay-fed dams. Feedlot performance among treatments was not different; however, calves from hay-fed dams required 8 and 10 more days on feed to reach a similar fat thickness when compared with calves from distillers- and corn-fed dams, respectively. Although final BW did not differ, Radunz (2009) reported greater HCW in steers from corn-fed dams compared with steers from dams fed dried distillers grains during late gestation, and a trend for increased marbling score

### Table 2. Effects of level of feed input provided to dam and to female progeny on progeny performance later in life

<table>
<thead>
<tr>
<th>Item</th>
<th>Marginal (1.1 kg/d)</th>
<th>Adequate (1.8 kg/d)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Restricted&lt;sup&gt;1&lt;/sup&gt;</td>
<td>Control&lt;sup&gt;1&lt;/sup&gt;</td>
</tr>
<tr>
<td>BW at 5 yr, kg</td>
<td>515</td>
<td>530</td>
</tr>
<tr>
<td>BCS at 5 yr, %</td>
<td>4.9</td>
<td>5.1</td>
</tr>
<tr>
<td>Retention at 5 yr, %</td>
<td>48</td>
<td>46</td>
</tr>
<tr>
<td>Calf BW at birth, kg</td>
<td>33.6&lt;sup&gt;4&lt;/sup&gt;</td>
<td>35</td>
</tr>
<tr>
<td>Calf BW at weaning, kg</td>
<td>196&lt;sup&gt;4&lt;/sup&gt;</td>
<td>201</td>
</tr>
</tbody>
</table>

<sup>1</sup>Differs (P < 0.05) from other means in same row (P < 0.001 for interaction of dam treatment and progeny treatment).

<sup>2</sup>Data from Roberts et al. (2009a).

<sup>3</sup>Amount of winter supplement to dam.

<sup>4</sup>Progeny treatment: restricted = 80% of feed provided to control during 140-d postweaning development and 1.1 kg/d supplement each subsequent winter; control = fed ad libitum during postweaning and 1.8 kg/d supplement each winter.

<sup>5</sup>P < 0.01 for effect of dam treatment and progeny treatment.

<sup>6</sup>Additional years of data analyzed since Roberts et al. (2009a).

<sup>7</sup>Data on calves of progeny.
for steers born to hay-fed cows compared with steers from corn-fed dams.

Stalker et al. (2006, 2007) reported steer progeny from dams supplemented the equivalent of a 0.45 kg/d (42% CP on a DM basis) cube during late gestation had no difference in calf birth BW compared with steers from nonsupplemented dams. Conversely, Larson et al. (2009), using the same cow herd, reported an increase in calf birth BW when comparing calves born with dams supplemented the equivalent of a 0.45 kg/d (28% CP, DM basis) cube during late gestation with calves from nonsupplemented dams. In the study reported by Stalker et al. (2006), cows were utilized in a switchback design, whereas cows utilized by Larson et al. (2009) remained on the same treatment over the 3-yr study.

Protein supplementation during late gestation increased weaning BW, ADG to weaning, and proportion of calves weaned when comparing calves from supplemented to nonsupplemented dams grazing dormant winter range (Stalker et al., 2006, 2007; Larson et al., 2009; Table 4). Stalker et al. (2006) reported no differences in steer progeny feedlot performance and carcass characteristics when comparing progeny from supplemented and nonsupplemented dams. However, Larson et al. (2009) reported increased ADG, HCW, and marbling scores in steers from supplemented dams. Furthermore, a greater proportion of steers from supplemented dams graded USDA Choice or greater when compared with steers from nonsupplemented dams. Nonsupplemented cows in the study by Larson et al. (2009) may have been under greater nutritional stress than Stalker et al. (2006) because average weaning date was approximately 1 mo later and possibly had a greater impact on fetal development.

In a review on fetal programming of skeletal muscle, Du et al. (2010) reported results on steer progeny from beef cows fed 1 of 3 diets: 100% of NRC (2000) nutrient requirements, 70% of NRC requirements, or 70% of NRC requirements plus supplementation of ruminal bypass protein from d 60 to 180 of gestation. Steer progeny from dams fed 70% of nutrient requirements plus a supplement had numerical decreases in marbling scores compared with steers from dams fed 100% of requirements. Underwood et al. (2010) also reported increased tenderness in steers from dams grazed on improved pasture compared with steers from dams grazed on native range during mid-gestation.

Male counterparts to the control or restricted heifers from cows in the long-term research project at Fort Keogh discussed above also exhibited dam nutrition treatment × individual feeding treatment interactions for carcass traits and growth rate (Endecott et al., 2011). As with the heifers, bull calves from this study were developed on

### Table 3. Effect of maternal nutrition on steer progeny performance

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NR</td>
<td>IP</td>
</tr>
<tr>
<td>Birth BW, kg</td>
<td>39^a</td>
<td>37^a</td>
</tr>
<tr>
<td>Weaning BW, kg</td>
<td>242^a</td>
<td>256^b</td>
</tr>
<tr>
<td>ADG, kg/d</td>
<td>1.49^a</td>
<td>1.66^b</td>
</tr>
<tr>
<td>HCW, kg</td>
<td>330^a</td>
<td>348^b</td>
</tr>
<tr>
<td>12th-rib fat, cm</td>
<td>1.24^a</td>
<td>1.64^b</td>
</tr>
<tr>
<td>Marbling score</td>
<td>420</td>
<td>455</td>
</tr>
</tbody>
</table>

^a,bMeans within a study with different superscripts differ (P ≤ 0.05).

^x,yMeans within a study with different superscripts differ (P ≤ 0.10).

1NR = dams grazed native range from d 120 to 180 of gestation; IP = dams grazed improved pasture from d 120 to 180 of gestation.

2Hay = dams offered a diet of grass hay beginning on d 209 of gestation; corn = dams offered limit-fed diet of corn beginning on d 209 of gestation; DDGS = cows offered a limit-fed diet of distillers grains with solubles beginning on d 209 of gestation.

3Where 400 = Small^b.

### Table 4. Effect of maternal protein supplementation on steer progeny performance

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NS SUP</td>
<td>NS SUP</td>
<td>NS SUP</td>
</tr>
<tr>
<td>Weaning BW, kg</td>
<td>200^a 210^b</td>
<td>211^a 218^b</td>
<td>235^a 241^b</td>
</tr>
<tr>
<td>DMI, kg/d</td>
<td>11.15^a 12.05^b</td>
<td>8.48 8.53</td>
<td>8.94^x 9.19^y</td>
</tr>
<tr>
<td>ADG, kg/d</td>
<td>1.60 1.68</td>
<td>1.57 1.56</td>
<td>1.66 1.70</td>
</tr>
<tr>
<td>F:G</td>
<td>6.97 7.19</td>
<td>5.41 5.46</td>
<td>5.37 5.38</td>
</tr>
<tr>
<td>HCW, kg</td>
<td>347^a 365^b</td>
<td>363 369</td>
<td>364^a 372^b</td>
</tr>
<tr>
<td>Choice, %</td>
<td>— —</td>
<td>85 96</td>
<td>71^a 86^b</td>
</tr>
<tr>
<td>Marbling score</td>
<td>449</td>
<td>461</td>
<td>467 479</td>
</tr>
</tbody>
</table>

^a,bMeans within a study with different superscripts differ (P ≤ 0.05).

^x,yMeans within a study with different superscripts differ (P ≤ 0.10).

1NS = dams did not receive protein supplement while grazing dormant Sandhills range during the last third of gestation; SUP = dams were supplemented 3 times per week with the equivalent of 0.45 kg/d of 42% CP cube (DM basis) while grazing dormant Sandhills range during the last third of gestation.

2NS = dams did not receive protein supplement while grazing dormant Sandhills range or corn residue during the last third of gestation; SUP = dams were supplemented 3 times per week with the equivalent of 0.45 kg/d of a 28% CP cube (DM basis) while grazing dormant Sandhills range or corn residue during the last third of gestation.

3Where 400 = Small^b.
2 levels of nutrition during a 140-d period after weaning; fed to appetite (i.e., control, 1.16 kg ADG) or fed at 80% of that consumed by controls adjusted to a common BW basis (i.e., restricted, 0.63 kg ADG). Carcass ultrasound evaluation of bulls at the end of the 140-d period revealed LM area differed due to interaction of individual and dam nutritional treatment, being smallest in restricted bulls from MARG-supplemented dams, intermediate in restricted bulls from ADEQ-supplemented dams, and greatest for control bulls from either dam treatment group (Table 5). After the 140-d feeding trial, bulls were castrated and managed together through the finishing phase. As would be expected, restricted animals during postweaning exhibited compensatory growth during the finishing phase. Magnitude of this compensatory growth response was influenced by level of supplement provided to dams during pregnancy. Differences between growth of restricted and control animals were greater for MARG dam progeny than ADEQ dam progeny (Table 5). When considered collectively, these studies provide evidence that animal responses to variations in nutritional inputs throughout life may be dependent on uterine programming resulting from variations in nutritional environment of the dam during pregnancy.

**PROGENY HEALTH**

Several reports have linked maternal nutrition during gestation to calf health. Research conducted by Corah et al. (1975) demonstrated increased morbidity and mortality rates in calves born to primiparous heifers receiving 65% of their dietary energy requirement over the last 90 d of gestation compared with calves from primiparous heifers receiving 100% of their energy requirement. A possible factor contributing to increased morbidity and mortality is decreased birth BW. Calves born to nutrient-restricted dams weighed 2 kg less at birth compared with calves from dams receiving adequate nutrition (Corah et al., 1975).

Mulliniks et al. (2008) and Larson et al. (2009) indicated that there were reduced proportions of steers treated for bovine respiratory disease (BRD) in the feedlot from cows supplemented with protein compared with calves from nonsupplemented dams. Stalker et al. (2006) reported increased proportions of live calves weaned to dams offered supplement during late gestation; however, there was no difference in the number of calves treated for BRD before weaning or in the feedlot. Furthermore, Larson et al. (2009) reported no difference in the number of steer calves treated for BRD before weaning. Similarly, Funston et al. (2010b) reported no differences in illness of cohort heifers.

Snowder et al. (2006) reported that incidence of disease is more likely after 5 d on feed and remains high through the first 80 d in the feedlot, and steers were more likely to become sick compared with heifers in the feedlot. Postweaning stress is a factor influencing calf health. As mentioned earlier, Funston et al. (2010b) did not report any difference in heifer calf health. These heifers, unlike their steer cohorts, remained at the ranch postweaning and were maintained on a forage-based diet, likely reducing the amount of stress placed on the animal compared with their steer cohorts who were transported to the feedlot 2 wk postweaning and adapted to a concentrate-based diet.

**POTENTIAL MECHANISMS OF FETAL PROGRAMMING**

Establishment of functional uteroplacental and fetal circulation is one of the earliest events occurring during embryonic and placental development (Patten, 1964; Ramsey, 1982). Studies have been conducted to determine how maternal nutrition can influence placental development, or placental programming. Zhu et al. (2007) reported that nutrient restriction of beef cows from d 30 to 125 of gestation resulted in reduced caruncular and cotyledonary weights from nutrient-restricted cows compared with control cows, and fetal weights from nutrient-restricted cows tended to be less compared with control cows. After realimentation during d 125 to 250 of gestation, caruncular and cotyledonary weights were still reduced for nutrient-restricted cows; however, fetal weight was not different.

Because 75% of fetal growth occurs during the last 2 mo of gestation (Robinson et al., 1977), nutrient requirement during early gestation is minimal compared with later in gestation. Thus, inadequate nutrition during early gestation was thought to be of less significance. However, during the early phase of fetal development, critical events for normal conceptus development occur, including differentiation, vascularization, fetal organogenesis, and as previously mentioned, placental development (Funston et al., 2010a).

A review by Caton et al. (2007) lists examples of fetal programming in livestock models in individual organs, including heart (Han et al., 2004), lung (Gnanalingham et al., 2005), pancreas (Limesand et al., 2005, 2006), kidney (Gilbert et al., 2007), placenta (Reynolds et al., 2006), perirenal fat (McMillen et al., 2004; Matsuzaki et al., 2006), and small intestine (Greenwood and Bell, 2003).

The fetal stage is also crucial for skeletal muscle development because of the lack of a net increase in muscle fiber numbers after birth (Stickland, 1978; Zhu et al., 2004). Skeletal muscle is particularly vulnerable to nutrient deficiency because it is a lower priority in nutrient partitioning compared with the brain, heart, or other organ systems (Bauman et al., 1982; Close and Pettigrew, 1990); thus, a decrease in nutrient availability to the dam.
during gestation can result in a reduced number of muscle fibers through fetal programming, reducing muscle mass and affecting animal performance. Both muscle fiber number and intramuscular adipocytes, which provide the sites for intramuscular fat accumulation or marbling formation, are influenced during fetal development (Tong et al., 2008; Du et al., 2010). Because of the importance that fetal stage plays in adipocyte formation, it is proposed that the effectiveness of nutritional management on altering marbling is most important during the fetal stage followed by (in descending order of importance) neonatal stage, early weaning stage (i.e., 150 to 250 d of age), weaning, and older stages (Du et al., 2010).

**SUMMARY AND CONCLUSIONS**

Management of maternal diet beginning during early gestation will ensure proper placental programming, resulting in adequate nutrient transfer to the fetus. Maternal nutrition later in gestation has been reported to influence fetal organ development, muscle development, and postnatal calf performance, including carcass characteristics and reproduction. Although the mechanisms by which placental and fetal programming occur are not clear, managing resources to ensure proper cow nutrient intake during critical points of gestation can improve lifetime performance and progeny health.

**LITERATURE CITED**


Radunz, A. E. 2009. Effects of prepartum dam energy source on progeny growth, glucose tolerance, and carcass composition in beef and sheep. PhD Diss. The Ohio State Univ., Columbus, OH.


