INFLUENCE OF PREPARTUM NUTRITION ON COW PERFORMANCE AND SUBSEQUENT CALF PERFORMANCE, GLUCOSE TOLERANCE, CARCASS CHARACTERISTICS, EFFICIENCY, AND GENE EXPRESSION

BY

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DISSERTATION

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Abstract

Previous research has demonstrated the potential for cow nutrition during mid- and late gestation to have lasting effects on progeny growth, carcass characteristics, and insulin sensitivity. With the advancement of nutrigenomics, the ability to evaluate the effects of maternal nutrition on gene expression in tissues of subsequent progeny has grown. The objective of this dissertation was to evaluate potential fetal programming effects of beef cow nutrition within beef production systems.

Fall-calving cows grazing endophyte-fescue experience a decline in forage quality during late gestation, when fetal growth occurs at a high rate. Fall-calving, mature cows and their progeny were used to evaluate the effects of late gestation dried distillers grains plus solubles (**DDGS**) supplementation on cow performance, and progeny growth and carcass characteristics. Cows were offered daily DDGS supplementation or offered no supplement 69 ± 9 d prepartum through calving. Cow BW and BCS change during late gestation were greater ($P \leq 0.02$) for cows offered supplement. Supplementation had no effect ($P \geq 0.11$) on calving date, calf birth or weaning BW, or pre-weaning ADG, milk production, AI conception, or overall pregnancy rate. For steer progeny, dam DDGS supplementation had no effect ($P \geq 0.19$) on feedlot performance or carcass characteristics.

Use of corn coproducts in drylot beef gestation rations has increased over the last decade. Because of the elevated energy and CP content of corn coproducts, cow drylot rations may easily exceed cow energy and CP requirements. The effects of excessive prepartum dietary energy and CP intake of subsequent progeny needs to be further investigated. In one experiment, spring-calving, mature cows and their progeny were used to evaluate the effects of prepartum dietary energy on cow performance as well as performance and carcass characteristics of subsequent

progeny. Cows were limit-fed isonitrogenous rations that provided 100% or 125% of TDN requirements, respectively, from 83 ± 10 d prepartum to calving. Cow BW change through breeding was greater ($P < 0.01$) and BCS change tended to be greater ($P = 0.09$) for cows 125% of TDN requirement. Birth BW was greater ($P = 0.02$) for calves born to cows fed excessive dietary energy with no increase ($P = 0.30$) in percentage of unassisted births. There were no effects ($P \geq 0.27$) of dietary energy on calving date, milk production, or subsequent pregnancy rate. Calf feedlot performance was not affected ($P \geq 0.20$) by prepartum energy. Although progeny born to dams fed excessive dietary energy tended ($P = 0.10$) to have greater marbling scores at weaning, prepartum dietary energy had no effect ($P \geq 0.60$) on carcass marbling score or other carcass characteristics.

Two experiments were conducted to investigate the effects of prepartum dietary CP intake on cow performance as well as subsequent progeny growth, carcass characteristics, and plasma glucose and insulin concentrations. Spring-calving, mature cows in both experiments were limit-fed rations formulated to be isocaloric, and provide 100% or 129% of CP requirement, respectively, from 92 ± 10 or 78 ± 12 d prepartum to calving in Exp. 1 and 2, respectively. Prepartum CP intake had no effect on cow BW, BCS, milk production, and subsequent reproduction or progeny pre-weaning growth in either experiment. In Exp. 1, post-weaning ADG, final BW, and HCW were decreased in progeny born to dams fed excessive dietary CP. In Exp. 2, progeny post-weaning growth was not affected by treatment; yet, 12^{th} rib fat thickness, KPH, and yield grade were greater for progeny born to dams fed excessive dietary CP. Progeny born to dams fed excessive dietary CP had decreased glucose and insulin concentrations, and insulin to glucose ratios, indicating greater insulin sensitivity.

Mid-gestation is a critical time for the development of skeletal muscle and adipogenesis, two tissues of great interest to the beef industry. Much of the work that has demonstrated promising fetal programming effects, was done in nutrient restricted or overfed dams, 50% or 150% or energy and protein requirements, respectively. One experiment was conducted to investigate the effects of divergent plane of nutrition during mid-gestation on cow performance and progeny growth, feed efficiency, methane production, glucose tolerance, carcass characteristics, and gene expression in LM. Mature cows were limit-fed 3 planes of nutrition from 196 ± 14 to 114 ± 14 d prepartum: 100% energy and protein requirement (**REQ**), 70% requirement (**70%REQ**), or 130% requirement (**130%REQ**). Cow ADG during mid-gestation was greatest ($P < 0.01$) for 130%REQ, least for 70%REQ, with REQ intermediate. Transition period (30 d post-weaning) ADG was greatest ($P < 0.01$) for 70%REQ progeny, least for REQ progeny, with 130%REQ progeny intermediate. Treatment had no effect ($P \geq 0.21$) on progeny RFI or 24 h methane emissions; but, REQ progeny tended ($P = 0.06$) to have decreased RG relative to 70%REQ and 130%REQ progeny. Treatment had no effect ($P \geq 0.12$) on progeny glucose and insulin concentrations, AUC, glucose clearance rate, or insulin to glucose ratio during glucose tolerance test. Progeny of REQ dams had greater ($P = 0.04$) HCW than 70%REQ progeny, with 130%REQ intermediate and not different from either. Treatment had no effect ($P \geq 0.27$) on other carcass characteristics. Treatment had no effect ($P \geq 0.24$) on expression of 13 selected genes in LM, with the exception of MYH1 ($P = 0.07$). Expression of all target genes, except MYH7, changed ($P \leq 0.03$) as progeny d of age increased. There was a treatment by d of age interaction ($P = 0.04$) for expression of *MYH1*, in which expression of *MYH1* was least in progeny born to 70%REQ dams at 392 ± 14 d of age relative to REQ and 130% progeny. There were treatment by progeny sex by d of age interactions ($P \leq 0.01$) for expression of *SLC2A4*,

YY1, and *MYH7*. In conclusion, prepartum DDGS supplementation improved cow BW and BCS but did not alter milk production, subsequent reproduction, or subsequent calf performance or carcass characteristics. Feeding cows 125% of TDN requirement during late gestation increased cow BW change and progeny birth body weight; but, had no effect on pregnancy rate or progeny performance. Although feeding cows 129% of CP requirement during late gestation did not affect cow performance, progeny post-weaning growth was decreased and carcass adiposity was increased. Differing mid-gestation plane of nutrition diverged cow BW and affected transition period ADG and HCW of progeny; yet, did not dramatically impact methane production, insulin resistance, or gene expression in LM.

To my parents, Wayne and Deborah Wilson,
You two have provided a solid example of how to conduct myself,
I hope I am smart enough to apply these lessons to my own life

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CHAPTER 1

LITERATURE REVIEW

Introduction

A discussion of the potential long-term effects beef cow nutrition can impart on subsequent progeny is one that encompasses a wide variety of topics in the beef production cycle. An understanding must be gained regarding the array of cow/calf production systems that are found throughout the United States beef industry. Production systems differ by region, animal type, feedstuffs used, and environmental challenges faced. Heterogeneity in cow/calf operations presents challenges in interpreting research results across production models.

Significant research has been devoted to investigating the link between maternal gestation diet and progeny predisposition to disease, metabolism, and body composition in humans and nonruminants (Bee, 2004; Barker, 2012). The concept that maternal nutrition has long lasting impacts on the lives of progeny is known as fetal programming (Barker, 2007b). Fetal programming is related to the concept of developmental programing that states that pre- or early postnatal nutrition can impart lifelong, lasting effects (Du et al., 2010). Fetal programming and developmental programming theories have garnered substantial attention in the field of Animal Science. However, the long, seasonal nature, and regional specificity of the cow/calf cycle has limited the ability to discern the potential fetal programming effects of cow gestational nutrition in beef production systems (Funston et al., 2010a).

Goals of Cow/calf Operations

Feed Costs

Despite the diversity in cow/calf operations, progressive producers operate with two overarching goals in mind: to manage input costs and achieve an acceptable level of cow performance. The primary input cost to be managed is feed. After conducting an economic analysis of commercial cow/calf operations from 1996 to 1999, with 225 herd-year observations, Miller et al. (2001) found that feed costs represent 63% of total annual cow costs. Miller et al. (2001) further explained feed costs accounted for over 50% of the variation in production costs between cow/calf operations and the difference in feed costs between high and low cost producers was over $\$1.00/d \cdot cow^{-1}$. The economic analysis conducted by Miller et al. (2001) may be outdated, as feed costs may represent an even greater portion of annual cow costs in 2014.

Acceptable Cow Performance

Acceptable cow performance is often defined when cows achieve moderate BCS, maintain a 365 d calving interval, and maintain a desirable level of milk production. The BCS system (1 = severely emaciated, 9 = very obese) is a useful indicator of body energy reserves in beef cows (Wagner et al., 1988). Managing cow nutritional status through assessment of BCS is a common practice because it can be assessed without gathering cows does not require investment in ultrasound technology required to measure subcutaneous fat thickness. Because body composition is independent of BW, BCS predicts differences in body composition with greater accuracy than BW (Wagner et al., 1988). Cow BCS is best used as an indicator of long-term energy status.

There is substantial evidence that BCS has significant impact on reproductive efficiency. Richards et al. (1986) determined that BCS at time of calving had greater effects on cyclicity and

subsequent pregnancy rates than postpartum plane of nutrition. Cows calving with a BCS of 5 or greater displayed quicker return to estrus and decreased postpartum interval relative to cows calving with a BCS of 4 or less. Spitzer et al. (1995) observed greater cyclicity and pregnancy rate at d 40 of a 60 d breeding season when cows calved at BCS of 6 rather than 4, cows calving at a BCS of 5 were intermediate and different from both. At the end of the calving season, d 60, cyclicity was greater in cows that calved with a BCS of 5 or 6 relative to those that calved with a BCS of 4. At d 60 of the breeding season, pregnancy rate was greater for cows that calved with a BCS of 5 or 6 relative to those that calved with a BCS of 4; although, cows calving with a BCS of 6 tended to have greater pregnancy rate relative to cows calving at a BCS of 5. The data of Richards et al. (1986) and Spitzer et al. (1995) provide evidence that there is threshold at which reproduction is significantly improved when cows are managed to achieve BCS of 5 or greater. Decreased postpartum interval via quicker return to estrus carries substantial economic value. Heifers calving during the first 21 d of a 55 d calving season weaned calves that were 32 kg heavier and approximately $40 more valuable than the calves weaned by heifers calving from 43 to 55 d of the calving season (Marshall et al., 1990).

Calf weaning BW is thought to be heavily affected by dam milk production; however, this relationship is quite difficult to evaluate. Clutter and Nielsen (1987) determined that the correlation between milk intake and pre-weaning calf gain can be as high as 0.60 at 50 d postpartum and as low as 0.11 at 158 d postpartum. The regression of calf 205 d pre-weaning gain on milk intake was 0.32, 0.32, and 0.53 kg gain / kg milk intake for groups of cows with high, medium, and low genetic milk potential, respectively (Clutter and Nielsen, 1987). This would indicate that ADG for calves born to cows with low milk potential is more dependent on milk intake. Calves born to cows with low milk potential may also become more dependent on

alternative feeds such as forage or creep feed earlier in lactation. Clutter and Nielsen (1987) also reported that calves born to cows with high milk potential were 16.9 kg heavier than calves born to cows with low milk potential. In a companion paper to Clutter and Nielsen (1987), Lewis et al. (1990) reported that level of dam milk production did not significantly affect final BW or carcass characteristics of steer progeny. These two studies indicate that level of dam milk production can have significant economic ramifications for beef producers that market calves shortly after weaning, because calves will be heavier at weaning; but, not for those who retain ownership through the feedlot, because the added milk production does not appear to have lasting impacts on growth and carcass characteristics. Any discussion about appropriate level of cow milk potential is operation specific, and must also consider input costs and environment. Maintenance requirements of beef cows are influenced by milk potential and mature size. It is generally accepted that cows with low milk potential and moderate mature size will maintain BCS and greater reproductive efficiency than cows with high milk potential and large mature size. However, the relationships between milk potential, mature size, BCS, and reproduction are not so clear. When different breeds varying in milk potential and mature size were compared, no clear effects of milk potential or mature size of breed were observed (Sinclair et al., 1998a). No differences in conception rate or postpartum interval were observed between Angus (small size, low milk potential) and Simmental (large mature size, high milk potential) cows (Sinclair et al., 1998b)

Cow Feeding Systems

Grazing Supplementation

Supplementation is a common strategy to improve the nutritional status of grazing cattle. The goal of supplementation is to supply the difference between cattle nutrient requirements and available nutrients from forage, which vary by season and forage specie. Cattle grazing warm season forages typically require supplementation from late fall when forage begins to senesce until mid-spring when forage regrowth occurs. Cattle grazing cool-season forages tend to require supplementation during late summer when forage growth slows, with many species going dormant during this time. For cool-season forages, this period of slow forage growth during late summer is often referred to as the "summer slump" by beef producers. After a period of fall growth, forage growth declines during the winter as forage senescence occurs; thus, creating a need to supplement grazing cattle during this time. The need to supplement grazing cattle is also heavily dependent on climate and length of growing season.

The feedstuffs cattlemen use to supplement grazing cattle are often chosen based on commodity markets that can be quite volatile. Increasing forage dry matter digestibility is the goal of an effective supplementation strategy, as forage represents the majority of DMI when cattle are grazing. It is generally accepted that supplements that are high in CP, particularly those that are high in RDP concentration, are more effective at enhancing forage digestibility than supplementation of high energy feedstuffs. This concept is proven by an experiment conducted by Olson et al. (1999) in which steers were ruminally dosed with combinations of RDP and starch. Ruminal dosing of RDP, Na-caseinate, increased intake of forage OM and NDF and increased forage OM and NDF digestibility linearly. Ruminal dosing of starch, as cornstarch grits, decreased intake of forage OM and NDF and decreased forage OM and NDF digestibility

linearly. Stalker et al. (2006) and Larson et al. (2009) demonstrated the benefits of supplementing CP to cows grazing low quality, dormant native range during late gestation. In both studies, cows offered CP supplement had greater BW and BCS at time of calving when compared to cows offered no supplement. Supplemental CP during late gestation did not improve subsequent pregnancy rate in either study. Larson et al. (2009) also saw no differences in milk production when cows were offered CP supplementation during late gestation.

There has been considerable interest in supplementing grazing cattle with supplements high in RUP to improve nutritional status. Bohnert et al. (2002) observed greater NDF intake and total tract digestibility when wethers consuming hay (5.2% CP) were fed a CP supplement that was 60% RUP when compared to wethers fed a supplement that 82% RDP. However, in a companion cow performance study, using the same supplements, no differences in cow BW or BCS change were observed. When gestating and lactating cows were fed low quality hay (5.8% CP), Sletmoen-Olson et al. (2000b) determined that as long as RDP requirement was met, additional RUP had no effect on forage OM intake or cow BW and BCS.

With the expansion of the ethanol industry in the early 2000's, there has been increasing availability of dried distillers grains plus solubles (DDGS), the primary coproduct produced by the dry grind process, available to be fed to ruminants. At times, this coproduct has represented a cost-effective alternative to traditional true protein sources that have been fed to grazing cattle, such as soybean meal or cottonseed meal. Distillers grains are a good supplement for grazing cattle because they are high in protein (30% CP), contain highly digestible fiber (46% NDF), and contain a considerable amount of energy in the form of fat (11%; NRC, 1996). The high fat content off DDGS is concerning as dietary fat is known to negatively affect fiber digestibility. Hess et al. (2008) suggests that supplemental fat to cattle consuming a forage-based diet should

not represent more than 3% of diet DM to avoid negative associative effects of fiber digestibility. It is also suggested that dietary fat should not exceed 6% of DM when cattle are fed concentrate diets. There is growing evidence that DDGS supplementation does not negatively impact fiber digestion. Leupp et al. (2009) supplemented steers consuming average quality hay (10.6% CP) with 0.3 to 1.2% of BW of DDGS. Forage DMI decreased linearly, total tract NDF digestibility increased linearly, and total tract CP digestibility increased quadratically with increasing level of DDGS supplementation. Leupp et al. (2009) concluded that supplementation of 0.3 to 1.2% of BW of DDGS resulted in no adverse effects on forage digestion. Winterholler et al. (2012) conducted three experiments to evaluate cow performance, diet digestibility, and milk production and composition when DDGS were supplemented at three levels of intake to cows consuming low quality prairie hay (5.6% CP). A comparison was also made between a DDGS supplement formulated to meet RDP requirement and an isonitrogenous supplement consisting of more true protein sources, such as wheat middlings and cottonseed meal. In one experiment conducted by Winterholler et al. (2012), decreased BW and BCS loss was observed as level of DDGS supplementation (0.77, 1.54, or 2.31 kg / d) increased over a 119 d period encompassing the last 106 d of gestation and the first 13 d of lactation. These BW and BCS differences from DDGS supplementation lasted through pre-breeding. No differences in cow BW and BCS were observed between cows fed isonitrogenous amounts of DDGS or a supplement with greater RDP concentration. There is evidence that efficiency of nitrogen use is greater in cows supplemented DDGS because serum urea nitrogen was greater when cows were fed the traditional high RUP supplement containing wheat middlings and cottonseed meal relative to when an isonitrogenous amount of DDGS was fed. When cows in a second experiment conducted by Winterholler et al. (2012) were fed similar diets, no differences were observed on forage intake or NDF digestibility

with increasing amount of DDGS supplementation. In a third experiment conducted by Winterholler et al. (2012), it was observed that milk protein yield increased, protein percentage increased, and milk fat decreased with increasing level of DDGS supplementation. As level of DDGS supplementation increased, there was a numerical increase in milk yield, a decrease in milk energy per kg of milk produced; resulted in no difference in total milk energy produced per day. Cows fed DDGS incorporated more dietary protein into milk protein and had lower milk urea nitrogen than cows fed an isonitrogenous level of traditional high RDP supplement. These data reported by Winterholler et al. (2012) provide further evidence that DDGS are a viable form of supplementation to cows consuming low quality forage. In recent years, ethanol distillers have begun to produce de-oiled DDGS with decreased fat content relative to traditional DDGS. The removal of additional corn oil from DDGS did not affect NDF digestibility of finishing diets when DDGS were included at 20 or 40% of DM (Jolly et al., 2014).

As previously mentioned, it may be necessary to supplement cattle grazing cool-season forages during late summer, or during the "summer slump" period. Cattle consuming endophyte-infected tall fescue forage are susceptible to experiencing a condition known as fescue toxicosis. Symptoms of tall fescue toxicosis include retained winter hair coat, impaired thermoregulation, decreased time spent grazing, and a potential reduction in DMI that culminate in reduced weight gain (Paterson et al., 1995). Level of circulating prolactin is reduced when cattle exhibit symptoms of fescue toxicosis; and thus, is used as an indicator of fescue toxicosis (Paterson et al., 1995). Symptoms of fescue toxicosis also include reduced milk production and reproductive efficiency (Porter and Thompson, 1992; Paterson et al., 1995). The symptoms of fescue toxicosis appear to be exacerbated by environmental temperatures above 32°C (Aldrich et al., 1993). Periods of elevated environmental temperatures during late summer (July and August) coincide

with the time when forage declines and forage growth slows. The cause of fescue toxicosis has been determined to be caused by an ergot alkaloid producing endophyte known as *Acremonium coenophialum* that lives within the fescue plant (Bacon, 1995). Hoveland (1993) estimated that fescue endophyte infestation costs the beef industry $354 million in reduced calf number and $254 million in reduced calf weaning weights annually, totaling $609 million annually.

The efficacy of providing supplement to growing cattle to alleviate fescue toxicosis has been investigated with regard to ADG, prolactin level, and shedding of winter hair coat. Aiken et al. (2008) and Carter et al. (2010) observed greater ADG when growing cattle grazing endophyte-infected fescue were provided 2.3 kg steer·d^{-1} of pelleted soybean hulls during the summer grazing season relative to steers that received no supplement. Carter et al. (2010) also observed greater serum prolactin levels, and improved hair coat rating when steers received soybean hull supplementation. It should be noted that grazing season in the experiment conducted by Carter et al. (2010) only lasted an average of 81.5 d over 2 yr and did not occur during late July and August when the effects of fescue toxicosis are intensified. In contrast to the findings of Carter et al. (2010), Aiken et al. (2008) observed no differences in serum prolactin levels or hair coat rating when cattle were provided soybean hull supplement over a grazing season that lasted an average 107 d over 2 yr that included late summer. The differences between these two experiments may also serve to highlight the variation between grazing years as the experiment conducted by Aiken et al. (2008) was conducted during 2004-2005 and the experiment conducted by Carter et al. (2010) was conducted during 2007-2008.

There has been limited research regarding the supplementation of beef cows grazing endophyte-infected fescue during late summer as a means to improve cow performance during the "summer slump". Forcherio et al. (1995) conducted an experiment in which lactating cows

grazing endophyte-infected fescue during June and July were provided 1.1 to 1.3 kg of supplements which consisted of cracked corn or soybean hulls as energy sources and 100 g or 200 g of RUP in 2 x 2 factorial design. Cow ADG was not improved by providing supplement when compared to cows who did not receive supplement. There was an energy source by RUP level interaction in which cows fed cracked corn and 200 g of RUP gained 0.33 kg/d and cows fed cracked corn and 100 g of RUP lost 0.10 kg/d. Difference in BW gain when soybean hulls were fed was much less substantial as cows fed soybean hulls and 200 g of RUP lost 0.10 kg/d and cows fed soybean hulls and 100 g of RUP gained 0.07 kg/d. Calf ADG was not improved by providing their dams supplement when compared to calves nursing cows who did not receive supplement. There was an effect of supplemental RUP concentration on calf ADG. Calves nursing cows who received 100 g of RUP had greater ADG when compared to calves nursing cows who received 200 g of RUP. This coincides with greater milk consumption by calves nursing cows who received 100 g of RUP when compared to calves nursing cows who received 200 g of RUP. Calves nursing cows who received supplement consumed more milk than calves nursing cows who did not receive supplement. It would appear that under the conditions of the study conducted by Forcherio et al. (1995), elevated level of supplemental RUP is detrimental to milk production and resulting calf ADG. Forcherio et al. (1995) attributes the difference in cow ADG when cracked corn-containing supplements were fed to a nutrient repartitioning effect in which nutrients were partitioned to increase maternal BW gain at the expense of milk production. This repartitioning effect when supplements supplying greater RUP are fed to lactating cows has also been observed by Hunter and Magner (1988) and Shike et al. (2009). Despite the interesting differences in cow/calf performance observed by Forcherio et al. (1995)

between supplement types, the benefits of offering supplement when compared to not offering cows grazing endophyte-infected fescue are much less clear.

Drylot Feeding

Drylot feeding is a management practice employed when grazing is not a viable option to maintain beef cows. The need to drylot feed is precipitated by limited forage availability; often caused by limited pasture availability during winter or drought conditions. During certain periods of the year, drylot feeding of cattle may be preferable to grazing to protect forage from being trampled and maintain long-term pasture health. An effective drylot feeding strategy successfully manages feed costs. Wintering cows in a drylot can be the most expensive time for beef producers to feed cows as reliance on stored feeds is greatest (Braungardt et al., 2010).

A traditional method used to drylot cows is to provide ad libitum access to hay, often in the form of large round bales. Many beef producers prefer feeding ad libitum large round bales due to their ease of handling and management (Miller et al., 2007). Although easy to manage, feeding ad libitum hay can be costly. Aside from purchase/production costs, hay feeding comes with unseen costs of storage and feeding losses.

Much effort has been spent investigating storage methods for large round bales that reduce storage losses that are caused by DM losses due to weathering. In one experiment conducted by Brasche and Russell (1988), DM losses of large round bales were 9.7% when stored on the ground and not covered when compared to DM losses less than 1% when bales were elevated off the ground and covered during a storage period of 20 to 28 weeks. Turner et al. (2007) conducted a study in which storage losses of large round bales of cool-season grass hay stored for 7 or 15 months were compared using five storage systems: on the ground uncovered, on pallets uncovered, on the ground covered, on pallets covered, and on pallets in a barn. Storage

losses after 7 months were 22.7% when hay was left uncovered, either on the ground or on pallets, 10.0% when covered, either on the ground or on pallets, and 2.7% when stored in a barn. Storage losses after 15 months were 30.7% when hay was left uncovered, either on the ground or on pallets, 19.3% when covered on the ground, and 11.1% when stored on pallets and covered or in a barn. An economic analysis conducted by Turner et al. (2007) concluded that for a storage period of 7 months, storing hay covered on the ground had the lowest cost and storing hay uncovered on pallets was most expensive. For a storage period of 15 months, storing hay covered on pallets had the lowest cost and storing hay uncovered on pallets was still the most expensive storage system.

Round bales that are protected during storage generally have increased DM and decreased NDF and ADF concentrations when compared to bales left unprotected during storage (Brasche and Russell, 1988; Turner et al., 2007). The effects of weathering on CP content of large round bales appear to be mixed (Turner et al., 2007). No differences in cow DMI or BW change were observed when cows were fed hay that was protected or left unprotected during storage despite differences in the nutritive value due to storage method (Brasche and Russell, 1988).

Storage method of large round bales can also affect feeding losses. Belyea et al. (1985) observed feeding losses of 24.7% and 12.4% when feeding large round bales that were stored outside, uncovered and inside a barn, respectively. These data indicate that DM and spoilage loses from storing hay have a greater economic impact than changes in nutritive content caused by weathering of hay.

Hay feeding losses are also affected by feeding method. Landblom et al. (2007) evaluated waste and economics of feeding large round bales in tapered-cone feeders, unrolling bales on the

ground, and using a PTO driven flail-type bale processor to feed hay on the ground over three years. Tapered-cone feeders are ring type feeders that have an inverted cone to suspend hay off the ground and in the center of the feeder. Unrolling large round bales on the ground is a feeding method commonly used in the Great Plains when feeding hay to cows maintained on dormant pastures. Hay waste can be increased when unrolling large round bales due to cows bedding in or defecating on hay. Use of a bale processor is desirable as hay particle size is reduced, making sorting of stems more difficult when average quality hay is fed. Feeding hay with bale processors also increase machinery costs and are known to create appreciable amounts of dust when processing hay that represents feeding loss. Landblom et al. (2007) determined that feeding round hay using tapered-cone feeders reduced the amount of hay required per cow to maintain BCS by 5.0% and 15.3% compared to when hay was unrolled on the ground or a bale processor was used, respectively. However, there was an interaction between feeding method by hay type for hay waste type and firmness of bales fed. When tightly-tied mixed alfalfa-grass bales were fed without removing strings during yr 1 and 2, hay wastage was lowest when tapered-cone feeders were used; but, when loosely-tied oat bales were fed with strings removed, hay wastage was greatest when tapered-cone feeders were used, lowest with a bale processor, and intermediate when unrolling bales on the ground. In herds of 100 or 300 cows, feed costs per cow were cheapest when tapered-cone feeders were used, most expensive with a bale processor, and intermediate when unrolling bales on the ground.

A feeding method to reduce hay feeding losses is to limit time of access to large round bales (Miller et al., 2007). Mature cows were offered large round bales of high (127 RFV) or average (96 RFV) quality hay in fence-line feeders ad libitum or limited access to 3, 6, or 9 h. As time of access to hay decreased, cows maintained acceptable BW and BCS gain with decreased

DM disappearance and feed costs. When high quality hay was fed, hay wastage was minimized when cows were allowed access to large round bales for 6 h. When average quality hay was fed, hay wastage was minimized when cows were allowed access to large round bales for 9 h. Miller et al. (2007) posed that the most precise method of feeding hay would be to feed processed forage in a bunk. This method would reduce over consumption of forage and reduce forage wastage. However, the additional equipment required for processing forage is cost prohibitive for small and medium size cow-calf producers.

It is well documented that feeding method affects hay wastage of large round bales (Landblom et al., 2007; Miller et al., 2007); however, hay wastage may also be impacted by round bale feeder design. Buskirk et al. (2003) evaluated hay wastage when four different hay feeder designs were used: ring, cone, trailer, or cradle-type feeder. Hay wastage was reduced for ring and cone feeders when compared to trailer and cradle feeders (Ring = 6.1%, Cone = 11.5%, Trailer = 11.4%, Cradle = 14.6%). Estimated hay intake per day was not different, regardless of feeder type. Buskirk et al. (2003) posed that the differences in hay wastage between feeder designs were because cow eating behavior in cone and ring-type feeders most closely mimicked natural grazing behavior; and cone, ring, and trailer feeders have bars that keep hay centered in the middle of the feeder. Agnostic interactions (fighting) per h were greatest with cradle-type feeders, with no differences between other feeder types. This was attributed to the lack of vertical bars with cradle feeders that created feeding positions that deterred cows from interacting with one another.

Limit feeding corn has been investigated as an alternative to feeding cows hay ad libitum that has been investigated is limit-feeding corn (Loerch, 1996). Concentrates, such as corn, contain more energy, thus cows can eat less DM to meet their energy requirement. This method

of maintaining drylot cows was especially attractive during the 1990's when long-term corn prices were approximately $2.00 / 25.4 kg (bushel) and hay approximately $0.09 / kg ($80 / ton). Loerch (1996) conducted three experiments in which gestating cows were either offered ad libitum orchardgrass hay or limit-fed 5 kg whole shelled corn, 1.2 kg CP supplement, and 1 kg of hay. Performance of limit-fed cows was similar to those offered ad libitum access to hay with limit-fed cows experiencing few off-feed issues. It was noted by Loerch (1996) that limit-feeding cows corn resulted in greater variation in BW change than those fed hay ad libitum. Galyean (1999) explains that this variation in BW change occurs when limit-feeding as individuals are likely to over- or under-consume targeted feed intake; while average pen performance is as expected. Loerch (1996) reported that the cost of limit-feeding corn was 55% of feeding ad libitum hay. It should be noted that this economic analysis was conducted at a time when corn was valued at $2.00 / 25.4 kg and hay at $0.09 / kg ($80/English ton). At the time of the study conducted by Loerch (1996), corn and other feedstuffs were priced much lower than they are in today's market. The economics of limit-feeding cows in drylots corn should be reevaluated prior to implementation.

As mentioned previously, the expansion of the ethanol industry in the early 2000's led to increased availability of DDGS, which have been used to supplement grazing cattle. Corn coproducts such as DDGS, wet distillers grains plus solubles (WDGS), and corn gluten feed (CGF) are also attractive feedstuffs to include in drylot rations of beef cows. A major coproduct of the corn wet milling process, CGF, is lower in CP (24%), RUP (25% of CP), NDF (36%), and fat (3%) than DDGS (NRC, 1996). Traditionally, corn coproducts have been viewed as a protein source; yet, high concentrations of readily digestible fiber has led to increased use as an energy source in beef cattle diets (Klopfenstein et al., 2008).

While easily digested, the fiber found in corn coproducts is of small particle size and cannot be expected to replace forage in the diets of beef cattle. This is highlighted by comparing the NDF and effective neutral detergent fiber values (eNDF) values for DDGS and corn silage. DDGS contain 46% NDF and 4% eNDF while corn silage contains 45% NDF and 81% eNDF (NRC, 1996). Limit-feeding diets containing corn coproducts is often necessary in order to prevents over-consumption of feed and over-conditioning of cows. Shike et al. (2009) conducted an experiment that investigated the efficacy of limit-feeding lactating beef cows diets that consisted of ground alfalfa and either DDGS at 55% or CGF at 57% DM. Both diets were fed as a total mixed ration (TMR) and were formulated to be isocaloric and meet or exceed protein requirements. Cows fed CGF from calving until breeding lost more BW and tending to lose more BCS than those fed DDGS. Cows fed CGF produced more milk which coincided with a trend for increased calf ADG. The fact the DDGS containing diet fed by Shike et al. (2009) contained greater RUP than the CGF containing diet provides further support of the nutrient repartitioning effect of RUP described by Hunter and Magner (1988) in which nutrients are diverted from milk production and towards maternal bodily reserves. Despite the fact that cows fed CGF lost more BW over the course of the experiment, no difference in AI or overall pregnancy rates when compared to cows fed DDGS were observed. The results of Shike et al. (2009) indicate that both CGF and DDGS can be incorporated with ground alfalfa hay into TMRs fed to lactating cows at an inclusion rate of approximately 56% DM.

High quality alfalfa hay, similar to that fed by Shike et al. (2009), may not be the ideal forage source to match with corn coproducts due to the high CP content and low NDF content of both alfalfa hay and corn coproducts. Poor quality forages, such as cornstalk residue and wheat straw, are low in protein and fail to meet the cow's energy requirement when fed alone; yet, are

extremely complementary with high protein, energy dense corn coproducts. In the upper Midwest, matching corn coproducts with cornstalk residue in beef cattle diets has great potential due to the vast acres of cropland planted in corn annually. Cornstalk residue also represents a feedstuff that is at a reduced cost when compared to hay. Shike et al. (2009) conducted a second experiment that investigated the efficacy of limit-feeding lactating beef cows diets that contained cornstalk residue and either DDGS at 76% or CGF at 77% DM. As with the previously discussed experiment conducted by Shike et al. (2009), both diets were fed as a total mixed ration (TMR) and were formulated to be isocaloric and meet or exceed protein requirements. Cows fed CGF from calving until breeding tended to lose more BW than those fed DDGS. In contrast to the first study conducted by Shike et al. (2009), no differences in milk production or calf ADG were observed. In agreement with the first study, no difference in AI or overall pregnancy rates when compared to cows fed DDGS were observed. When considering the results of both experiments conducted by Shike et al. (2009), it can be concluded that corn coproducts can be included in limit-fed cow diets at levels up to 75% of diet dry matter. Inclusion of DDGS and CGF resulted in variable differences in cow BW change and milk production with no effects on subsequent reproduction resulting in acceptable cow performance when matched with either ground alfalfa hay or cornstalk residue.

The price of corn coproducts is seasonal, with prices generally being cheaper in the late summer (Warner et al., 2011). Thus, it would be advantageous for beef producers to have the ability to purchase corn coproducts under favorable market conditions and store feed, in a way to prevent spoilage, up to 9 months until feedout. Warner et al. (2011) conducted an experiment that evaluated performance of non-lactating, non-pregnant cows consuming an ad libitum forage diet when compared to those limit-fed diets consisting of ground cornstalks and either WDGS or

condensed corn distillers solubles (CCDS) that had been packed and stored in a bunker for 30 d. Distillers solubles and WDGS were stored at 41:59 and 70:30 coproduct to cornstalk ratios, respectively. At feedout, additional ground cornstalks were added to the bunker DDGS so that both coproduct diets were fed at a 41:59 coproduct to cornstalk ratio. The all forage diet consisted of 43% bromegrass, 34% cornstalks, and 23% alfalfa haylage. At the end of the 76 d feeding period, cows fed WDGS were heavier than cows fed CCDS or ad libitum forage. A trend for cows fed WDGS to have greater ADG than those fed ad libitum forage, with cows fed CCDS being intermediate, was observed. There were no differences in final BCS. Warner et al. (2011) posed that the reason for lower BW gains by cows fed ad libitum forage was because actual DMI was lower than DMI predicted by the NRC (1996) model. Increased BW gains by cows limit-fed coproducts may be attributed to a reduction in maintenance requirement as a result of lower visceral masses observed in limit-fed animals (Sainz and Bentley, 1997). Warner et al. (2011) concluded that limit-feeding bunkered corn coproduct diets does not negatively affect cow performance and allows selection of feedstuffs for nutrition programs to be based on economic opportunity.

As the ethanol industry continues to refine the dry grind process and maximize coproduct value, additional corn coproducts are being derived (Braungardt et al., 2010). For example, further fractionation is being utilized to remove the germ, rich in oil, prior to starch fermentation, resulting in DDGS that are higher in protein with lower fat content relative to traditional DDGS. Braungardt et al. (2010) evaluated the effects of modified corn coproducts on beef cow performance by providing them as supplements to lactating cows offered ad libitum access to cornstalk residue bales from calving until breeding. Supplements were formulated to be isocaloric and consisted of blends of DDGS, high protein dried distillers grains (40% CP, 5.5%

fat), and corn bran (13% CP). Cows fed coproduct supplements lost less BW when compared to cows offered ad libitum access to alfalfa mixed hay. Whether cows were offered hay ad libitum or cornstalk residue bales and coproduct supplements, no differences in milk production, calf ADG, or AI conception rates were reported. Substantial differences existed in daily feed cost between the treatment diets evaluated by Braungardt et al. (2010). There was a \$0.22/cow·d^{-1} range in costs of coproduct supplements. However, the greatest difference in feed costs came as average feed cost for cows receiving cornstalk residue bales and coproduct supplements were \$1.00/cow·d^{-1} cheaper than for cows given ad libitum access to alfalfa mixed hay. The high cost of feeding hay is brought into further focus when considering that cows fed hay in the experiment conducted by Braungardt et al. (2010) lost more BW than those fed a less expensive diet consisting of low quality forage and corn coproducts.

Multiple studies have compared different energy sources in drylot beef cow diets; yet, few have compared feeding beef cows hay, corn, and DDGS in the same experiment under similar conditions. Radunz et al. (2010) conducted an experiment that evaluated performance of cows fed isocaloric diets consisting of ad libitum hay, limit-fed corn, or limit-fed DDGS from mid-gestation through calving. Cows limit-fed DDGS gained more BW prior to calving than cows fed ad libitum hay or limit-fed corn; however, no differences in BCS change, milk production, or subsequent pregnancy rates were observed.

Research has demonstrated that multiple energy sources are capable of supporting acceptable cow/calf performance. Along with the variation in drylot feed costs, cost associated with feeding method should also be accounted for. This is pertinent due the diversity in size and associated economies of scale for cow/calf operations. Braungardt et al. (2010) conducted a second experiment that evaluated the effects of diet type and feeding method on lactating cow

performance and beef herd economics. Diets evaluated were: ad libitum access to cornstalk residue bales and DDGS supplement, two TMRs consisting of DDGS at either 50% or 63% of DM and ground cornstalks, or ad libitum access to alfalfa mixed hay. Consistent with the first experiment conducted by Braungardt et al. (2010), cows fed hay lost more BW than those fed corn coproducts, regardless of feeding method. Cows offered ad libitum access to cornstalk residue bales had greater BCS loss than cows fed either TMR diet; but, no differences were observed in BW change. The authors noted that cows offered ad libitum access to cornstalk residue bales had lower bale dry matter disappearance than expected and tended to produce more milk than cows fed a TMR, possibly contributing to greater BCS loss. Despite the tendency for differences in milk production between coproduct fed cows, calf ADG was not affected by maternal diet. Cows fed hay ad libitum tended to have lower AI conception rates. Braungardt et al. (2010) hypothesized that numerically greater conception rates when cows were fed corn coproducts may be due to greater levels of unsaturated fatty acids or RUP in coproduct diets relative to hay. This hypothesis is substantiated by Bellows et al. (2001) who reported improved conception rates with increased level of unsaturated fats in the diets of beef heifers. Increased BW loss experienced by cows fed hay also likely contributed to lower conception rates. Daily feed costs were in agreement with the first experiment conducted by Braungardt et al. (2010), in which feeding hay costs an additional \$1.00/cow·d^{-1} relative to the coproduct diets evaluated. The costs associated with delivering the diets to herds of 50 to 300 cows via hand or tractor feeding of DDGS supplement, grinding cornstalks and using a TMR mixer, or using a tractor to feed hay were evaluated. For herds of 50 cows, hand feeding DDGS supplement and providing access to cornstalk residue bales represented the cheapest method to winter cows. For herds of 100 cows, hand feeding DDGS supplement remained the least expensive feeding method,

feeding ad libitum hay was most expensive, with feeding DDGS supplement with a tractor or a TMR being intermediate. For herds larger than 100 cows, feeding DDGS supplements with a tractor and feed wagon became cheapest feeding method with feeding ad libitum hay the most expensive, with both TMR diets being intermediate. Differences in feed and delivery costs existed because cost of equipment ownership were spread over more cows in larger herds.

While proven to be an attractive component of beef cow diets, there are several considerations that should be made when feeding corn coproducts, primarily DDGS. These include: mineral concentrations, determining their feeding value, possible overconsumption of dietary CP, and increased calf birth BW when fed to gestating cows. The NRC (1996) lists calcium and phosphorous values of 0.32% and 1.40% of DM, respectively. As with other concentrates, diets with high inclusion of DDGS require an additional calcium source so that dietary calcium to phosphorus ratio is maintained at an appropriate physiological level. A dietary calcium to phosphorus ratio of 2:1 is often recommended; however, research has demonstrated that animal growth is not negatively impacted when a ratio of 1:1 to 7:1 is fed (NRC, 1996). A dietary calcium phosphorus ratio less than 1:1 is known to cause urinary calculi. High sulfur concentration of corn coproducts gain substantial attention as inclusion of DDGS and CGF has increased in beef cattle diets. The NRC (1996) lists the sulfur value of DDGS at 0.40% of DM; however, DDGS sulfur concentrations commonly average 0.6% to 0.80% of DM (Drewnoski et al., 2014). Maximum tolerable limit of sulfur given by NRC (1996) is 0.4%, but can range between 0.3% and 0.5% given dietary considerations (Drewnoski et al., 2014). Sulfur content of corn coproducts varies by plant and by load within plant; largely due to the amount of sulfuric and sulfurous acid used in the production of ethanol. Another source of sulfur is sulfur concentration in water, which is variable by location and is additive to dietary sulfur

concentration. The primary concern associated with high dietary sulfur concentration is polioencephalomalacia which is softening of grey matter in the brain and caused by inhalation of H_2S gas produced in the rumen.

The NRC (1996) lists a TDN value of 88% for both corn and DDGS and 80% for CGF. Much of the analysis conducted to determine the feeding value of corn coproducts has been done with feedlot diets. Klopfenstein et al. (2008) conducted a meta-analysis that determined the feeding value of DDGS relative to corn is 153% and 100% when DDGS inclusion was 10% and 40% of diet DM, respectively. Green et al. (1987) conducted a meta-analysis that determined the feeding value of CGF relative to dry rolled corn is 87% and 100% when CGF inclusion was 23% and 46% of diet DM, respectively. Fewer studies have sought to determine the feed value of DDGS when fed to cattle consuming forage-based diets. Loy et al. (2008) conducted an experiment that evaluated the feeding value of DDGS relative to corn when supplemented to beef heifers consuming ad libitum grass hay. It was determined that DDGS had 118% and 130% the feeding value of corn when supplemented at 0.21% and 0.81% of BW, respectively. This equated to TDN values for DDGS of 120% and 95.8% when supplemented at 0.21% and 0.81% of BW, respectively.

Excessive amounts of protein can be consumed when feedstuffs high in CP, such as DGS and CGF, are used as an energy source. Gunn et al. (2014) fed gestating and lactating heifers isocaloric diets that either met or exceeded CP requirement. No differences in heifer BW was observed; but, heifers fed excessive CP produced less energy corrected milk, due to reduced milk fat, while tending to have decreased anestrous period when compared to heifers fed protein to requirement.

The effects of drylot diets containing DDGS, and other concentrates, on cow performance have been documented; however, diet of gestating cows also impacts the subsequent calf. Calf birth BW has been increased when cows are limit-fed concentrate diets, both corn or DDGS, as a primary energy source relative to cows fed hay (Loerch, 1996; Radunz et al., 2010). Despite increased calf birth BW when gestating cows are fed concentrates, neither Loerch (1996) nor Radunz et al. (2010) reported increased incidence of dystocia. Gunn et al. (2014) observed a similar increase in calf birth BW, while also observing an increase in dystocia, when feeding excessive dietary CP to pregnant heifers during mid- and late gestation.

Fetal Programming

Link between Cow/calf Production and Fetal Programming

Much research has been devoted to how nutrition affects performance of the beef cow; yet, knowledge of how maternal nutrition during gestation affects the developing calf is much more limited. As previously discussed, many decisions regarding how beef cows are managed are based the production goals of reducing feed costs and maintaining acceptable cow performance. It has been observed for several decades that certain beef cow nutrition programs result in increased or decreased calf birth BW (Corah et al., 1975; Loerch, 1996; Radunz et al., 2010). These observations provide evidence that maternal nutrition during gestation impacts developing calves; much fewer data exist concerning the long-term impacts of these effects on the lives of progeny. If maternal nutrition can substantially impact subsequent progeny, positively or negatively, perhaps these impacts should be considered when managing nutrition of pregnant beef cows. Alterations to prepartum nutrition have translated to differences in adiposity,

BW, cyclicity, LM area, and marbling scores of resulting progeny (Du et al., 2010; Funston et al., 2010a).

The Fetal Programming Concept

The concept that maternal nutrition can have lasting effects on subsequent progeny performance is known as fetal programming (FP). This concept is based off of the principle that living creatures are plastic in their development and stimuli at certain points during development can cause permanent changes in body structure, function, or metabolism (Barker, 2012). The fetus is reliant on the flow of nutrients it receives from its dam through the placental membranes. Hence, the maternal environment is responsible for "programming" the growing and developing fetus for postnatal life.

Origins of the Fetal Programming Concept

The concept of FP applies to all mammalian species and was developed by analyzing public human health data (Barker, 2007a; Barker, 2007b; Barker, 2012). The origins of this theory are grounded in human cohort studies that investigated the geographical prevalence of chronic diseases such as coronary heart disease, type-two diabetes, and hypertension (Barker, 2007b). These cohort studies typically involve children born during short-term, geographically isolated food shortages in developed countries. Using birth and health records collected throughout early life, investigators are able to track these children through adulthood to ascertain lifelong effects of maternal nutrition. Examples of the historical events that have been analyzed for potential FP effects are food shortages in England and Wales early in the twentieth century, and famines that resulted from the Nazi occupation of Europe; such as the well-documented famine of Helsinki, Finland (Barker, 2007a; Barker, 2007b). Incidence of disease was elevated in children who were conceived, born, or spent infancy in specific geographic regions in which

widespread food shortages were present. Many of these food shortages were associated with difference in social class within the same nation, reflecting differences in living conditions. It is thought that increased prevalence of chronic diseases, such as coronary heart disease, is related to the rise in living conditions and prosperity following World War 2. Human cohort studies have shown a greater correlation chronic disease and adverse maternal conditions, such as poor living conditions and food shortage, experienced by affected offspring in utero (Barker, 2007b). Adults predisposed to coronary heart disease and type-two diabetes later tended to grow slowly in utero, had below average BW at birth and through the first two years of life, and then gained BW and body mass index rapidly (Barker, 2007a; Barker, 2012). Barker (2013) commented that public health programs intended to promote a balanced diet in pregnant women are the key reducing incidence of chronic adult diseases in contemporary times.

Timing of Fetal Growth and Development

Fetal growth and development is a complex process with different organs and body systems being developed at specific time points during gestation (Du et al., 2010; Funston et al., 2010a). Generally, fetal development and growth occurs in two stages. Many organs and body systems are developed during the first two thirds of gestation, while the majority of fetal growth occurs during the final third of gestation. Since the great amount of fetal growth that occurs during the final trimester, dam nutrient requirement is greatest during this time. Meeting short-term nutrient requirements are of great importance; yet, it is an oversimplification to believe that the developing fetus is supplied directly by maternal diet during pregnancy (Barker, 2012). The fetus is directly supplied maternal nutrient supply via the uterus, which is dependent on maternal diet and the dam's stored bodily reserves (Barker et al., 2013). Thus, fetal nutrient supply is closely tied to the long-term, lifetime nutrition of its dam. When applied to beef production, the

influence of long-term plane of nutrition, reflected by body condition score, potentially has as much of an impact on fetal development as short-term nutrition provided to the cow.

Trajectory of Growth, and Nutrient Partitioning

Fetal growth trajectory is determined at time of conception by placental size and resulting ability to transfer nutrients across placental membranes, directly affecting birth BW (Vonnahme et al., 2007; Barker, 2012). An abundant nutrient flow during early gestation sets a rapid growth trajectory demand for maternal nutrients greatest during late gestation. Nutrient restriction at time of conception would set a slow growth trajectory. A rapid growth trajectory sets a high demand for maternal nutrients. Nutrient restriction later in development would challenge the dam to meet the high requirements of fetal developing set by a rapid growth trajectory. The fetus has the ability to exhibit accelerated growth, also known as compensatory growth, to overcome instances of brief undernutrition. The concept of compensatory growth is familiar to livestock producers as this is often referred to for postnatal growth patterns. However, nutrients devoted to compensatory growth decrease allocation of maternal nutrients to other developmental processes as an inexhaustible flow of the nutrients across the placenta is not present. It is accepted that fetal growth trajectory is faster for male fetuses. Thus, male fetuses could be more susceptible to adverse developmental consequences caused by in utero undernutrition. Barker (2012) reasons that this may be partially explain the shorter lives of men.

A hierarchy of nutrient partitioning towards fetal growth and development exists. If maternal nutrient flow to the fetus is compromised, development of certain bodily systems takes precedence for nutrient partitioning over others. For example, brain growth is a higher priority when compared to development of organs that are non-functioning in the womb, kidneys and lungs, or skeletal muscle that is of lower priority (Barker, 2012). The delayed development of

low-priority organs is done to protect those that are vital to further development of the fetus. An extreme example of the hierarchy of nutrient partitioning is a phenomenon known as intra-uterine growth restriction (IUGR). Wu et al. (2006) defines IUGR as impaired growth and development of the mammalian embryo/fetus or its organs during pregnancy. Severe nutrient restriction during gestation is a common cause of IUGR in livestock production. The need for adequate cow nutrition is brought into focus when considering that tissues of greatest economic performance, muscles and adipose, are of low priority during fetal growth and development.

It widely recognized that primiparous heifers give birth to smaller calves. This reduction in birth BW is due to smaller physical size of heifers relative to cows and heifer's continued nutrient requirement for growth (Greenwood and Cafe, 2007). Beef cows continue to grow to mature until 4 yr of age and experience decreased growth rate from 4 to 7 yr of age (Long et al., 2009). During periods of maternal nutrient restriction, growth requirement of heifers and young cows would be expected to result in greater restriction in fetal nutrient supply when compared to mature cows. Heifers respond to pre-calving nutrient restriction with reduction in calf birth BW more so than older cows (Bellows and Short, 1978).

Placental Development and Intra-uterine Growth Restriction

The importance of proper nutrition during early gestation is often overlooked as cow nutrient requirements are much lower during early gestation relative to late gestation. Early gestation is of great importance because development of the placenta facilitates maternal nutrient flow for further growth and development to occur. An issue closely related to placental development is IUGR. While IUGR can occur during any stage of gestation, impaired placental development during early gestation significantly impedes the flow of maternal nutrients to the fetus.

To evaluate the effects of nutrient restriction during early gestation, Long et al. (2009) conducted an experiment that fed multiparous beef cows to 100% of NRC (1996) requirement or restricted cows to 68.1% of NE_m and 86.7% of MP requirements from d 30 to 125 of gestation. Cows were either slaughtered on d 125 of gestation or realimented to achieve similar BW and BCS by d 190 of gestation. Remaining cows were slaughtered on d 245 of gestation. Of the nutrient restricted cows slaughtered at d 125 of gestation, 60% did not display IUGR and carried fetuses similar in weight to cows fed to requirement (Requirement = 947.6 g, Nutrient restricted non-IUGR = 973.8 g). The remaining 40% of nutrient restricted cows slaughtered at d 125 of gestation exhibited IUGR and carried significantly lighter fetuses (772.6 g) than non-IUGR nutrient restricted cows or those fed to requirement. It was noted by Long et al. (2009) that of nutrient restricted cows, IUGR cows were significantly younger than non-IUGR cows (3.5 vs. 5.0 yr of age). At d 125, fetal brain weight as a percentage of fetal weight was greater for fetuses carried by IUGR dams than fetuses carried by the other two groups. Also at d 125, fetal heart weight as a percentage of fetal weight tended to be greater for fetuses carried by IUGR dams than fetuses carried by the other two groups. These differences in fetal weight and organ weight were attributed to reduced placental vasculature. At d 125, cotyledonary weights were reduced and total placentome surface area tended to be reduced for nutrient restricted cows when compared to non-IUGR nutrient restricted and requirement-fed cows. At d 245 of gestation, fetal and caruncular weights were similar between requirement-fed and realimented cows. None of the nutrient restricted cows displayed IUGR on d 245 of gestation. However, cotyledonary weights were reduced for previously nutrient restricted cows; providing evidence of reduces placental vasculature caused by previous nutrient restriction. Despite no differences in fetal weight at d 245, organ structure and function may have been detrimentally impacted by nutrient restriction.

At d 245 total glomerular and glomeruli per g of liver tissue were significantly reduced in fetuses carried by nutrient restricted dams when compared to requirement-fed dams. These differences in liver structure could result in decreased filtration rate and renal function. Long et al. (2009) concluded that IUGR may go unnoticed if cows that were nutrient restricted during early gestation received improved nutrition during mid- and late gestation.

Vonnahme et al. (2007) conducted a similar experiment that investigated the possible FP effects of nutrient restriction during early gestation on placental vascularity. Cows were nutrient restricted in similar manner as Long et al. (2009) from d 30 to 125 of gestation. In contrast to Long et al. (2009), when slaughtered at d 125 of gestation, fetal weights were similar between nutrient restricted and requirement-fed cows with no reported incidence of IUGR. Caruncular and cotyledonary weights were reduced in nutrient restricted cows. At d 125, nutrient restricted cows had similar uterine vasculature when compared to cows fed to requirement. When slaughtered a d 250 of gestation, nutrient restricted cows that had been realimented had similar fetal weight and caruncular weight, and reduced cotyledonary weight relative to requirement-fed cows. Also at d 250, nutrient restricted cows had greater caruncular capillary density and decreased cotyledonary capillary surface density when compared to cows fed to requirement. These two studies show that nutrient restriction during early gestation can negatively affect placental development and the developing fetus. Nutritional realimentation later in gestation may mask some of these effects; yet, irreversible alterations to organ structure and function occur.

Development of Skeletal Muscle

Development of skeletal muscle is of obvious importance to beef cattle production; yet, is of lower priority for maternal nutrient partitioning than organs or systems like the brain and central nervous system. Thus, risk of inhibited development of skeletal muscle is greater during

periods of nutrient restriction. No net increase in muscle fiber number, hyperplasia, occurs following parturition, making proper development of fetal skeletal muscle extremely important (Du et al., 2010).

Du et al. (2010) outlines the process of skeletal muscle development. Prior to development of specific cell types, differentiation, a pool of pluripotent and multipotent mesenchymal stem cells exists in embryonic and fetal tissues. Muscle fibers, myofibers, develop in two waves during fetal development. In cattle, the primary wave occurs during the first two months of gestation with few myofibers generated in this stage. The myofibers generated during this phase serve as a framework for myofiber development during the second wave of myogenesis. This secondary stage is when the majority of muscle fibers are formed and is thought to occur during the second through eighth month of gestation. Consequently, nutrient restriction that were to occur during the second wave of myogenesis would have permanent effects on resulting progeny. In cattle, fetal skeletal muscle matures during late gestation, around d 210 of gestation. Nutrient restriction after this point would result in minimal impact on muscle hyperplasia, but could significantly decrease muscle fiber diameter and mass, hypertrophy. Greenwood et al. (2004) reported that progeny born to nutrient restricted cows had reduced BW and HCW relative to those born to adequately fed cows. These differences were attributed to reduced muscle mass as a consequence of maternal nutrient restriction. Nutrient restriction lasting from early to mid-gestation has caused alterations in muscle fiber type, with type two, oxidative fiber types being favored in lambs (Zhu et al., 2006). Altering myofiber type has potential implications on postnatal muscle growth, growth efficiencies, and carcass characteristics later in life.

Development of Adipose Tissue

Development of marbling, or intramuscular fat, is of great economic importance to the beef industry. Intramuscular adipocytes are formed during fetal development. Intramuscular adipocytes do not experience a great amount of growth during fetal development, but do determine future marbling potential. To realize maximum postnatal marbling potential, multipotent cells must be committed to adipocyte formation in utero because few undifferentiated cells exist post-parturition. Adipogenesis is initiated approximately the fourth month of gestation, partially overlapping with the second wave of myogenesis. Du et al. (2010) poses that Adipogenesis coinciding with the wave of myogenesis in which the majority of myofibers form represents a major opportunity for maternal nutritional to positively or negatively affect stem cell differentiation. Fibroblasts which form connective tissue found in muscle also form at this time.

Since the number of multipotent stems cells decrease as cattle mature, strategies to increase marbling during early life would be more effective than later in life. After 250 d of age, nutritional influences have little chance of increasing adipocyte development (Du et al., 2010). After 250 d of age, marbling is enhanced only through the growth of pre-existing adipocytes. Early weaning has been used to increase development of adipocytes early in life (Wertz et al., 2002; Meteer et al., 2013). Calves that were early-weaned and immediately transitioned to a high concentrate diet, often with substantial amounts of starch, had higher marbling scores than normal-weaned calves (Shike et al., 2007). Nutritional stimuli that optimize muscle adipocyte differentiation during fetal development theoretically could surpass early weaning in ability to enhance marbling in beef calves. However, effective strategies that are repeatable and economical for large scale cow/calf production systems have yet to be refined. Periods of

nutrient restriction during mid-gestation may negatively affect marbling potential of subsequent progeny; however, this is not known. To preserve marbling potential of progeny, Funston et al. (2010a) proposed ideally management would allow cows to achieve adequate body condition prior to exposure to conditions in which nutrients are limited. Strategies to achieve this include early weaning or altering time of breeding and subsequent parturition to avoid nutrient restriction during mid-gestation.

Health

Skeletal muscle and adipose tissue are not the only body systems affected by maternal nutrition as there is evidence that the immune system is affected. Data derived from cattle and sheep imply that nutrient restriction during pregnancy affects the health of neonates. Hammer et al. (2011) conducted two experiments that investigated immunoglobulin transfer and neonatal health of lambs born to dams that were fed either 60%, 100%, or 140% of NRC (1985) requirement during mid- and late gestation. In one experiment, serum IgG concentrations were greatest for lambs born to nutrient restricted dams and lowest for lambs born to overfed dams, with serum IgG concentration being intermediate for those born to dams fed to maintenance. At 57 d of age, incidence of morbidity and mortality was greatest for lambs born to overfed dams. In the second experiment conducted by Hammer et al. (2011), serum IgG concentration was greater in lambs born to nutrient restricted dams when compared to those born to dams overfed or fed to maintenance. These findings lead to a hypothesis that lambs born to nutrient restricted dams were programmed to survive in harsher environments than those developed with an overabundance of nutrients. Despite evidence that immunoglobulin transfer was greater for progeny born to nutrient restricted dams, it does not appear that neonatal health was consistently improved. Corah et al. (1975) observed differences in calf morbidity and mortality when cows

were fed either 50% of NRC (1970) requirement 100 d prepartum or restricted to 50% of NRC requirement beginning 100 d prepartum and then fed 117% of NRC requirement 30 d prepartum. Incidence of scours was 19% greater for calves born to continuously-restricted dams relative to those born dams who been fed high energy diets 30 d prior to calving. Calf pre-weaning mortality was 29% greater and weaning BW reduced when cows were continuously-restricted 100 d prepartum. Nutrient restriction may lead to improved immunoglobulin uptake; however, this does not necessarily translate to healthier, thriftier calves.

In a review, Funston et al. (2010a) summarized research using various animal models explaining that nutritional insults in utero may contribute to increased incidence of bovine respiratory disease (BRD). It has been observed in rats that maternal undernutrition elevates blood pressure in the fetus and throughout postnatal life via altered lung vascularity. Altered lung vascularity increases susceptibility to respiratory disease. Increased incidence of BRD has serious economic ramifications, representing the primary cause of feedlot mortality. When Larson et al. (2009) supplemented cows grazing dormant winter range with protein-based supplement; differences in feedlot health of subsequent steer progeny was observed. There were no differences in number of calves treated for BRD or metabolic disorders from birth to weaning; however, steers whose dams were provided protein supplement were healthier in the feedlot, with fewer calves treated from weaning until slaughter.

Plane of Nutrition

As indicated by previous discussion of placental and fetal development, maternal plane of nutrition has substantial effects on subsequent progeny. Cattlemen often prescribe to management that maintains beef cows at a moderate level of body condition, especially at calving, during lactation, and through the breeding season when cow nutrient requirements are

greatest. Due to emphasis on meeting nutrient requirements during early lactation and at breeding, the importance of providing adequate nutrition during early and mid-gestation may be overlooked. This is understandable as cow nutrient requirements are less, relative to late gestation and early lactation. The fetal programming effects of maternal nutrient restriction garner significant attention as possible nutritional deficiencies exist for grazing and drylot cattle consuming low quality forages with little or no supplemental nutrition. Maternal overnutrition is most common in a drylot setting when intake of energy dense diets is excessive. This condition has been studied to a lesser extent in beef cows as proper diet management and feeding management can alleviate instance of over feeding. However, investigation of the fetal programming effects of maternal overnutrition may have great bearing on human disease states, such as diabetes.

Nutrient Restriction

Effects of severe maternal restriction during early to mid-gestation on subsequent progeny has been studied using both sheep and beef models. Ford et al. (2007) fed ewes to 100% of NRC (1985) requirement or restricted ewes to 50% of NRC requirement from d 28 to 78 of gestation. Nutrient restricted ewes were fed to 100% of requirement from d 79 of gestation through lambing. This nutrient restriction model had been previously shown to induce IUGR (Vonnahme et al., 2003). Wethers born to nutrient restricted dams had similar birth BW as those born to requirement-fed dams. Wethers born to nutrient restricted dams were heavier and had more backfat than those born to dams fed to requirement at 4 months of age and remained heavier throughout life. At 140 d of age, wethers born to nutrient restricted dams had greater leptin concentrations, which correlate with greater adiposity. Ford et al. (2007) posed that maternal nutrient restriction and greater adiposity and growth rate of progeny may be associated

with a programmed increase in appetite; however, DMI was not reported. At slaughter, wethers born to nutrient restricted dams tended to have greater HCW, reduced LM and semitendinosus weights as percentage of BW, and greater kidney and pelvic fat as a percentage of BW.

Maternal nutrient restriction during early or mid-gestation does not necessarily culminate in substantial alterations in post-weaning growth of subsequent progeny; yet, differences in carcass composition can still result. Long et al. (2012a) conducted an experiment that evaluated the effects of nutrient restriction with or without protein supplementation from d 45 to d 185 of gestation on progeny growth, carcass characteristics, and adipocyte size. Mature cows were fed to 100% of NRC (1996) requirement, restricted to 70% of requirement, or restricted to 70% of requirement and provided supplemental RUP formulated to provide similar duodenal AA flow to requirement-fed cows. At d 185 of gestation, cows fed to requirement or offered supplemental protein had similar BW and BCS, with both being greater than those that were nutrient restricted and not offered protein supplement. Maternal nutrient restriction had no effect on calf BW at birth, weaning, or slaughter. Calves born to requirement-fed or protein supplemented dams had lower yield grades than those born to nutrient restricted dams. Higher yield grades for calves born to nutrient restricted dams may be due to decreased muscle mass indicated by a trend for decreased semitendinosus muscle weight as a percentage of HCW. Long et al. (2012a) analyzed adipocyte diameter of adipose tissue from subcutaneous, perirenal, mesenteric, and omental depots. In all four depots, progeny of nutrient restricted dams had greater or tended to have greater adipocyte diameter than progeny of requirement-fed dams. Progeny born to protein supplemented dams had adipocyte diameters that were either intermediate and not different from either treatment or similar to those of progeny from requirement-fed dams. The experiment

conducted by Long et al. (2012a) indicates that supplemental AA may be essential to prevent detrimental effects on subsequent progeny when dams are energy restricted.

Long et al. (2010a) restricted cows to 55% of energy and 50% of CP requirements from d 32 to d 83 of gestation and observed no differences in birth and weaning BW when compared to progeny born to dams fed to 100% of requirement. Despite trends for differences in BW at the beginning and end of the finishing period, no differences were observed in HCW. Long et al. (2010a) observed no differences in typical carcass characteristics; but, muscle fiber area was reduced in the complexus muscle of steers born to nutrient restricted dams. Progeny born to nutrient restricted dams had reduced lung and trachea weight, possibly signifying reduced respiratory capacity. However, Long et al. (2010a) did not report incidence of respiratory disease in this experiment. The work of Long et al. (2010a) and Long et al. (2012a) show that nutrient restriction during early to mid-gestation does not automatically lead to obvious changes in growth rate of progeny, but can lead to more subtle differences in body composition.

Overfeeding

Interest in effects of maternal obesity on FP has grown due to an obesity epidemic in human populations. Extreme maternal obesity tends to less common in livestock production due to the economic implications of maintaining animals in obese body condition. Thus, much more research has focused on the FP effects of nutrient restriction. Long et al. (2010b) evaluated the FP effects of maternal obesity in ewes on growth and body composition of subsequent progeny. Ewes were either fed 100% or 150% (obese) of NRC (1985) nutrient requirements 60 d prior to breeding through parturition. Ewes fed 150% of requirement increased their BW by 52% from initiation of feeding through d 135 of gestation when compared to BW change of 7%for requirement-fed ewes. Lamb birth BW and BW through 19 mo of age. At 19.5 mo of age, lambs

were individually fed an ad libitum high energy diet for 12 wk. At the beginning of the ad libitum feeding period, no differences were observed in body composition. Over the feeding period, lambs born to obese dams consumed 10% more feed and tended to gain more weight; yet, G:F was not improved relative to lambs born to requirement-fed lambs. Long et al. (2010b) concluded that greater appetite is more likely responsible for greater adiposity than differences in metabolic rate. This conclusion is supported by the fact that lambs born to obese dams had similar BW as those born to requirement-fed dams up to 19 mo of age when raised under typical production conditions. At the end of the feeding period, percentage of body fat and lean were increased and decreased, respectively, in lambs born to obese dams relative to lambs born to requirement-fed dams. Plasma leptin concentrations were greater in lambs born to obese dams at wk 7 and 12 of the feeding period. Plasma leptin is associated with increased feed intake and adiposity. It is unclear if greater plasma leptin is result of increased feed intake or greater adiposity that results from increased feed intake (Long et al., 2010b). It was noted by Long et al. (2010b) that maternal obesity during gestation leads to several phenotypic similarities found in lambs born to nutrient restricted dams.

Long et al. (2012b) used the same ewe obesity model as (Long et al., 2010b) to evaluate maternal and fetal blood metabolites and hormones during late gestation as well as fetal adiposity. Ewes and fetuses were necropsied on d 135 of gestation. Fetal weight was similar across treatments; yet, fetal carcass weight was reduced in fetuses carried by obese dams relative to those born to requirement-fed dams once internal organs and internal fat were removed. Similarly, greater differences in fetal weight were observed when fetuses carried by obese ewes were necropsied during mid-gestation (Ford et al., 2009). Long et al (2012b) posed that fetal growth in obese ewes slows during late gestation, possible due to reduced placental vascularity

and angiogenic factor production. Perirenal and pericardial adipose depots represented a greater percentage of fetal carcass weight and subcutaneous fat thickness was greater in fetuses carried by obese dams relative to those born to requirement-fed dams. Differences in subcutaneous fat thickness were not anticipated by (Long et al., 2010b) since this depot is the last to form in the ovine fetus. Average adipocyte diameter was greater in perirenal and tended to be greater pericardial adipose tissue of fetuses carried by obese dams relative to those born to requirement-fed dams. At d 135 of gestation, maternal plasma glucose and thyroxine concentrations tended to be greater in obese ewes. Fetal plasma cortisol, insulin-like growth factor 1 (IGF-1), and thyroxine concentrations were reduced in fetuses carried by obese to dams relative to those born to requirement-fed dams. Cortisol is a glucocorticoid that functions to increase glucose through stimulation of gluconeogenesis. Thyroxine is thyroid hormone that function to increase basal metabolic rate and necessary for cell differentiation and development. Increased concentrations of cortisol, IGF-1, and thyroxine indicate more rapid growth of fetuses carried by requirement-fed dams during late gestation and reduced growth of fetuses carried by obese dams. Fatty acid concentration was greater in perirenal adipose depots, the first depot to form in ovine fetuses, and tended to be greater in subcutaneous adipose depots, the last depot to form in ovine fetuses, of fetuses carried by obese dams relative to lambs born to requirement fed dams. Insulin-like growth factor 1 is a hormone similar in insulin structure that serves mediate the effects of growth hormone. Concentrations of fatty acids longer than 16 carbons (18:0, 18:1 c-9, and 18:1 c-10/11) were greater in perirenal adipose tissue of fetuses carried by obese dams. Concentration of 18:1 c-9 fatty acid was greater and 18:1 c-10/11 fatty acid tended to be greater in pericardial adipose tissue of fetuses carried by obese dams. Concentrations of 16:0, 18:1 c-9, and arachidonic fatty acids were greater in subcutaneous adipose tissue of fetuses carried by obese dams. These

differences in fatty acid profile in various adipose depots indicate altered fatty acid synthesis in fetuses carried by obese dams relative to those born to requirement-fed dams.

Fetal Programming and Beef Production Systems

Much of the previous research that has investigated the potential FP effects of maternal nutrition has analyzed only certain portions of the beef production cycle or has used nonruminant models. The number of studies that have investigated FP effects of maternal nutrition in the context of applied beef production systems are much more limited. Studies concerning the long-term effects of maternal nutrition on subsequent progeny have focused on improved plane of nutrition of gestating cows during grazing or energy source of drylot cow diet.

Grazing systems and fetal programming

As discussed previously, grazing cattle are susceptible to experiencing periods of nutrient restriction caused by sharp seasonal differences in forage quality and growth. This is especially true for spring-calving cows gazing dormant warm-season forage during late gestation. Evidence exists that CP supplementation of cows can improve performance of gestating cows and also impart FP effects on steer (Stalker et al., 2006; Larson et al., 2009) and heifer progeny (Martin et al., 2007; Funston et al., 2010b).

Stalker et al. (2006) and Larson et al. (2009) conducted separate three year experiments that evaluated the effects of CP supplementation on cow and pre-weaning progeny performance as well as post-weaning performance and carcass characteristics of steer progeny. Stalker et al. (2006) offered cows wintered on native range pastures the equivalent of 0.45 kg of 42% CP supplement/cow·d^{-1} fed 3 d per wk or no supplement 90 d prior to the start of the calving season. Cows offered CP supplement were able to maintain BW and BCS through the prepartum supplementation period, while cows not offered supplementation lose both BW and BCS.

Differences in BW did not persist at breeding; however, cows that received prepartum supplementation had greater BCS. Prepartum supplementation had no effect of post-partum interval or conception rate during the first 21 d of the breeding season. Stalker et al. (2006) reasoned that no differences in subsequent reproduction were observed as differences in BCS between supplemented and non-supplemented cows were not great enough to affect pregnancy rates. Stalker et al. (2006) observed no differences in calf birth BW; however, calves born to supplemented dams were heavier at weaning and had greater pre-weaning ADG. Winterholler et al. (2012) observed increased calf birth BW as CP in supplement was increased with greater level of DDGS supplementation. This response in weaning BW to gestational protein supplementation agrees with the findings of Beaty et al. (1994) and Winterholler et al. (2012) who observed increased calf weaning BW as CP in supplement fed during gestation elevated. Stalker et al. (2006) observed greater weaning percentage for cows offered CP supplement when compared to those not offered supplement. Corah et al. (1975) reported a 29% reduction in weaning percent when cows were continuously nutrient restricted 100 d prepartum when compared to cows that were nutrient restricted and offered a high energy diet 30 d prepartum. No differences were observed for feedlot ADG, DMI, gain efficiency, or carcass characteristics of steer progeny, regardless of whether dams received CP supplementation or not. Ciminski (2002) observed improved growth of calves born to CP supplemented dams in an experiment conducted under similar conditions to Stalker et al. (2006). Stalker et al. (2006) explained that the difference between the two studies was that Ciminski (2002) weaned the previous calf crop later in the year (November vs. early October), reducing maternal BCS and making fetuses carried by non-supplemented dams more susceptible to nutrient restriction. When sold at weaning, net returns of steer calves from CP supplemented dams were $25.38 greater, driven by greater calf

weaning BW and weaning percentage when compared to calves from non-supplemented dams. When ownership of steer calves was retained through the feedlot, net returns of steer calves from CP supplemented dams were $45.76 greater when compared to steer calves from unsupplemented dams, attributed almost entirely to the greater weaning percentage of calves from CP supplemented dams.

Due to the abundance of corn residue following corn harvest in the Midwest, cow/calf producers graze standing corn residue as an alternative to feeding harvested forages in a drylot. Quality of corn residue is greatest immediately following harvest and declines through the winter (Klopfenstein et al., 1987). Corn residue quality is closely tied to the selective nature in which cattle graze cornstalks; tending to eat grain first, corn leaves and husks second, and low quality cornstalks last. The decline of crop residue quality necessitates that cows grazing crop residue be supplemented later in the grazing season.

Larson et al. (2009) investigated the influences of winter grazing system and protein supplementation on performance of both cows and subsequent progeny. Treatments were arranged in a 2 x 2 factorial in which cows were grazed on winter range or corn residue and offered the equivalent of 0.45 kg of 28% CP supplement/cow·d^{-1} fed 3 d per wk or no supplement 90 d prior to the start of the calving season. Analyzed nutrient value was similar between crop residue and winter range; however, analyzed nutrient value of corn residue may be misleading as diet selectivity may have been greater by cows grazed on corn residue. Cows wintered on crop residue had greater BW and BCS prior to calving when compared to those wintered on winter range; likely due to the superior quality of the corn residue early in the grazing period. In agreement with Stalker et al. (2006), cows offered CP supplement had greater BW and BCS prior to calving when compared to non-supplemented cows. Non-supplemented

cows grazed on winter range calved at least 5 d later than all other treatment combinations; with 16% fewer non-supplemented cows grazed on wither range calving in the first 21 d of the calving season. Larson et al. (2009) posed that this may have been a cumulative effect of BW loss and ensuing delay in conception as cows were maintained on the same treatment for all three years of the experiment. Greater BW and BCS for cows grazed on corn residue or offered supplement were maintained through breeding. Cow BW and BCS at weaning were not affected by prepartum CP supplementation. At weaning, cows grazed on corn residue were heavier than those grazed on winter range; yet, BCS was not different. There was no effect of prepartum CP supplementation on milk production. Milk production tended to be greater during early lactation and was greater during late lactation for cows grazed on corn residue when compared to those grazed on winter range during late gestation. Calf birth BW was greater when dams were wintered on corn residue compared to winter range. Prepartum supplementation had no effect on calf birth BW. This response agrees with Stalker et al. (2006), in which prepartum supplementation resulted in only numerical increases in calf birth BW when compares to calves born to non-supplemented dams. There was an interaction for calf weaning BW between winter grazing system and CP supplementation in which calves born to non-supplemented dams grazed on winter range were at least 15 kg lighter than all other treatment combinations, with no differences between any other treatment combinations. However, there was no interaction for calf adjusted 205-d BW; as 205-d BW was greater for calves born to dams grazed on corn residue and a trend for greater 205-d calf BW when dams were supplemented. In contrast to Stalker et al. (2006), no difference in percentage of calves weaned was observed.

Unlike the study conducted by Stalker et al. (2006), maternal nutrition had long-term influences on steer progeny in the feedlot. Feedlot ADG and DMI tended to be greater for steers

born dams offered supplement when compared to those born to un-supplemented dams; with differences if G:F. Treatment for respiratory and gastrointestinal disease was greater for steers born to non-supplemented dams when compared to those born to supplemented dams; despite no pre-weaning treatment differences. There were interactions for final BW and HCW between winter grazing system and prepartum supplementation. Calves born to supplemented dams grazed on winter range and those born to non-supplemented dams grazed on corn residue had greatest final BW and HCW, those born to non-supplemented dams grazed on winter range were lightest, with those born to supplemented dams grazed on corn residue being intermediate. Steers born to supplemented dams had greater marbling scores, equivalent to approximately half of a USDA quality grade; and as a result, percentage of calves grading low or average choice or better was greater when compared to those born to non-supplemented dams. This marbling difference indicates that improved maternal nutrition during late gestation can alter altered adiposity of skeletal muscle of subsequent progeny. Smith and Crouse (1984) determined that glucose is the preferred substrate for intramuscular adipocytes. Larson et al. (2009) posed that improved maternal nutrition through concentrates increased glucose uptake or increased the supply of glucogenic amino acids available to the cow; having a trickle-down effect on the fetus. The reason that Stalker et al. (2006) did not see a marbling response to protein supplementation under similar conditions may be because of differences in the supplement fed between the two studies. Stalker et al. (2006) fed a 42% CP supplement that was 31% RUP while Larson et al. (2009) fed a 28% CP supplement that was 48% RUP. Increased supplemental RUP concentration fed by Larson et al. (2009) changed maternal amino supply or glucose production, stimulating greater preadipocyte development in the fetus. However, g of supplemental RUP was similar for both studies. The increase in carcasses grading choice, without an increase in yield grade,

resulted in an additional $47 of carcass value for steers born to supplemented dams when compared to those born to non-supplemented dams. An alternate theory for the improved marbling observed by Larson et al. (2009) revolves around the previously discussed differences in steer post-weaning health. As fewer calves from supplemented dams were treated for BRD in the feedlot, it was posed that improved health lead to improved marbling scores. Larson et al. (2009) concluded that despite improvements in cow and calf performance with protein supplementation, supplementation was not cost-effective in all situations. When sold at weaning, calves born to non-supplemented dams grazed on corn residue were most valuable (average of $35 greater net return) with no differences between all other treatment combinations. Winter grazing system had no effect on steer carcass value or net return at slaughter. Steers born to supplemented dams had greater average net returns of $30 at slaughter when compared to steers born to non-supplemented dams.

Few experiments have investigated the effects of maternal nutrition on productivity of subsequent heifer progeny including pregnancy rate and growth performance through calving. For example, Corah et al. (1975) reported that heifer calves born to dams restricted to 65% of NRC (1970) requirement 100 d prepartum reached puberty 19 d later than those born to dams fed to meet requirement; however, pregnancy rate was not measured. To investigate the potential FP effects of CP supplementation during late gestation on heifer progeny and their productivity when retained in the herd Martin et al. (2007) and Funston et al. (2010b) evaluated the female progeny resulting from the studies conducted by Stalker et al. (2006) and Larson et al. (2009), respectively.

Martin et al. (2007) observed no differences in birth date or birth BW of heifer calves regardless of whether dams received supplement or no supplement. In agreement with Stalker et

al. (2006), greater weaning BW was observed for calves born to dams offered CP supplement when compared to those born to non-supplemented dams. In contrast to Stalker et al. (2006), heifers born to dams offered CP supplement were also heavier at time of first breeding, pregnancy diagnosis, and beginning of the second breeding season. Considering that these studies were conducted under similar conditions, there appears to be an interaction between calf sex and maternal nutrient status for mature weight. Steer final BW was not different due to prepartum supplementation; yet, heifer progeny had persistent BW differences when measured at multiple time points. The difference between these studies may be the greater fetal growth trajectory of male fetuses. If true, female fetuses would require fewer nutrients to achieve an equivalent level of fetal development; and when provided with same flow of maternal nutrients, female fetuses would have the potential for further growth and development. Maternal nutrition had no effect on the percentage of heifers cycling prior to the breeding season or on age at puberty. It was posed that delayed estrus was not observed in heifer progeny as dams in the experiment conducted by Martin et al. (2007) only experienced moderate nutrient restriction when compared to the significant nutrient restriction imposed by Corah et al. (1975). A greater percentage of heifers born to supplemented dams calved within the first 21 days of the calving season; 77% and 49% for calves born to supplemented and non-supplemented dams respectively. Overall pregnancy was effected by maternal prepartum CP supplementation, 93% and 80% and heifers born to supplemented and non-supplemented dams, respectively. Martin et al. (2007) commented that late gestation, corresponds with fetal ovarian folliculogenesis and endometrial gland development. Thus, it appears that moderate nutrient restriction during late gestation negatively affects fertility of subsequent heifer progeny.

Funston et al. (2010b) evaluated the effects of winter grazing system and prepartum supplementation growth performance and reproduction of subsequent heifer progeny. There was an interaction for heifer adjusted 205-d BW between winter grazing system and CP supplementation in which heifers born to non-supplemented dams grazed on winter range were at least 11 kg lighter than all other treatment combinations, with no differences between any other treatment combinations. Heifers born to non-supplemented dams grazed on winter range maintained numerically lower BW through to first calving and the start of the second breeding season. Funston et al. (2010b) concluded that if cows are to be wintered on winter range, CP supplementation is necessary to achieve optimal production from progeny of either sex. Contrary to Martin et al. (2007), Funston et al. (2010b) observed that heifers born to CP supplemented dams reached puberty at a younger age when compared to heifers born to non-supplemented dams. Winter grazing system did not influence age at puberty. Age at puberty was independent of BW at puberty, as BW at puberty was similar for all treatments. Funston et al. (2010b) posed that the difference in age at puberty indicates maternal nutrient flow effects intrauterine environment and development of the female reproductive tract. Pregnancy rates were not affected by winter grazing system or prepartum supplementation. At time of first calving: calving date, calf birth BW, and percentage of calves born in the first 21 d of the calving season was not affected by maternal nutrition. The experiments conducted by both Martin et al. (2007) and Funston et al. (2010b) reveal that maternal nutrition can impact growth and reproductive performance of subsequent heifer progeny. Differences existed when fetuses of different sexes were developed under similar conditions and may be the result of differences in fetal trajectory of growth between male and female fetuses.

Improved Grazing During Mid-Gestation

Much of the previous research that has examined the influences of maternal nutrition on subsequent progeny has focused on late gestation. The focus on maternal nutrition during late gestation is understandable fetal nutrient requirement is at its greatest to support rapid fetal growth. For spring-calving herds, late gestation is the period of time when cow/calf producers are most reliant on stored feeds to meet cow nutrient requirements. Despite this, it has firmly established that that maternal nutrition during mid-gestation has great influence on fetal development (Du et al., 2010; Funston et al., 2010a). The importance of proper maternal nutrition during mid-gestation is easily overlooked as fall- and winter-calving herds are often maintained on pasture and require little supplemental nutrition during this time. In contrast, late spring-calving herds require significant supplemental nutrition during mid-gestation. Pasture quality affects maternal plane of nutrition and may influence fetal development.

Underwood et al. (2010) conducted an experiment that investigated the influence of grazing cows on improved pastures during mid- to late gestation on the growth and carcass characteristics of resulting steer progeny. Beginning at either d 120 or 150 of gestation, mature cows were grazed on either native range (6.5% to 5.4% CP) or irrigated, improved pastures (11.1% to 6.0% CP) for a period of 60 d. Cows grazed on improved pastures gained 11 kg more than those grazed on native range; however, there were no differences in cow BW or BCS prior to calving season. No differences in steer birth or adjusted 205-d BW were observed. Steers born to dams grazed on improved pastures had greater feedlot ADG and tended to have greater final BW, and had greater HCW when compared to those born to dams grazed on native range. No differences for LM area and semitendinosus weight were observed. The observation of similar muscle mass between treatments is perhaps a reflection on the stage of gestation that maternal

nutrition was manipulated via grazing. Subcutaneous backfat thickness was greater for steers born to dams grazed on improved pasture; marbling scores and KPH percentage were similar between treatments (455 for improved pasture and 420 for native range). In contrast to finding no difference in marbling score, ether extract of the LM at the 12th rib tended to be greater for steers born to dams grazed on improved pastures. Underwood et al. (2010) used light microscopy to determine if maternal plane of nutrition would alter adipocyte number and size. Steers born to dams gestated on improved pasture tended to have a greater number of subcutaneous adipose cells per field of view; however, no differences in adipocyte diameter were detected. Increased subcutaneous fat thickness would be attributed to an increased number of adipocytes and not an increase in adipocyte number. When commenting on the work of Underwood et al. (2010), Funston et al. (2010a) hypothesized that the difference in subcutaneous fat thickness was due to higher quality and digestibility of improved pasture relative to native range; resulting in increased acetate production by the cow. Smith and Crouse (1984) determined that acetate is the primary substrate used by subcutaneous adipocytes. It could be possible that grazing cows on improved pasture increased fetal acetate supply; thus, increasing recruitment of undifferentiated mesenchymal stem cells to formation of fetal adipocytes. Shear force was reduced for steers whose dams were grazed on improved pasture, indicating improved tenderness. Although tenderness has been related to proteolysis of the calpain/calpastatin system and degradation of Troponin-T, no differences in calpastatin content in LM or degraded Troponin-T were observed between steers born to dams grazed on improved pastures or native range. Underwood et al. (2010) also observed no differences in collagen content of LM. The differences in shear force do not appear to be attributed to differences in postmortem proteolysis or connective tissue content of LM. No difference in ratio of Type I / Type II muscle fibers was observed, indicating that

improved plane of nutrition during mid- to late gestation did not alter muscle fiber type in LM of steer progeny. These data indicate that maternal nutrition during mid- to late gestation can have lasting effects on growth and carcass characteristics of subsequent steer progeny. It is important to note that these treatment differences were enacted in a relatively short period of 60 d, indicating that the fetus is highly sensitive to nutritional changes during this period of fetal development.

Drylot feeding and Fetal Programming

A considerable amount of work that has investigated the FP effects of drylot diets have evaluated different dietary energy sources. Radunz et al. (2010) and Radunz et al. (2011a) investigated the effects of feeding isocaloric diets consisting of ad libitum hay or haylage, limit-fed corn, or limit-fed DDGS from mid-gestation through parturition on dam and progeny pre-weaning performance in beef cattle and sheep, respectively. Cows limit-fed DDGS gained more BW prior to calving than cows fed ad libitum hay or limit-fed corn (Radunz et al., 2010). Cow plasma glucose and insulin concentrations were analyzed before feeding and 3, 6, and 9 h post-feeding on d 210 of gestation. There were no differences in plasma glucose at any time post-feeding. Plasma insulin level was greater 3 h post-feeding for cows fed DDGS. Radunz et al. (2010) posed that greater post-feeding insulin concentration was due to greater CP and RUP content of DDGS. Increased insulin concentrations were observed with greater amounts of supplemental RUP by Sletmoen-Olson et al. (2000a). Cows fed hay or DDGS tended to have greater plasma NEFA concentrations that those fed corn before feeding. Cows fed hay tended to have greater plasma NEFA concentrations than those fed DDGS or corn 3 h post-feeding. Elevated NEFA concentrations before or 3 h feeding for cows fed hay may be a reflection of decreased BW gain when compared to those fed DDGS. Elevated NEFA concentrations before

feeding for cows fed DDGS may be a reflection of greater dietary fat content of DDGS. Cows fed DDGS had greater plasma BUN concentrations before and 3 h post-feeding when compared to those fed corn or hay. Cows fed DDGS and corn had greater plasma BUN concentrations 6 h post-feeding when compared to those fed hay. Greater plasma BUN concentrations for cows fed DDGS can be attributed to greater CP intake as cows were fed isocaloric but not isonitrogenous diets. Greater plasma BUN concentrations 6 h post-feeding for cows feed corn when compared to those fed hay may be due to the fact that cows were offered ad libitum access to hay and fed corn once daily.

Circulating progesterone during pregnancy is produced primarily by the placenta during mid- and late gestation. Progesterone concentration during late gestation has been correlated with placental function (Sullivan et al., 2009). Sullivan et al. (2009) observed increased progesterone concentrations when heifers were fed high levels of dietary protein during early and late gestation. Radunz et al. (2010) greater plasma progesterone concentrations at d 210 of gestation for cows fed DDGS when compared to those fed hay or corn. No differences in plasma progesterone concentrations were observed at d 189 or 231 of gestation. Radunz et al. (2012) reported birth BW, pre-weaning growth, and ultrasonic composition of progeny resulting from the experiments conducted by Radunz et al. (2010) and birth BW, pre-weaning growth of progeny resulting from Radunz et al. (2012), which managed similarly to those of Radunz et al. (2010). Calf birth BW was greater for calves born to dams fed DDGS or corn when compared to those fed born to dams fed hay (Radunz et al., 2010; Radunz et al., 2012). This agrees with Loerch (1996) who observed greater calf birth BW for cows were limit-fed corn when compared to those fed ad libitum hay during late gestation. Neither Loerch (1996) nor Radunz et al. (2010) reported increased incidence of dystocia when cows were fed concentrates during late gestation.

No differences in calving BCS, milk production, or subsequent pregnancy rates were observed (Radunz et al., 2010). Calves born to dams fed corn were heavier at 100 d of age than those born to dams fed hay, with those born to dams fed DDGS being intermediate and not different from either (Radunz et al., 2012). Weaning BW of calves born to dams fed corn tended to be greater than those born to dams fed hay, with those born to dams fed DDGS being intermediate. Despite differences in BW at birth and 100 d of age, no differences in ultrasonic LM area were observed at birth or weaning. No difference in ultrasonic backfat thickness was observed at weaning.

Radunz et al. (2011a) conducted an experiment similar to Radunz et al. (2010) in which ewes were fed isocaloric diets consisting of ad libitum haylage, limit-fed corn, or limit-fed DDGS from mid-gestation through parturition. Ewes limit-fed DDGS or corn maintained BW and gained BCS from mid-gestation to post-lambing when compared to ewes fed ad libitum haylage that lost both BW and BCS during the same period of time. When analyzed at d 80 (mid-gestation) and 122 (late gestation) of gestation, plasma glucose concentrations were greater before feeding for ewes fed corn when compared to those fed DDGS or haylage. During mid-gestation, plasma glucose concentrations were greater 3 h post-feeding for ewes fed corn and DDGS when compared to those fed haylage. Greater concentrations of glucose may be the result of greater propionate production in the rumen, which may lead to greater gluconeogenesis in the liver (Radunz et al., 2011). Plasma insulin concentrations during mid-gestation were greater 3 h post-feeding and during late gestation 3 and 6 h post-feeding for ewes fed DDGS when compared to those fed corn of DDGS. Increased insulin concentrations 3 h post-feeding for ewes fed DDGS agrees with the findings of Radunz et al. (2010) when insulin concentrations were analyzed during late gestation. Higher dietary fat supplied by DDGS may also lead to a greater post-feeding insulin response. In pregnant women, insulin activity is lower during late gestation,

leading to insulin insensitivity, and greater circulating insulin (Butte, 2000). Plasma BUN concentration before feeding was greater for ewes fed DDGS when compared to those corn or haylage. As with Radunz et al. (2010), greater BUN concentrations for ewes fed DDGS may be a reflection of greater dietary CP. Plasma BUN concentrations 6 and 9 h post-feeding were lowest for ewes fed corn, possibly be due to lower dietary CP intake and greater ruminal uptake of CP. During mid-gestation, plasma NEFA concentrations were greater for ewes fed DDGS and haylage when compared to those fed corn. No differences were observed in plasma NEFA concentrations during late gestation. Greater NEFA concentrations before feeding for ewes fed DDGS during mid-gestation may be due to greater dietary fat of DDGS, as with Radunz et al. (2010) when NEFA concentration was analyzed during late gestation. Increased NEFA concentrations before feeding for ewes fed haylage may be attributed to negative energy balance indicated by losses in BW and BCS. Lamb birth BW tended to be greater for lambs born to dams fed corn or DDGS when compared to those from dams fed haylage. This is in agreement with previous literature in which birth BW was increased in calves born to concentrate-fed dams (Loerch, 1996; Radunz et al., 2010). Radunz et al. (2012) reported no differences in serum IgG concentrations or passive immunity classification and pre-weaning morbidity or mortality regardless of maternal energy source. No differences in milk production or composition were observed. No differences in lamb weaning BW or pre-weaning ADG were observed. No differences in body composition, muscle and organ weights, were observed in a subset of lambs were slaughtered at birth. Severe nutrient restriction during mid- to late gestation reduces birth BW and muscle weight of lambs, but not muscle weight relative to BW (Fahey et al., 2005). No differences in lamb body composition should not be surprising as lambs were not born to nutrient restricted dams.

To investigate the lasting effects of maternal dietary energy source on subsequent progeny, Radunz et al. (2012) and Radunz et al. (2011b) evaluated post-weaning growth and carcass characteristics of progeny resulting from the experiments conducted by Radunz et al. (2010) and Radunz et al. (2011a), respectively. Radunz et al. (2012) observed no differences in final BW, feedlot ADG, DMI, or G:F regardless of maternal energy source. However, days on feed tended to be greater calves born to dams fed hay when compared to those born to dams fed corn or DDGS. No difference for percentage of calves treated for respiratory disease was observed. Carcass characteristics were similar among treatments, with the exception of marbling score. Calves born to dams fed hay had greater marbling scores when compared to those fed corn, with those born to dams fed DDGS being intermediate and not different from either. This coincides with a greater percentage of calves born to dams fed corn grading select. Mid- and late gestation are known to be critical times for adipocyte development (Du et al., 2010), yet the mechanisms by which maternal energy source affects marbling of subsequent progeny is unknown.

When evaluating the post-weaning growth of progeny resulting from Radunz et al. (2011a), no differences were observed ADG, DMI, G:F, or days on feed; yet, BW at slaughter tended to greater for lambs born dams fed DDGS when compared to those born to dams fed haylage, with lambs born to dams fed corn being intermediate. There were no differences in HCW, but dressing percentage of lambs born to dams fed DDGS was decreased when compared to those from dams fed corn or haylage. This difference in dressing percentage may be attributed to the fact that lambs born to dams fed DDGS tended to have greater kidney and pelvic fat when compared to those born to dams fed haylage, lambs born to dams fed corn were intermediate. Lambs born to dams fed DDGS also tended to have smaller LM areas and lower leg scores;

leading to lower percentages of boneless trimmed retail cuts than lambs born to dams fed haylage or corn. These data indicate that maternal energy source had substantial impacts on both adiposity and muscularity of progeny. It is difficult to determine whether the FP effects observed by Radunz et al. (2011b) in sheep or by Radunz et al. (2012) in cattle were a result differences in maternal energy source being fed during mid- or late gestation specifically. Maternal treatment diets in both studies were not isonitrogenous as DDGS diets would have exceeded dietary CP requirement; thus, some FP effects observed may be attributed to excess dietary protein that could be deaminated and used as additional energy supply.

Gunn et al. (2014) observed greater birth and weaning BW when calves were born to heifers fed excessive dietary CP during late gestation. Maternal dietary treatments were also fed during lactation, which may confound potential FP effects of excess dietary CP during late gestation. However, calves born to dams fed excessive dietary CP had greater weaning BW despite no differences in milk production and decreased energy corrected milk production by dams fed excess dietary CP. These data may provide additional evidence that feeding dietary CP above requirement to gestating dams alters progeny growth through weaning.

Glucose Tolerance

Mechanisms behind observed differences in progeny growth and carcass characteristics caused by maternal nutrition are poorly understood. Altered metabolism of glucose, mediated by insulin response, may be a possible explanation phenotypic responses to maternal nutrition. Multiple experiments have conducted glucose tolerance (GTT) tests to evaluate the FP effects of maternal plane of nutrition or diet on insulin sensitivity of resulting progeny.

To investigate the effects of maternal nutrient restriction to 50% requirement during early to mid-gestation on insulin sensitivity in wethers, Ford et al. (2007) conducted a GTT at 63 and

250 d of age. At 63 d of age, wethers born to nutrient restricted dams had greater glucose and insulin area under the curve (AUC) than wethers born to requirement-fed dams. Baseline glucose concentration was greater for wethers born to nutrient restricted dams, with no difference in baseline insulin concentration at d 63 of age. At 250 d of age, wethers born to nutrient restricted dams had greater glucose AUC but lower insulin AUC than wethers born to requirement-fed dams. There were no differences in baseline glucose and insulin concentrations at d 250 of age. Also at 250 d of age, wethers born to nutrient restricted dams had reduced initial insulin response (sum of insulin concentration at 2 and 5 minutes post i.v. glucose infusion minus baseline insulin concentration) when compared to wethers born to requirement-fed dams. The results of the first GGT at 63 d of age indicate insulin resistance, caused by maternal nutrient restriction, because wethers were both hyperglycemic and hyperinsulinemic. The second GTT at 250 d of age indicates pancreatic dysfunction caused by maternal nutrient restriction as wethers remained hyperglycemic but were also hypoinsulinemic. The reduction in initial insulin secretion may be due to β-cell deterioration following hyperinsulinemia earlier in life. Ford et al. (2007) discussed previous findings that indicated that reduction in initial response has been correlated to insulin dependent diabetes later in life.

In retrospective human studies, maternal nutrient restriction only during early gestation increased risk of coronary heart disease; maternal nutrient restriction only during late gestation impacted glucose and insulin homeostasis (Gardner et al., 2005). With this in mind, Gardner et al. (2005) sought to evaluate the effects of maternal nutrient restriction on glucose and insulin metabolism of sheep during early or late gestation in the same experiment. Ewes were fed 100% of nutrient requirements throughout gestation or nutrient restricted to 50% of requirement either during the first 30 d or last 30 d of gestation. No differences in lamb birth BW or BW through 1

yr of age were observed. Lambs born to nutrient restricted dams during late gestation had more omental and perirenal adipose tissue when compared to lambs born requirement-fed dams or those nutrient restricted during early gestation. During a GTT conducted at 1 yr of age, baseline and peak glucose and insulin concentrations were not different among treatments. Glucose AUC was greater for lambs born to nutrient restricted dams during late gestation when compared those born to requirement-fed dams, with lambs born to nutrient restricted dams during late gestation intermediate. Insulin AUC and Insulin:Glucose AUC ratio was greater for lambs born to nutrient restricted dams during late gestation when compared to lambs born to requirement-fed dams and nutrient restricted dams during early gestation. It was concluded by Gardner et al. (2005) that undernutrition during late gestation had a more distinct effect on glucose and insulin metabolism than undernutrition during late gestation. When glucose-insulin homeostasis was measured via GTT a 1 yr of age, it appeared that glucose intolerance was related to insulin resistance and not increased insulin insensitivity that has been observed by Ford et al. (2007) in lambs as d of age increased.

Effects of maternal obesity of ewes on glucose and insulin sensitivity of subsequent progeny were investigated by Long et al. (2010b). Frequently sampled i.v. glucose tolerance tests (FSIGT) were conducted at the initiation and conclusion of a 12 wk ad libitum feeding period. The FSIGT was conducted by taking baseline glucose and insulin samples prior to glucose infusion and through 19 min post-glucose infusion. At 20 min post-glucose infusion, exogenous insulin was infused, and glucose and insulin sample collected through 240 min post-glucose infusion. Variables used to measure glucose-insulin homeostasis include: insulin sensitivity (SI), glucose effectiveness (Sg), acute insulin response to glucose (AIRg), and disposition index (DI). Insulin sensitivity represents the acceleration of glucose clearance by endogenous insulin; AIRg

is the insulin AUC prior to infusion of exogenous insulin, Sg is the glucose clearance at basal insulin concentration, DI is an index of potential for insulin action and is calculated as AIRg × SI (Long et al., 2010b). Prior to the first FSIGT, fasting plasma glucose concentrations tended to be greater in lambs born to obese dams when compared to lambs born to requirement-fed dams; with no difference in fasting in insulin concentrations. During the first FSIGT, SI and Sg were greater in lambs born to obese dams relative to lambs born to requirement-fed dams, with no differences in AIRg and DI. Prior to the second FSIGT, fasting glucose and insulin concentrations were greater in lambs born to obese dams. During the second FSIGT, SI, Sg, AIRg, and DI were all reduced in lambs born to obese dams. Prior to the beginning of the ad libitum feeding period, lambs born to obese mothers had decreased insulin sensitivity with decreased ability of glucose infusion to mediate glucose uptake. These FP effects of maternal obesity on glucose-insulin homeostasis were exacerbated after s 12 wk of ad libitum intake of a high energy diet; resulting in insulin resistance and decreased initial insulin response. Insulin resistance in lambs born to obese dams is supported by greater fasting glucose concentrations at the beginning and end of the ad libitum feeding period and by greater fasting insulin concentrations at the end of the period. It is interesting that maternal obesity during gestation results in similarly challenged glucose and insulin dysregulation in subsequent progeny as those born to nutrient restricted dams (Ford et al., 2007).

To evaluate the effects of maternal energy source during mid- and late gestation on glucose tolerance of progeny, GGTs were conducted by Radunz et al. (2011b) and Radunz et al. (2012) during their respective experiments. At 93 d of age, Radunz et al. (2011b) analyzed glucose and insulin concentrations of wethers prior to feeding and 3 h post-feeding. Maternal energy source had no effect on pre- or post-feeding glucose or insulin concentrations analyzed

under what was considered by Radunz et al. (2011b) to be normal feeding conditions. When a GTT was conducted at 96 d of age, no differences were detected in baseline glucose or insulin concentrations. Wethers born to DDGS-fed ewes had decreased glucose concentrations at 2, 5, and 10 min post-glucose infusion relative to wethers born to ewes fed haylage or corn. At 15 min post-infusion, wethers born to haylage fed ewes had greater glucose concentrations than those born to ewes fed DDGS or corn. At 5, 10, and 15 min post-infusion, wethers born to ewes fed DDGS had greater insulin concentrations relative to those born to haylage and corn-fed ewes. Greater insulin concentration immediately post-infusion coincide with a trend for greater initial insulin response in wethers born to ewes fed DDGS relative to wethers born to haylage or corn-fed ewes. Despite differences in glucose and insulin concentrations at certain time post-infusion, no differences for AUC for glucose or insulin were observed. No differences in glucose clearance rate or ratio of Insulin:Glucose AUC were observed. Ewes fed DDGS during mid- and late gestation had greater insulin concentrations and BCS (Radunz et al., 2011a). Progeny born to DDGS-fed ewes tended to have greater insulin response during a GTT, and reduced LM area, and have greater kidney and pelvic fat (Radunz et al., 2011b).

In another study that evaluated the FP effects of maternal energy source during mid- and late gestation, Radunz et al. (2012) analyzed glucose and insulin concentrations in progeny born to dams fed hay, corn, or DDGS. During a weigh-suckle-weigh conducted at 93 d of age, calf glucose and insulin concentrations were analyzed prior to nursing and 2 h post-nursing. Pre-nursing glucose concentrations were lowest for progeny of dams fed DDGS and greatest for dams fed corn, with progeny of hay-fed dams being intermediate and not different from either. Maternal energy source had no effect on pre-nursing insulin concentration or post-feeding glucose and insulin concentrations. For GGTs conducted at 41 d and 111d post-weaning,

maternal energy source during mid- and late gestation had no effect on baseline concentrations or AUC of glucose or insulin. Progeny born to dams fed corn had faster glucose clearance rates than those born hay and corn-fed dams. Initial insulin response was greater for progeny born to dams fed corn or DDGS when compared those born to dams fed hay. No differences in glucose clearance rate or Insulin:Glucose AUC ratio were observed for maternal energy source. The combination of slow glucose clearance rate and high initial insulin response would indicate insulin resistance in progeny born to cows fed DDGS. Similar to Radunz et al. (2011a), dams fed DDGS had greater insulin concentrations during pregnancy and gained more BW prior to calving than dams fed hay or corn. When compared to d 41 post-weaning, cattle had greater glucose and insulin AUC, faster glucose clearance rate, higher baseline insulin concentration, greater initial insulin response, and greater ratio of Insulin:Glucose AUC at d 111 post-weaning. These data indicate that cattle consuming a high energy diet become more insulin resistant as d post-weaning increases. A calf sex by maternal energy source interaction existed in which heifers born to cows fed corn had lower fasting glucose concentrations, faster glucose clearance rate, and greater initial insulin response when compared to steers born to cows fed corn. There were no other sex differences within maternal energy source treatments. Progeny, of either sex, born to cows fed corn spent the fewest days on feed, had the lowest marbling scores, and had the greatest percentage of carcasses grade Select. Performance of heifers vs. steers was not reported, but this sex difference for insulin sensitivity may explain the accepted differential between sexes.

Epigenetics

The FP effects of maternal nutrition has been studied most extensively on the resulting phenotypes of subsequent progeny with the underlying mechanisms for observed phenotypic differences not understood. Nutritional influences on gene expression, through epigenetics and

nutrigenomics, may be partially explained by how maternal plane of nutrition or diet impart indirect effects on progeny growth and body composition. Because skeletal muscle and adipose tissue are economically important tissues for the beef industry, several experiments have analyzed differential gene expression in these tissues when maternal nutrition is manipulated.

To analyze the effects of maternal nutrient restriction during early or late gestation on glucose-insulin homeostasis, Gardner et al. (2005) investigated abundance of proteins involved in insulin signaling and glucose uptake in lambs. Western blot analysis was used to quantify protein of insulin receptor β-subunit (Irβ), phosphatidylinositol 3-kinase (PI3K) p110 β -subunit (p110β), PI3K p85 α-subunit (p85α), and glucose transporter 4 (GLUT4) in perirenal fat and muscle in lambs slaughtered at 1 yr of age. Insulin receptor β-subunit is part of the transmembrane insulin receptor that phosphorylates insulin receptor substrate protein, which binds to PI3K (composed of p110β and p85α subunits). Activation of PI3K ultimately leads to the translocation of GLUT4, the primary insulin-dependent intracellular glucose transporter, to the plasma membrane to uptake glucose into the cell. In perirenal adipose tissue, protein for Irβ and p110β were greater with protein for GLUT4 decreased in lambs born to nutrient restricted dams during late gestation, with no differences in p85α. In muscle, Irβ protein expression was greatest in lambs born to nutrient restricted dams during early gestation, with no differences in p85α or GLUT4. It was noted by Gardner et al. (2005) that expression of p110β in muscle was less than 10% of expression in perirenal adipose tissue. It was concluded that the underlying mechanisms for observed insulin resistance were downstream of insulin receptors (Gardner et al., 2005). It was hypothesized that insulin-signaling proteins, located downstream to the insulin receptor, are programmed during late gestation before increased adiposity and glucose intolerance manifest; however, this is not known. Impaired glucose uptake can be largely

attributed to decreased GLUT4 expression in adipose tissue of lambs born to nutrient restricted dams during late gestation.

Long et al. (2010a) evaluated the effects of maternal nutrient restriction during early gestation on DNA concentration and gene expression in subcutaneous and perirenal adipose and complexus muscle tissue. Heifers were fed to 100% or restricted to 55% of NRC (1996) requirements from d 32 to d 115 of gestation. Concentration of DNA in tissue can be used as an indicator of hyperplasia; protein:DNA ratio can be used as an indicator of hypertrophy (Long et al., 2010a). However, muscle fibers are multinucleated and DNA concentration cannot be used to infer cell number. Concentration of DNA in subcutaneous adipose tissue was not different but tended to be greater in the perirenal adipose tissue of steers born to nutrient restricted dams. This indicates a greater number of adipocytes in perirenal tissue or less lipid in adipocytes. Long et al. (2010a) used qPCR to quantify abundance of mRNA for GLUT4, fatty acid binding protein 4 (FABP4), and fatty acid translocase (CD36) in subcutaneous and perirenal adipose and complexus muscle tissue. Fatty acid binding protein 4 activates hormone-sensitive lipase that facilitates uptake of NEFA into adipocytes. Fatty acid translocase also facilitates uptake of NEFA into adipocytes. In perirenal adipose tissue, abundance of FABP4, CD36, and GLUT4 mRNA were reduced in steers born to nutrient restricted dams. Abundance of mRNA was not different in subcutaneous adipose tissue. Abundance of GLUT4 tended to be greater in complexus muscle of steers born to nutrient restricted dams. Decreased abundance of mRNA for FABP4, CD36, and GLUT4 indicate decreased ability to use NEFA and glucose for fatty acid synthesis in perirenal tissue. The trend for increased mRNA for glucose transporters in muscle of steers born to nutrient restricted heifers indicate increased uptake of glucose into muscle and may explain the observation for greater muscle fiber area.

Long et al. (2012a) evaluated the effects of maternal nutrient restriction with or without CP supplementation during early to mid-gestation on gene expression in subcutaneous adipose tissue. Cows were fed 100% of NRC (1996) requirements, restricted to 70% of requirement, or restricted to 70% of requirement and provided supplemental RUP formulated to provide similar duodenal AA flow to requirement-fed cows. Average adipocyte diameter was greater in subcutaneous, mesenteric, and omental and tended to be greater in perirenal adipose tissue of calves born nutrient restricted dams when compared to calves born to requirement-fed dams, with adipocyte diameter of calves born to protein supplemented dams intermediate or similar to requirement-fed dams. Differences in adipocyte diameter in adipose depots were confirmed by reduced DNA concentration in adipose tissue on calves born nutrient restricted dams. Abundance of mRNA for GLUT4, fatty acid transport protein 1 (FATP1), fatty acid transport protein 4 (FATP4), and lipoprotein lipase (LPL) were quantified using qPCR. Fatty acid transport protein 1 is an insulin sensitive that enhances uptake of long chain fatty acids (LCFA). Fatty acid transport protein 4 is associated with uptake and metabolism of LCFA and very LCFA. Lipoprotein lipase hydrolyzes triglycerides in lipoproteins into two FFA and one monoacylglycerol, aiding in the uptake of lipids into cells. No difference in abundance of mRNA for GLUT4, FATP4, or LPL were observed in subcutaneous adipose tissue. Abundance of mRNA for FATP1 was approximately 15 fold greater in subcutaneous adipose tissue of calves born to nutrient restricted dams when compared to calves born requirement-fed and protein supplemented dams. Long et al. (2012a) commented that changes in adipocyte size are associated with activity of fatty acid transporters. It would be expected that observed differences in adipocyte diameter were caused by greater fatty acid transport into the adipocyte. Adipocyte

size has been shown to have no effect on GLUT4 content; yet, ability of insulin to illicit translocation to the plasma membrane is reduced in large adipocytes (Long et al., 2012a).

Long et al. (2012b) evaluated the effects of maternal obesity on lipid and glucose metabolism of ovine fetuses at d 135 of gestation. Abundance of mRNA for CD36, FATP1, FATP4, GLUT4, fatty acid binding protein 1 (FABP1), fatty acid binding protein 3 (FABP3), FABP4, fatty acid binding protein 5 (FABP5), fatty acid synthase (FASN), and acetyl-coA carboxylase (ACC) from perirenal, pericardial, and subcutaneous adipose tissue was quantified using qPCR. Western blots were used to quantify abundance of CD36, FATP1, FATP4, and GLUT4 protein in the same adipose depots. Fatty acid binding proteins are proteins that function to carry fatty acids within the cell, such as from extra- to intracellular membranes. These proteins tend to be distributed in certain tissues; FABP1, FABP3, FABP4, and FABP5 are known to be primarily distributed in liver, muscle, adipocytes, and epidermal tissues, respectively. Fatty acid synthase (FAS) is an enzymatic system that functions to synthesize palmitate (16:0) from acetyl-CoA and malonyl-CoA and is encoded by the FASN gene. Acetyl-CoA and CO_2 are converted to malonyl-CoA enzymatically by ACC for use by FAS. Abundance of CD36, FATP1, FATP4, and GLUT4 mRNA were greater in all adipose depots measured in fetuses carried by obese ewes when compared to those carried by requirement-fed ewes. Abundance of mRNA for FABP1 and FABP5 were greater and FABP4 tended to be greater in subcutaneous adipose tissue of fetuses carried by obese dams, with no difference in FABPs in other adipose depots. Abundance of mRNA for both ASN and ACC were greater in fetuses carried by obese dams. Greater abundance of mRNA for fatty acid transporters, the primary insulin-dependent glucose transporter, and lipogenic enzymes in fetuses carried by obese dams is a reflection of greater nutrient intake and adiposity. Greater expression of FATPs would be expected to be the result of

greater lipids in fetal circulation. It was posed that increased expression of GLUT4 could be due to increased fetal plasma glucose concentrations observed during mid-gestation by Ford et al. (Ford et al., 2009). It is also possible that greater nutrient transporters in adipose tissue are a result of greater adipocyte maturity in fetuses carried by obese ewes (Long et al., 2012b). As previously discussed, fatty acid profile of adipose tissue was altered in fetuses born to obese dams in that concentrations of fatty acids longer than 18 carbons were greater. Long et al. (2012b) posed that this was because of greater expression of FASN and ACC genes which encode the rate-limiting steps of fatty acid synthesis; thus, a greater degree of fatty acid elongation could occur in adipose tissue of fetuses carried by obese dams.

Feed efficiency and Methane Production

Feed efficiency can be measured using traditional feed conversion ratio (F:G), gain efficiency (G:F), or other measures of feed efficiency such as residual deed intake (RFI). Calculation of RFI is the difference between actual DMI and expected DMI based on BW and growth rate (Nkrumah et al., 2006; Hegarty et al., 2007). A negative value for RFI is desirable because it means an animal consumed less DM than expected. Mechanisms that are thought to cause variation in RFI include: feed intake and digestion, heat increment, protein turnover and issue metabolism, feeding behavior, body composition, rate of gain, and BW (Nkrumah et al., 2006). When evaluating feedlot performance of cattle classified into high, medium, or low RFI groups, Nkrumah et al. (2006) determined that low RFI cattle had reduced DMI, lower F:G, and reduced feeding duration (min/d) when compared to high RFI cattle. RFI classification had no effect on metabolic BW or ADG. When fed 2.5 times estimated NRC (1996) requirement, cattle classified as low RFI tended to have greater DM and CP digestibility, decreased methane and

heat production, and greater retained energy when compared to those classified as high RFI (Nkrumah et al., 2006).

In ruminant animals, methane gas is released, primarily through eructation, during the process of feed fermentation and digestion. The relationship between feed efficiency and methane production garners particular interest as methane represents a lost dietary energy and is the primary greenhouse gas produced by ruminants (Freetly and Brown-Brandl, 2013). Estimates of energy lost as methane account for 2.3% to 4.9% of energy intake (GE) when cattle consume high energy grain diets (Hegarty et al., 2007; Freetly and Brown-Brandl, 2013) and 3.6% to 8.4% of energy intake when cattle consume forage-based diets (Freetly and Brown-Brandl, 2013). A positive association between energy intake and methane production is found; greater energy intake provides greater substrate for ruminal fermentation and greater supply of hydrogen for methanogens (Hegarty et al., 2007). Thus, selecting cattle for reduced DMI would be expected to decrease methane production. There is evidence that both OM digestibility and methane production per unit of feed intake increase as cattle age; suggesting that cattle more completely ferment their feed with age, resulting in more methane produced per unit of feed (Freetly and Brown-Brandl, 2013). Research conducted on RFI, and other feed efficiency measures, exhibit that genetic diversity for feed intake exists among cattle of similar growth rates. The moderate heritability of RFI provides the opportunity to select for cattle with decreased DMI and methane production without sacrificing growth rate (Hegarty et al., 2007). Hegarty et al. (2007) observed that when cattle selected for divergent RFI over 2.4 generations were fed a high-grain diet, low RFI cattle had reduced DMI, greater G:F, and reduced daily methane production when compared to high RFI cattle with no sacrifice in ADG. Methane production expressed as g/kg of ADG tended to be reduced in low RFI cattle with no difference in methane production when expressed

as g/kg of DM. These data show that the reduction in DMI when selecting for low RFI was largely responsible for reduced daily methane production; yet, animal differences independent of DMI exist (indicated by the trend for decreased g methane/kg of ADG when selecting for low RFI). When feeding cattle 2.5 times NRC requirements, Nkrumah et al. (2006) observed a reduction in L methane/kg $BW^{0.75}$ in cattle classified as low RFI, relative to cattle classified as medium or high RFI. Energy lost as methane was reduced in cattle classified as low RFI relative to cattle classified as medium or high RFI.

Freetly and Brown-Brandl (2013) evaluated methane production in two populations known to vary in feed efficiency: steers consuming a high-grain diet and heifers consuming a forage-based diet. Unlike Nkrumah et al. (2006) and Hegarty et al. (2007), methane production was not measured in cattle selected for feed efficiency; but, a survey of each population was represented. Cattle furthest from the confidence ellipse were selected for measurement of methane production when BW gain was regressed on DMI. Regression analysis was used to determine the influence of G:F and RFI on methane production. Previous 24 h DMI was included as a covariate in the regression analysis of G:F and RFI since feed intake is known to influence methane production. There was considerable difference in the contribution of variance for G:F, previous 24 h DMI, and RFI between the two populations. Neither G:F and previous 24 h DMI or RFI and previous 24 h DMI accounted for a considerable amount of the variance in methane production in the steers consuming the high-grain diet. In heifers consuming the forage-based diet, G:F accounted for 28% and previous 24 h DMI accounting for 72% of the variance in methane production. Methane production was increased as G:F increased, indicating that more feed efficient animal produce more methane. When RFI and previous 24 h DMI were regressed, 24 h DMI accounted for 96% of the variance in methane production while the regression

coefficient for RFI did not differ from 0. These findings are contrary to those of Nkrumah et al. (2006) and Hegarty et al. (2007) who found that more feed efficient cattle produce less methane. Freetly and Brown-Brandl (2013) concluded that selection programs aimed at solely reducing methane emissions may decrease feed efficiency and increase days on feed to achieve desired endpoints, possibly increasing methane production over the life on the animal. Due to the differences between steer and heifer populations evaluated, it was also concluded that the beef industry would realize greater improvement if it selected for efficiency and methane production on animals consuming forage (Freetly and Brown-Brandl, 2013).

Effects of maternal plane of nutrition during late gestation on feed efficiency of heifers were evaluated by Martin et al. (2007) and Funston et al. (2010b). In the experiment conducted by Martin et al. (2007) cows grazing dormant range pastures were either offered CP supplement or not supplemented during late gestation. During early lactation, cows also grazed improved meadow pastures or fed hay in a drylot. Heifer progeny from yr 3 of the experiment were fed a forage-based diet individually for 84 d to evaluate ADG, DMI, G:F, and RFI. Late gestation CP supplementation or early lactation diet had no effect on heifer ADG, DMI, G:F, or RFI. However, there were interactions between late gestation and early lactation planes of nutrition for heifer DMI and RFI. Heifers born to protein supplemented dams fed hay consumed greater DMI than heifers born to non-supplemented dams fed hay; heifers born to dams grazed on meadows during early lactation, regardless of supplementation level, were intermediate and not different from either. Heifers born to protein supplemented dams fed hay had higher RFI than heifers born to non-supplemented dams fed hay; heifers born to dams grazed on meadows during early lactation, regardless of supplementation level, were intermediate and not different from either. These data indicate heifers born to protein supplemented dams were less efficient than

heifers born to non-supplemented dams fed hay. There was also no correlation between heifer RFI and ADG; yet, heifers with desirable RFI had numerically lower ADG. There were no differences in ADG and G:F steer mates due to maternal plane of nutrition during late gestation or early lactation (Stalker et al., 2006).

In the experiment conducted by Funston et al. (2010b) cows grazing on native range or corn residue were provided CP supplement of no supplement during late gestation. Heifer progeny from all 3 yr of the experiment were fed a forage-based diet for 85 to 92 d for evaluation of ADG, DMI, G:F, and RFI. Grazing system and CP supplementation during late gestation had no effect on heifer DMI or RFI. There were interactions between grazing system and CP supplementation for heifer ADG and G:F. Heifers born to dams grazed on corn residue and provided CP supplement had lower ADG and decreased G:F than any other treatment combination. Cows grazed on corn residue and offered CP supplement would have been least nutrient restricted during late gestation; yet, heifer progeny from these cows grew least efficiently. This indicates that nutrient restriction during late gestation can result in progeny that grow more efficiently later in life. Similar to Martin et al. (2007), steer mates to the heifers used by Funston et al. (2010b) did not exhibit any differences in feedlot feed efficiency (Larson et al., 2009). Funston et al. (2010b) posed that that high rate of gain of steers may mask any fetally programmed feed efficiency differences expressed by heifers managed for lower rates of gain.

Conclusions

Cow/calf producers manage herd in such a way that management of feed costs is balanced with maintaining an acceptable level cow performance. Acceptable level of performance is typically characterized by maintenance of BW and BCS, adequate milk

production, and a 12 mo calving interval. These goals can be met by effective grazing supplementation or economical, balanced drylot diets. Research demonstrates that maternal nutrition during gestation affects not only cow performance, but potentially has lasting effects on subsequent progeny; a concept known as fetal programming. Thus, management of breeding females should account for effects on growth and body composition of the future calf crop.

The concept of fetal programming has been developed by studying the incidence of chronic disease in humans; then further investigated using different mammalian models. Maternal plane of nutrition during different stages of gestation can affect placental, muscle, and adipose tissue development as well as postnatal growth, insulin resistance, and body composition. Generally, both extreme maternal nutrient restriction and overfeeding result in increased adiposity, decreased muscle development, and greater insulin resistance of progeny; with variable result on postnatal growth. A limited number of studies have investigated the potential fetal programming effects of maternal nutrition in practical beef production systems, such as supplementation to grazing cows and evaluation of different drylot diet types. Research demonstrates the enhanced maternal nutrition during gestation may impart desirable effects of the growth and carcass characteristics of subsequent progeny; however, results are conflicted and underlying mechanisms not completely understood.

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CHAPTER 2

EFFECTS OF LATE GESTATION DISTILLERS GRAINS SUPPLEMENTATION ON BEEF COW PERFORMANCE AND STEER CALF GROWTH AND CARCASS CHARACTERISTICS

Abstract

Fall-calving, mature Angus and Simmental × Angus cows (n = 251 total) and their progeny were used to evaluate the effects of late gestation dried distillers grains plus solubles (**DDGS**) supplementation on cow performance, and progeny growth and carcass characteristics. Cows were blocked by breed and allotted to 12 pastures. Pastures were randomly assigned to 1 of 2 treatments within breed block: offered 2.1 kg DM DDGS·cow^{-1}·d^{-1} (CP = 23%, fat = 7%; **SUP**, n = 6 pastures) daily or offered no supplement (**CON**, n = 6 pastures) 69 ± 9 d before expected calving date. Cows remained on treatments until calving. Once weekly, cows that had calved were removed from treatment pastures and moved to new pastures where treatments were comingled without further supplementation. Cows calving more than 30d after expected calving date were removed from study. Cow BW and BCS were recorded at the beginning of the supplementation period, after calving, and at breeding. Calf BW was taken at birth and early-weaning (82 ± 14 d of age). Milk production was determined via the weigh-suckle-weigh technique at 82 ± 14 d postpartum. After weaning, 71 steer progeny were transitioned to a common feedlot diet with individual feed intake monitored using GrowSafe. Steers were slaughtered at a commercial facility 47 ± 4 d after a minimum 12th rib fat thickness (**backfat**) estimation of 0.6 cm, in such a way that cattle were shipped in 3 groups. Forage availability was not different between treatments (P = 0.69). Cows offered SUP gained more BW (P < 0.01) and

lost less BCS ($P = 0.02$) during the supplementation period. There were no differences ($P \geq 0.12$) in calving date, calf birth or weaning BW, or pre-weaning ADG. Cow BW at breeding was not different ($P = 0.19$); yet, BCS at breeding was greater ($P < 0.01$) for cows offered supplement. No differences ($P \geq 0.11$) in milk production, AI conception, or overall pregnancy rate were detected. For steer progeny, initial feedlot BW, final BW, and days on feed were not different ($P \geq 0.35$); and as a result, no difference ($P = 0.77$) in feedlot ADG was detected. Feedlot DMI and G:F were not different ($P \geq 0.52$) across treatments. No differences ($P = 0.62$) in morbidity were observed in the feedlot. No differences ($P \geq 0.19$) were detected for HCW, LM area, marbling score, or yield grade. Prepartum DDGS supplementation improved cow BW and BCS but did not alter milk production, subsequent reproduction, or subsequent calf performance or carcass characteristics.

Key Words: beef cow, distillers grains, fall-calving, fescue, fetal programming, supplementation

Introduction

Supplementation is a common strategy to improve the nutritional status of grazing beef cows. As growth of cool-season forages slows during late summer, supplementation may be required to meet cow nutrient requirements. For cows grazing endophyte-infected tall fescue, late summer also coincides with when symptoms of fescue toxicosis are expected to be greatest. Symptoms of fescue toxicosis include: reduced BW gain, reduced milk production, and reduced reproductive efficiency (Porter and Thompson, 1992; Paterson et al., 1995). A strategy to alleviate fescue toxicosis is to dilute the concentration of endophyte in the diet, possibly through supplementation. Dried distillers grains plus solubles (**DDGS**) provide an excellent source of dietary CP and highly-digestible fiber and have been proven to represent a viable form of

supplementation to improve BW and BCS of beef cows consuming low quality forage (NRC, 1996; Winterholler et al., 2012). The work of Stalker et al. (2006) and Larson et al. (2009) demonstrate that maternal protein supplementation to cows grazing dormant, winter range during late gestation has the potential to improve weaning BW and marbling scores of subsequent steer progeny. Late gestation is known to be a period of fetal muscle hypertrophy and adipogenesis (Du et al., 2010). Data concerning the effects of supplementation of DDGS to fall-calving cows grazing tall fescue during late gestation on performance of cows and subsequent progeny is limited. It was our hypothesis that maternal DDGS supplementation would improve cow BW gain and pregnancy rate, as well as calf growth and marbling scores. It was our objective to evaluate the effects of late gestation DDGS supplementation to fall-calving cows grazing fescue/clover pastures on cow performance, and growth and carcass characteristics of subsequent progeny.

Materials and Methods

Animals, Experimental Design, and Treatments

Experimental animals were managed according to the guidelines recommended in the Guide for the Care and Use of Agriculture Animals in Agriculture Research and Teaching (Federation of Animal Science Societies, 2010). All experimental procedures followed were approved by the University of Illinois Institutional Animal Care and Use Committee. Fall-calving, mature, multiparous Angus and Simmental x Angus cows (n = 251; BW = 603 ± 62 kg; age = 6.1 ± 2.2 yr) and their progeny were used to evaluate the effects of dried distillers grains plus solubles (DDGS) supplementation during late gestation on cow and calf performance as

well as the growth and carcass characteristics of subsequent steer progeny during the finishing period. Cows were fed at the Dixon Springs Agricultural Center in Simpson, IL.

A randomized complete block design was used with cows blocked by breed (6 pastures per breed; Angus or Simmental × Angus). Within block, cows were stratified by BW and then allotted to pastures (12 total pastures, 6 pastures total per treatment). Each block consisted of 3 replicates per treatment. Pastures were randomly assigned to 1 of 2 treatments within breed block: offered 2.1 kg DM pelleted DDGS·cow^{-1}·d^{-1} (CP = 23%, fat = 7%; **SUP**, n = 6 pastures) daily or offered no supplement (**CON**, n = 6 pastures) 69 ± 9 d before expected calving date. Supplementation began in mid-June and the average calving date was in mid-August. The beginning of the treatment period was targeted for 90 d prepartum to cover the last third of gestation; however, actual calving distribution was earlier than expected.

Pasture groups were grazed on endophyte-infected tall fescue (*Festuca arundinacea*)/red clover (*Trifolium pretense*) mixed pastures of similar size and forage availability. Forage availability was measured before grazing using a rising plate meter (Barnhart, 2009). Data concerning availability and forage quality are found in Table 2.1. Supplement was offered daily at 0800 h in feed bunks. Cows were given free access to trace-mineral salt (Table 2.1). Cows remained on treatments until calving. At least once weekly, cows that had calved were removed from treatment pastures and moved to new pastures where treatments were comingled. No supplement was offered to either treatment after calving. Cows that had not calved 30 d after expected calving date were removed from the experiment.

Pre-calving and Pre-weaning Management of Cows and Calves

Full cow BW was recorded on 2 consecutive d and BCS was assigned at the start of the supplementation period. Full post-calving BW was recorded and BCS assigned on the d cows

were moved from treatment pastures. Thus, cow BW at calving reflects loss of fetus, placental membranes, and associated fluids. Cow initial and post-calving BW and BCS were reported for 6 pastures per treatment and included data from 177 cows and excluded data for those who lost calves (CON, n = 7; SUP, n = 13), failed to calve within 30 d of expected calving date (CON, n = 26; SUP, n = 25), had injured calves before breeding (CON, n = 1; SUP, n = 0), or were euthanized (CON, n = 0; SUP, n = 2) before calving. Incidence of pre-weaning calf loss was not related to treatment ($P = 0.40$). Milk production was estimated via the weigh-suckle-weigh technique at 82 ± 14 d postpartum (6 pastures per treatment, CON = 80 cows, SUP = 85 cows). Cows and calves were separated at 1200 h, allowed to nurse at 1900 h, and then were separated overnight. At 0700 h the next d, an empty calf BW was recorded, calves were allowed to nurse, and a full calf BW was recorded. The BW difference between full and empty calf BW was estimated to be 12 h milk production. Estimate of 12 h milk production was multiplied by 2 to calculate 24 h milk production. Estimation of milk production at 82 ± 14 d postpartum coincides with time of early-weaning. Subsequent reproduction was reported for 6 pastures per treatment and included data from 169 cows (CON, n = 83; SUP, n = 86) and excluded those culled at breeding (CON, n = 3; SUP, n = 5). At rebreeding (89 ± 14 d postpartum), cows were synchronized using a 5-day Co-Synch + CIDR protocol (Johnson et al., 2013) with a 2nd $PGF_{2\alpha}$ injection given 6 h after CIDR removal. Cows were artificially inseminated in 3 groups on consecutive days. Full cow BW was taken and BCS assigned at time of CIDR removal to evaluate lasting effects of treatments. Cows were exposed to clean-up bulls beginning 11 ± 1 d after AI for a period of 51 d. Conception rates for AI were determined via transrectal ultrasonography at 41 ± 1 d after insemination, and overall pregnancy rates were determined via transrectal ultrasonography at 63 ± 1 and 96 ± 1 d after insemination.

Calf BW was taken within 24 h of birth and at time of early weaning (82 ± 14 d of age; early November) to measure pre-weaning calf ADG. Early-weaning has been a standard practice in the cow herd used in the current experiment. For steer progeny performance, early-weaning was not expected to interact with dam treatment. Shoup (2014) observed no interactions between dam plane of nutrition and early-weaning for progeny growth when using the same cow herd as the current experiment. Pre-weaning calf performance is reported for steer and heifer calves (6 pastures per treatment; CON: 44 steers, 41 heifers; SUP 47 steers, 44 heifers) raised by cows placed on treatments.

Post-weaning Management

In order to accommodate feedlot pen space, an equal amount of steers per treatment that were furthest from the mean weaning BW were removed from the experiment (10 steers removed per treatment). Thus, after weaning (82 ± 14 d of age), early-weaned steers (6 pastures per treatment, CON = 34; SUP = 37) were transported via commercial trucking to the Beef and Sheep Field Laboratory, Urbana, IL for the duration of the finishing period. Heifers were not early-weaned and were retained in the herd as potential replacements

Steers were vaccinated with the following: Bovishield Gold FP5 L5 HB (Zoetis, Florham Park, NJ), One Shot Ultra 7 (Zoetis), and Pulmo-Guard MpB (AgriLabs, St Joseph, MO). Steers were dewormed with Eprinex pour-on (Merial, Duluth, GA) and tagged with an electronic identification tag (Allflex USA, DFW Airport, TX). Upon entry to the feedlot, steers were adapted to a common, finishing diet (Table 2.2) fed for ad libitum intake over a transition period of 30 d. Steers were housed in 3 feedlot pens during the finishing period with maternal treatments represented equally in each pen. Steers were implanted with Component EC (10 mg estradiol benzoate, 100 mg progesterone, 29 mg tylosin 99 tartate; Elanco Animal Health,

Greenfield, IN) 40 d post-weaning and received a Component TE-IS implant (16 mg estradiol and 80 mg trenbolone acetate; Elanco Animal Health) 210 d post-weaning.

Initial feedlot BW was recorded and 12th rib backfat thickness (**backfat**) and marbling score were estimated 40 d post-weaning. At time of weaning, backfat and marbling score were estimated for all calves via compositional ultrasound. Ultrasound measurements were taken with an Aloka 500SV (Wallingford, CT) B-110 mode instrument equipped with a 3.5-MHz general purpose transducer array. Backfat measurements were taken in a transverse orientation between the 12th and 13th ribs approximately 10 cm distal from the midline. Ultrasound images were processed utilizing CPEC ultrasound imaging software (Cattle Performance Enhancement Company LLC., Oakley, KS).Individual feed intake was monitored using the GrowSafe automated feeding system (Model 4000E, GrowSafe Systems Ltd., Airdrie, Alberta, Canada) during the finishing period. Incidence of morbidity treatment during the finishing phase was recorded by animal care staff. Final BW was calculated from HCW using a standard dressing percentage of 63%.

Beginning on d 170 of the finishing period, backfat was estimated via ultrasound to determine slaughter date. Cattle were slaughtered at a commercial facility 47 ± 4 d after a minimum backfat estimation of 0.6 cm, in such a way that cattle were shipped in 3 groups with equal treatment representation in each group. Once selected for slaughter, steers were moved into a new pen equipped with GrowSafe, and fed 200 mg·steer^{-1} ·d^{-1} of ractopamine hydrochloride (Optaflexx 45, 99 g/kg, Elanco Animal Health) the last 40 d before slaughter. Trained personnel recorded slaughter order and HCW was taken on day of slaughter. Backfat, LM area, yield grade, and marbling score were taken after a 24h carcass chill with Video Image Analysis as part of the

USDA camera system. Carcass measurements from 1 steer from each treatment were excluded because of in-plant errors during data collection.

Feed Sampling and Analysis

Samples of forage from treatment pastures were hand-clipped at the initiation of the experiment. Samples of forage from common post-calving pastures were collected as cows were removed from treatment pastures. Forage samples were dried in a 55°C forced air oven for 3 d and then ground with a Wiley mill (1-mm screen, Arthur H. Thomas, Philadelphia, PA). Forage samples were analyzed for NDF and ADF (using Ankom Technology method 5 and 6, respectively; Ankom^{200} Fiber Analyzer, Ankom Technology, Macedon, NY), fat (using Ankom Technology method 2; Ankom XT10 Fat Analyzer, Ankom Technology), CP (Leco TruMac, LECO Corporation, St. Joseph, MI), and ash (600° C for 2 h ; Thermolyne muffle oven Model F30420C, Thermo Scientific, Waltham, MA). Nutrient composition of DDGS supplement was obtained from a load analysis provided by plant of origin (Archer Daniels Midland, Decatur, IL). Feed ingredients used in the common finishing diet were analyzed by Rock River Laboratory, Inc. (Watertown, WI) for CP, ADF, and fat using AOAC (1990) methods 990.03, 973.18, and 920.39, respectively. The method described by Goering and Van Soest (1970) was used for analysis of NDF. Reported NE_g of the finishing diet was back-calculated from observed animal performance using equations from NRC (1996).

Statistical Analysis

Cow treatment pasture was considered the experimental unit for all response variables. Measures of cow BW, BCS, and milk production as well as calf pre- and post-weaning growth and carcass characteristics were analyzed using the MIXED procedure of SAS (SAS Inst. Inc., Cary, NC). Measures of subsequent reproduction and carcass quality and yield grade

distributions were analyzed using the GLIMMIX procedure of SAS. The least square means function of SAS was used to separate treatment means. The statistical model included gestational treatment and breed block as fixed effects and cow treatment pasture as a random effect. Treatment effects were considered significant at $P \leq 0.05$ and trends at $0.05 < P \leq 0.10$.

Results and Discussion

Cow Performance

Cow BW, BCS, milk production and subsequent reproduction data are shown in Table 2.3. Initial cow BW was not different ($P = 0.82$); however, initial BCS tended ($P = 0.10$) to be greater for cows not offered supplement relative to supplemented cows. Post-calving BW was not different ($P = 0.17$); yet, cows offered supplement tended ($P = 0.07$) to have greater BCS than those not offered supplement. Since cows were removed from treatment pastures and BW recorded within 1 wk following calving, post-calving BW includes BW change during the supplementation period and loss of fetus, placental membranes, and associated fluids. Cow BW and BCS gain during the prepartum supplementation period were greater ($P \leq 0.02$) for cows offered supplement. Breeding BW was not different ($P = 0.19$); but BCS was greater ($P < 0.01$) for cows offered supplement. Prepartum supplementation of grazing cows is known to consistently improve cow BW and BCS. Stalker et al. (2006) observed maintenance of BW and decreased BCS loss when cows, grazing winter range (average CP = 5.4%, average TDN = 50.1%) during late gestation, were offered 0.45 kg/d of a 42% CP supplement. Larson et al. (2009) observed greater BW and BCS before calving and breeding when cows, grazing either dormant winter range (CP = 6.8%, ADF = 42.8%) or cornstalks (CP = 5.2%, ADF = 49.3%), were offered 0.45 kg/d of a 28% CP supplement during late gestation relative to those offered no

supplement. Bohnert et al. (2002) observed improved cow BW or BCS when late gestation cows, consuming prairie hay (CP = 5.2%, ADF = 32%), were supplemented to meet 100% RDP requirement or supplemented with a 60% RUP supplement that only provided 80% of RDP requirement. Winterholler et al. (2012) observed decreased BW and BCS loss when gestating cows consuming prairie hay (CP = 5.6%, TDN = 50%) were supplemented with increasing levels of DDGS (0.77, 1.54, or 2.31 kg/d) over a 119 d period that began 106 d prepartum.

Aside from providing additional CP, DDGS supplementation provides additional energy in the form of fat. The DDGS used in the current experiment contained 7% fat; thus, 2.1 kg DM DDGS·cow^{-1}·d^{-1} provided 0.15 kg·cow^{-1}·d^{-1} of supplemental fat. Winterholler et al. (2012) observed no effects on cow BW or BCS as level of supplemental fat from DDGS increased. The amount of supplemental fat from DDGS in the current experiment was less than the high level of supplemental fat from DDGS (0.28 kg·cow^{-1}·d^{-1}) fed by Winterholler et al. (2012).

No differences were observed in calving date (P = 0.24, Table 2.3). Data concerning the influence of maternal plane of nutrition on calving date are contrasting. In agreement with the current experiment, Bohnert et al. (2002) observed no difference in calving date between supplemented and unsupplemented dams. Stalker et al. (2006) observed that CP supplemented cows calved later in the calving season than unsupplemented cows. Larson et al. (2009) observed that CP supplemented cows calved earlier in the calving season relative to unsupplemented cows. In the 3 yr experiment conducted by Larson et al. (2009), cows remained on the same treatment throughout the experiment. Thus, it was hypothesized that unsupplemented cows were subjected to continual nutritional stress and conceived later in each following breeding season. This hypothesis was supported by a reduced number of unsupplemented cows calving during the first 21 d of the calving season. In the current experiment, AI conception rates were not different (P =

0.17, Table 2.3); however, the fact that 11% more cows offered prepartum DDGS supplementation conceived to AI relative to cows offered no supplement may be of biological significance. However, the current experiment only encompassed 1 yr, so it cannot be determined if carryover effects of supplementation on calving date in the subsequent calving season existed.

No differences were observed in calf birth BW (P = 0.13, Table 2.3). There is considerable data to indicate that prepartum CP supplementation to spring-calving cows consuming low quality forages during late gestation does not appear to increase calf birth BW (Bohnert et al., 2002; Stalker et al., 2006; Martin et al., 2007; Larson et al., 2009; Funston et al., 2010). In contrast, Winterholler et al. (2012) observed greater calf birth BW when cows were supplemented with DDGS relative to those only supplemented cottonseed hulls prepartum; calf birth BW was also increased as DDGS supplementation level increased. The contrasting results for effect of DDGS supplementation on calf birth BW observed between Winterholler et al. (2012) and the current experiment may be season of birth. Gaertner et al. (1992) observed greater calf birth BW of calves born to spring-calving cows relative to calves born to fall-calving cows. No differences in calf birth BW were observed when cows consuming ad libitum hay were provided 0.11 to 0.12 $kg \cdot cow^{-1} \cdot d^{-1}$ of supplemental fat from a high-fat range supplement relative to cows provided 0.03 $kg \cdot cow^{-1} \cdot d^{-1}$ supplemental fat from a corn-soybean meal supplement during the last 62 d of gestation (Alexander et al., 2002).

Subsequent pregnancy rates are shown in Table 2.3. As previously indicated, AI conception rate was not different (P = 0.17). Treatments also had no effect on overall pregnancy rate (P = 0.11). There is evidence that calving BCS, an indicator of long-term body reserves, has substantial influence on subsequent reproduction (Richards et al., 1986; Spitzer et al., 1995).

Richards et al. (1986) determined that a calving BCS of 5 represents a threshold at which additional BCS does not further improve pregnancy rates. In the current study, both treatments had a BCS greater than 5 at time of calving. However, at time of breeding, cows not offered supplement had a BCS lower than 5, considered to be in "borderline" body condition. This lower BCS at time of breeding may explain why 11% fewer cows not offered prepartum DDGS supplementation conceived to AI relative to cows offered supplement. Winterholler et al. (2012) observed numerical increases in luteal activity, AI conception rates, and overall pregnancy as level of prepartum DDGS supplementation increased during late gestation; however, these differences were not statistically significant as a result of the limited number of experimental animals used. Supplemental fat from prepartum DDGS supplementation may have the potential to affect postpartum reproduction. In a review of fat supplementation and reproduction in beef cattle, Funston (2004) concluded that the effects of supplemental fat prepartum on postpartum reproduction are inconclusive. Funston (2004) further concluded that prepartum fat supplementation may be most beneficial when no supplemental fat is provided postpartum. However, no beneficial effects of prepartum supplemental fat from DDGS were observed in the current experiment.

Milk production was not different ($P = 0.52$, Table 2.3) when measured at 82 ± 14 d postpartum. It is acknowledged that estimate of milk production was lower than in many other published experiments. However, the milk production estimates for the current experiment agree with those of Shike et al. (2013) who measured milk production within the same cow herd. Prepartum supplementation of CP to cows grazing winter range or cornstalks did not affect milk production (Larson et al., 2009). Winterholler et al. (2012) observed no differences in milk production with increasing level of DDGS supplementation prepartum through 13 d postpartum.

Forcherio et al. (1995) observed a trend for greater milk consumption when calves nursed cows grazed on endophyte-infected tall fescue and offered supplements of corn or soybean hull-based supplement when compared to cows offered no supplement. In the current experiment, supplementation ceased within one week after calving; thus, carryover effects of treatment on milk production would be unexpected. Prepartum supplementation has the potential to affect milk composition. Increasing level of prepartum DDGS supplementation decreased milk fat percentage, increased CP percentage, and tended to increase lactose percentage (Winterholler et al., 2012). Winterholler et al. (2012) observed decreased Mcal/kg of milk as level of prepartum DDGS supplementation increased; however, no difference in Mcal/d provided by milk were detected. In contrast, milk production or milk fat percentage was not different regardless of whether cows provided supplemental fat from a high-fat range supplement or a corn-soybean meal supplement during late gestation (Alexander et al., 2002). Because milk composition was not measured in the current experiment, no inferences about the effect of prepartum DDGS supplementation on the performance of subsequent progeny can be made.

Calf Performance

Pre-weaning performance of calves, steers and heifers, weaned by cows allotted to treatment pastures is shown in Table 2.3. As previously mentioned, calf birth BW was not different ($P = 0.13$). Weaning BW and pre-weaning ADG were also not different ($P \geq 0.12$). There were no differences ($P \geq 0.27$) in steer birth BW, weaning BW, or pre-weaning ADG (Table 2.4). Steer ultrasound backfat and marbling score were not different ($P \geq 0.19$) when measured at weaning. It is thought that calf weaning BW is more heavily influenced by milk consumption rather than maternal body reserves at calving, which more directly influence calf birth BW (Spitzer et al., 1995). This is in agreement with the current experiment in that

estimated milk production was not different, and weaning BW of progeny was not different among treatments. Because milk composition was not measured in the current experiment, no inferences about the effect of prepartum DDGS supplementation on the performance of subsequent progeny can be made. There is evidence that maternal plane of nutrition can have a programming effect on progeny growth independent of milk production or composition. Despite maternal CP having no effect on milk production, Larson et al. (2009) observed greater calf weaning BW when dams were supplemented during late gestation. Stalker et al. (2006) also observed greater calf weaning BW when dams were supplemented during late gestation. Winterholler et al. (2012) observed a trend for increased calf weaning BW as level of prepartum supplemental DDGS increased. The effects of prepartum fat intake on subsequent calf performance are contrasting. Alexander et al. (2002) observed no differences in calf ADG or weaning BW regardless of whether cows were provided prepartum supplemental fat from a high-fat range supplement or a corn-soybean meal supplement. In one experiment conducted by Bellows et al. (2001), greater 190 d calf BW was observed when dams were fed isocaloric diets containing 3.8 to 5.1% fat relative to a control diet containing 2.4% fat. However, in a 2nd experiment conducted by Bellows et al. (2001), no differences in 180 d calf BW were observed, regardless of prepartum dietary fat concentration (2.2 vs. 6.3% fat). In the current experiment, differences in nutrient status of CON cows relative to SUP cows may not have been great enough to cause a detrimental programming effect on progeny growth.

Post-weaning performance of steer progeny are shown in Table 2.4. There were no differences ($P \geq 0.35$) in initial feedlot BW, final BW, or days on feed. As a result, post-weaning ADG was not different ($P = 0.77$). Feedlot DMI was not different ($P = 0.52$) between CON and SUP and no difference ($P = 0.71$) in G:F was observed. Although Stalker et al. (2006) observed

greater calf weaning BW of calves born to supplemented dams, and as a result heavier steer initial feedlot BW, no differences were observed in steer feedlot ADG, DMI, or G:F. In contrast to this, Larson et al. (2009) observed trends for greater feedlot ADG and final BW for steers born to supplemented dams when compared to steers born to unsupplemented dams. During a post-weaning performance evaluation, heifer mates to the steer progeny fed by Larson et al. (2009) tended to have greater ADG and greater G:F when born to dams offered CP supplementation (Funston et al., 2010). As mentioned previously, cows used by Larson et al. (2009) remained on the same treatments throughout the 3 yr experiment unlike with Stalker et al. (2006), and this may explain the differences in post-weaning steer progeny performance. Unsupplemented cows over the course of the 3 yr experiment were fed a lower plane of nutrition, may have been more susceptible to nutrient restriction, and the subsequent progeny may have been more likely to experience reduced nutrient supply during development.

Data concerning post-weaning health of steer progeny are shown in Table 2.4. There were no differences in morbidity ($P = 0.62$) or steers requiring multiple treatments for bovine respiratory disease ($P = 0.38$). Larson et al. (2009) observed a greater percentage of steers born to unsupplemented dams requiring post-weaning treatment for respiratory or gastrointestinal disease relative to steers born to supplemented dams. This finding was surprising as Larson et al. (2009) saw no difference in percentage of calves treated from birth to weaning. Stalker et al. (2006) did not report post-weaning health of steer progeny followed through the feedlot; however, they did observe a 5% decrease in weaning percentage of calves born to unsupplemented dams relative to those born to supplemented dams. There were no differences in calf serum IgG concentrations when measured 24 to 48 h after birth. Similar serum IgG concentrations would infer that dam CP supplementation had no effect on passive immunity of

subsequent progeny and thus was not the cause for reduced weaning percentage observed by Stalker et al. (2006). Evidence exists of potential effects of prepartum CP supplementation on health of subsequent progeny; however, these data are inconclusive.

Carcass Characteristics

Data concerning carcass characteristics of steer progeny are shown in Table 2.5. There was no difference ($P = 0.56$) in HCW between steers born to CON and SUP dams. Backfat tended to be greater ($P = 0.08$) for steers born to CON dams relative to those born to SUP dams. This trend for a difference in backfat was unexpected as maternal treatment was approximately equal within each of the 3 slaughter groups. However, sorting steers into slaughter groups based on backfat reduced variation of carcass backfat, thus resulted in a small SEM, and allowing for small differences in carcass backfat to be detected. Longissimus muscle area was not affected ($P = 0.30$) by treatment. Neither yield grade nor marbling score were different ($P \geq 0.19$) among steers born to CON or SUP dams. The percentage of steers grading low choice or better was not different ($P = 0.66$) among treatments. The effects of maternal supplementation during late gestation on carcass characteristics of subsequent steer progeny is mixed. In agreement with the current experiment, Stalker et al. (2006) observed no differences in the carcass characteristics of steers born to supplemented or unsupplemented dams. In contrast, Larson et al. (2009) observed a trend for greater HCW, greater marbling scores, and greater percentages of steers grading low choice and average choice or greater when dams were supplemented CP during late gestation.

A primary difference between the current experiment and experiments evaluating prepartum supplementation using spring-calving cows consuming either native range, cornstalks, or prairie hay (Stalker et al., 2006; Larson et al., 2009; Winterholler et al., 2012) is the forage used in each experiment. The tall fescue grazed in the current experiment (Table 2.1) is higher in

CP and lower in ADF and NDF than forages utilized by Stalker et al. (2006), Larson et al. (2009), or Winterholler et al. (2012). Thus, cows in the current experiment may have been in a more positive nutrient balance, and their progeny less susceptible to nutrient restriction during prenatal development. However, despite the greater nutrient content of tall fescue, fescue toxicosis is a serious hindrance in realizing maximum cow/calf productivity (Paterson et al., 1995). Fescue toxicosis is associated with consumption of ergot peptide alkaloids which result in a complex of symptoms that culminate in decreased DMI; and thus, suboptimal animal performance. Retrospective to the current experiment, pastures at the site of the current experiment have been characterized as containing 1.165 mg/kg total ergot peptide alkaloid when forage was sampled in late October, which is greater than those reported by Belesky et al. (1988) and Peters et al. (1992) who observed fescue toxicosis in steers and lactating cows, respectively. Thus, high ergot peptide alkaloid consumption may explain the low estimates of milk production and poor AI conception rates observed in the current experiment (Table 2.3).

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The potential for prepartum supplementation of spring-calving cows consuming low quality forage to improve cow BW and BCS is well documented. Even though limited data exists, there are indications that prepartum supplementation during late gestation has the ability to positively affect the performance and carcass characteristics of subsequent progeny. The potential for prepartum supplementation of fall-calving cows grazing endophyte-infected tall fescue during late gestation to improve dam and progeny performance is much less clear. The results of our experiment indicate that late gestation supplementation of 2.1 kg DM pelleted

DDGS·cow^{-1}·d^{-1} to cows grazing endophyte-infected tall fescue elicits modest responses in cow BW and BCS change, but no effects on progeny growth or steer carcass characteristics.

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Tables

Table 2.1. Forage availability and nutrient composition at the initiation of grazing.

	Treatment[1,2]				TRT
Item	CON	SUP	Post-calving[3]	SEM	*P*-value[4]
Forage availability, kg DM	1205	1251	1095	114	0.69
Forage nutrient Composition, % DM					
DM	32.0	30.4	41.3	3.7	0.67
CP	12.7	14.4	12.2	1.0	0.12
ADF	39.0	36.1	38.2	1.2	0.03
NDF	59.6	57.4	63.2	2.6	0.41
Fat	2.2	2.3	2.6	0.4	0.87
Ash	7.7	7.2	8.0	1.0	0.61

[1]CON = offered no supplement; SUP = offered 2.1 kg DM pelleted DDGS·cow^{-1}·d^{-1}

[2]Cows were given free access to trace-mineral salt with the following composition: Salt = 21.45%, Ca = 14.75%, P = 7.84%, Mg = 5.96% (magnesium oxide), K = 1.07% (potassium chloride), S = 1.11%, Co = 29 mg/kg (cobalt carbonate), I = 35 mg/kg (calcium iodate), Cu = 1,005 mg/kg (copper sulfate), Fe = 5,549 mg/kg (ferrous sulfate), Mn = 2,2826 mg/kg (manganous oxide), Se = 26 mg/kg (sodium selenite), Zn = 2,539 mg/kg (zinc oxide), vitamin A = 535,497 IU/kg (vitamin A acetate), vitamin D = 14,991 IU/kg (vitamin D_3), vitamin E = 2,648 IU/kg (DL-alpha-tocpheryl acetate), chlortetracycline = 5,732

[3]Pastures in which cows from both treatments were comingled after calving

[4]TRT = comparison of CON and SUP pastures

Table 2.2. Diet and nutrient composition of common feedlot diet

Item	Inclusion, % DM
Ingredient, % DM	
Dried distillers grains plus solubles	43.3
Dry cracked corn	29.3
Corn husklage	22.4
Supplement, % Diet DM[1]	
Ground Corn	4.061
Limestone	0.750
Liquid fat	0.075
Trace mineral salt[2]	0.050
Urea	0.042
Rumensin 90[3]	0.006
Vitamin premix[4]	0.005
Thiamine	0.005
Tylan 40[5]	0.004
Copper sulfate	0.003
Analyzed nutrient content, % DM	
DM	68.1
CP	17.2
NDF	29.3
ADF	11.7
Fat	5.6
NE_g[6], Mcal /kg	1.31

[1]200 mg ractopamine hydrochloride·steer^{-1} ·d^{-1} fed 40 d before slaughter (Optaflexx 45, 99 g/kg, Elanco Animal Health, Greenfield, IN)

[2]Trace mineral salt = 80 to 85%, Fe = 2.57% (ferrous sulfate), Zn = 2.86% (zinc oxide), Mn = 5,710 mg/kg (manganous oxide), Cu = 2,290 mg/kg (copper sulfate), I = 100 mg/kg (calcium iodate), Se = 86mg/kg (sodium selenite)

[3]Monensin 198 g/kg (Elanco Animal Health)

[4]Vitamin A = 3,306,900 IU/kg, vitamin D_3 = 330,690 IU/kg, vitamin E = 44,092 IU/kg, vitamin K = 2,205 mg/kg, vitamin B_{12} = 18 mg/kg, riboflavin = 4,409 mg/kg, D pantothenic acid = 12,125 mg/kg, niacin = 16,535 mg/kg, choline = 143,189 mg/kg

[5]Tylosin 88 g/kg (Elanco Animal Health)

[6]NE_g value back-calculated from animal performance using NRC (1996)

Table 2.3. Effects of late gestation distillers grains supplementation on cow BW, BCS, calving, milk production, subsequent reproduction, and progeny pre-weaning performance.

	Treatment[1]			
Item	CON	SUP	SEM	*P*-value
BW, kg				
Initial[2]	601	599	7	0.82
Post-calving[2]	591	605	7	0.17
Supplementation BW change[2]	-10	6	4	<0.01
Breeding[3]	573	587	7	0.19
BCS				
Initial[2]	5.3	5.1	0.1	0.10
Post-calving[2]	5.2	5.3	0.1	0.07
Supplementation BCS change[2]	-0.1	0.1	0.1	0.02
Breeding[3]	4.6	5.1	0.1	<0.01
Calving date, Julian d	230	228	5	0.24
Milk production, kg[4]	5.4	5.6	0.2	0.52
Subsequent Reproduction[3]				
AI conception, %	32	43	--	0.17
Overall pregnancy, %	92	98	--	0.11
Progeny[2]				
Birth BW, kg	33	34	2	0.13
Weaning BW, kg	106	110	2	0.12
ADG, kg	0.91	0.92	0.02	0.78

[1]CON = offered no supplement; SUP = offered 2.1 kg DM pelleted DDGS·cow^{-1}·d^{-1}

[2]Supplementation period cow and progeny pre-weaning performance reported for 177 cows and calves (CON = 86; SUP = 91), 6 pastures per treatment

[3]Cow BW, BCS, and subsequent pregnancy rate reported for 169 cows (CON = 83; SUP = 86) , 6 pastures per treatment

[4]Cow milk production measured 82 ± 14 d postpartum and reported for 165 cows (CON = 80; SUP = 85) , 6 pastures per treatment

Table 2.4. Effects of late gestation distillers grains supplementation on pre- and post-weaning performance and health of steer progeny.

	Treatment[1]			
Item[2]	CON	SUP	SEM	*P*-value
Pre-weaning				
BW, kg				
Birth	36	36	1	0.87
Weaning[3]	112	116	3	0.27
ADG, kg	0.92	0.96	0.03	0.35
Post-weaning				
BW, kg				
Initial[4]	157	154	4	0.48
Final[5]	558	557	11	0.56
12th Rib Fat Thickness, cm[6]	0.3	0.3	0.1	0.19
Marbling Score[6,7]	350	342	9	0.55
Days on feed	243	251	6	0.35
ADG, kg/d	1.66	1.65	0.03	0.77
DMI, kg/d	8.7	8.5	0.2	0.52
G:F	0.194	0.195	0.003	0.71
Health				
Morbidity, %	38	33	--	0.62
Multiple Treatment[8], %	8	3	--	0.38

[1]CON = dams offered no supplement; SUP = dams offered 2.1 kg DM pelleted DDGS·cow^{-1} ·d^{-1}

[2]Performance reported for 71 steers (CON = 34; SUP = 37), 6 dam pasture groups per treatment

[3]Weaning BW taken on 82 ± 14 d of age

[4]BW of feedlot progeny taken on 122 ± 14 d of age

[5]HCW/standard dressing percent (63%)

[6]12th Rib fat thickness and marbling score measured via ultrasound on 122 ± 14 d of age

[7]400-499 = Small, 500-599 = Modest, 600-699 = Moderate, 700-799 = Slightly Abundant

[8]Steers treated two or more time for bovine respiratory disease

Table 2.5. Effects of late gestation distillers grains supplementation on carcass characteristics of steer progeny.

	Treatment[1]			
Item[2]	CON	SUP	SEM	*P*-value
HCW, kg	352	357	7	0.56
12th-rib fat thickness, cm	1.4	1.3	0.1	0.08
LM Area, cm^2	81.1	83.5	1.7	0.30
Yield Grade	3.3	3.1	0.1	0.19
Marbling Score[3]	466	452	18	0.60
≥ Low Choice, %	78	73	--	0.66

[1]CON = dams offered no supplement; SUP = dams offered 2.1 kg DM pelleted DDGS·cow^{-1} ·d^{-1}

[2]Carcass characteristics reported for 69 steers (CON = 33; SUP = 36), 6 dam pasture groups per treatment

[3]400-499 = Small, 500-599 = Modest, 600-699 = Moderate, 700-799 = Slightly Abundant

CHAPTER 3

INFLUENCE OF PREPARTUM DIETARY ENERGY ON BEEF COW PERFORMANCE AND CALF GROWTH AND CARCASS CHARACTERISTICS

Abstract

Objectives were to evaluate the effects of prepartum dietary energy intake on cow performance as well as performance and carcass characteristics of subsequent progeny. Spring-calving, mature cows (n = 106 total) were blocked by BW and allotted to 1 of 2 treatments: ground hay and dried distillers grains plus solubles (**REQ**: TDN = 61.8%, CP = 11.0%, RDP = 81.9% of CP, fat = 2.1%) or corn bran and ground cornstalks (**HE**: TDN = 70.3%, CP = 10.0%, RDP = 72.4% of CP, fat = 5.7%). Treatments were limit-fed as isonitrogenous rations with REQ and HE providing 100% and 125% of TDN requirements, respectively, and were fed from 83 ± 10 d prepartum to calving. All cows were fed a common diet postpartum. Cow BW and BCS were recorded at the beginning of the feeding period, 24 h post-calving, and at breeding. Milk production was estimated via the weigh-suckle-weigh technique 65 ± 9 and 120 ± 9 d postpartum. Calf BW was measured at birth and at weaning (120 ± 9 d of age). Calves (n = 86) were fed a common feedlot diet beginning 21 d after weaning, and individual feed intake was monitored using GrowSafe. Progeny were slaughtered in 3 groups at an average 12th rib fat thickness of 1.3 cm. From initiation of experiment to breeding, cow BW change was greater ($P <$ 0.01) and BCS change tended to be greater ($P = 0.09$) for HE relative to REQ cows. Birth BW was greater ($P = 0.02$) for calves born to cows fed HE with no increase ($P = 0.30$) in percentage of unassisted births. There were no effects ($P \geq 0.27$) of treatment on calving date, milk production, or subsequent pregnancy rate. Calf weaning BW, initial feedlot BW, final BW, and

days on feed were not affected ($P \geq 0.20$) by treatment. Feedlot DMI, ADG, and G:F were not different ($P \geq 0.35$). There was no effect ($P \geq 0.27$) of treatment on progeny pre- or post-weaning morbidity. Although progeny born to HE dams tended ($P = 0.10$) to have greater marbling scores at weaning, there was no effect ($P \geq 0.60$) of treatment on carcass marbling score or other carcass traits. Feeding cows 125% of TDN requirement during late gestation increased cow BW change and progeny birth body weight. Feeding cows 129% of TDN requirement during late gestation had no effect on pregnancy rate or progeny performance.

Key words: beef cow, prepartum, energy, fetal programming, gestation, progeny

Introduction

Beef cows may overconsume dietary energy when fed energy-dense rations ad libitum. Another opportunity for overconsumption of energy may be incorrect ration balancing. Late gestation is a critical period during which cow/calf producers have substantial control over the nutrition of spring-calving cows wintered in drylots (Braungardt et al., 2010).

Dietary energy level impacts body reserves of pregnant cows, but also fetal growth and development. In sheep, maternal overfeeding (150% of NRC [1985] requirement) from 60 d before breeding through parturition resulted in greater adiposity and reduced lean tissue mass of resulting progeny (Long et al., 2010). Few studies, especially those using beef cattle, have attempted to isolate the impact of greater prepartum dietary energy on subsequent progeny relative to global overnutrition alone.

There is evidence that dietary energy source has differing effects on both cow performance and of subsequent progeny. When comparing hay and corn coproducts as energy sources in isocaloric late gestation diets, both Radunz et al. (2010) and Wilson (2012) observed

greater cow BW and calf birth BW when cows were fed corn coproducts as an energy source relative to hay. Radunz et al. (2012) observed greater marbling scores for progeny born to dams fed dried distillers grains plus solubles (**DDGS**) as an energy source during late gestation relative to those born to dams fed hay. Greater fat and RUP of corn coproducts may contribute to greater cow performance relative to when hay is fed as an energy source. The current experiment uses both corn coproducts and hay as dietary energy sources; yet, corn coproducts are evaluated in a more energy-dense, but isonitrogenous ration relative to hay. We hypothesized that greater maternal dietary energy would increase cow BW, progeny birth BW, and increase marbling in subsequent progeny. Objectives were to evaluate the effects of increased dietary energy during late gestation on cow performance as well as growth performance and carcass characteristics of subsequent progeny.

Materials and Methods

Animals, Experimental Design, and Treatments

Experimental animals were managed according to the guidelines recommended in the Guide for the Care and Use of Agriculture Animals in Agriculture Research and Teaching (Federation of Animal Science Societies, 2010). All experimental procedures followed were approved by the University of Illinois Institutional Animal Care and Use Committee. Spring-calving, mature, multiparous Angus, Simmental, and Simmental × Angus cows (n = 106; BW = 688 ± 76 kg; age = 4.8 ± 2.4 yr) and their progeny were used to evaluate the effects of increased dietary energy during late gestation on cow performance as well as subsequent progeny pre-weaning and post-weaning growth and carcass characteristics. Cows were maintained at the Orr Beef Research Center in Baylis, IL.

A randomized complete block design was used with cows blocked by BW (light and heavy; 6 pens per block). Pregnancy was confirmed, via rectal ultrasonography, to determine whether cows were bred to either AI or cleanup bulls. Cows were blocked into light and heavy weight blocks of 636 kg or 727 kg BW, respectively. Within block, cows were stratified by breed and then allotted to pens (12 total pens, 6 pens total per treatment). Four light block pens contained 9 cows each and 2 pens contained 8 cows each (52 cows total). The 6 heavy block pens contained 9 cows each (54 cows total).

Pens were randomly assigned to 1 of 2 late gestation rations within block (Table 3.1): limit-fed ground, mixed, cool-season, grass hay and DDGS (**REQ**, n = 6 pens) or limit-fed corn bran and ground cornstalks (**HE**, n = 6 pens) 83 ± 10 d prepartum. The REQ and HE treatment rations were formulated to provide 100% and 125% of NRC (1996) energy requirement, respectively. Both treatments were formulated to be isonitrogenous. Rations were formulated using requirements of 636 kg or 727 kg cows with 9.1 kg peak milk production. Using the table generator function of NRC (1996), treatments were balanced using TDN and CP. Dry matter intake of treatments was increased each 30d of the prepartum feeding period to reflect changing nutrient requirements of cows during late gestation. Treatments were evaluated retrospectively with Level 1 of the NRC (1996) model using observed initial BW and BCS, milk production, and calf birth BW, and DMI of each treatment (Table 3.2). Rations were fed in concrete, fence-line bunks as a total mixed ration daily at 0900 h. Before feeding, hay and cornstalks were ground through a 2.54 cm screen. Cows were provided trace-mineral salt, free choice (Table 3.1). Cows remained on treatments until calving. Within 48 h after calving, cows were moved to new pens, comingled among treatment groups, and limit-fed a common diet formulated to meet or exceed

NRC (1996) requirements. The common post-calving diet was 50% pelleted corn gluten feed (**CGF**) and 50% ground cornstalks, (Table 3.1).

Pre-calving and Pre-weaning Management of Cows and Calves

During the prepartum feeding period and early lactation, cows were maintained in 11.0 x 10.7 m or concrete lots with a 7.3 x 7.3 m open-front shed and provided with a minimum of 0.73 m of fence-line bunk space. Cow BW was recorded on 2 consecutive d and BCS was assigned at the start of the prepartum feeding period. Within 48 h after calving, cow BW was recorded and BCS assigned to evaluate cow performance at the end of the treatment period. Thus, post-calving cow BW reflects loss of fetus, placental membranes, and associated fluids. Cow BW, BCS, incidence of dystocia, and milk production was reported for 6 pens per treatment and included data from 87 cows and excluded those who lost calves during parturition (REQ, n = 4; HE, n = 3), twinned (REQ, n = 0; HE, n = 3), failed to calve (REQ, n = 1; HE, n = 1), had injured calves before breeding (REQ, n = 2; HE, n = 3), or died (REQ, n = 1; HE, n = 1) over the course of the experiment. Incidence of calf loss during parturition was not related to treatment (P = 0.18). Milk production was estimated via the weigh-suckle-weigh technique (Boggs et al., 1980) at 65 ± 9 d and 120 ± 9 d postpartum. Subsequent reproduction was reported for 6 pens per treatment and included data from 82 cows and excluded those culled prior to breeding (REQ, n = 1; HE, n = 4). At rebreeding (66 ± 9 d postpartum), cows were synchronized using a CoSynch + CIDR protocol (Bremer et al., 2004) and were artificially inseminated as a single group. Cow BW was recorded and BCS assigned at time of CIDR removal to evaluate lasting effects of treatments. After AI, all cows went to pasture and were exposed to clean-up bulls for 2 subsequent estrous cycles. Conception rates for AI were determined via transrectal ultrasonography at 46 d after insemination. Overall pregnancy rates were determined via transrectal ultrasonography at 88 d

after insemination. During spring and summer, cow/calf pairs were rotated through mixed pastures of orchardgrass (*Dactylis glomerata L.*), endophyte-infected tall fescue (*Festuca arundinacea*), red clover (*Trifolium pretense*), and bluegrass (*Poa pratensis L.*).

Calf BW was recorded within 48h after birth and at weaning (120 ± 9 d of age) to measure pre-weaning calf ADG. At time of weaning, 12th rib backfat thickness (**backfat**) and marbling score were estimated for all calves via compositional ultrasound. Ultrasound measurements were taken with an Aloka 500SV (Wallingford, CT) B-110 mode instrument equipped with a 3.5-MHz general purpose transducer array. Backfat measurements were taken in a transverse orientation between the 12th and 13th ribs approximately 10 cm distal from the midline. Ultrasound images were processed utilizing CPEC ultrasound imaging software (Cattle Performance Enhancement Company LLC., Oakley, KS). Pre-weaning calf performance was reported for 6 pens per treatment and included data from all calves (n = 86; REQ: n = 45; 21 steers, 24 heifers; HE: n = 41; 20 steers, 21 heifers) raised by cows placed on treatments, minus twins, those injured or deceased before weaning (REQ, n = 0; HE, n = 1), or retained in the breeding herd (REQ, n = 0; HE, n = 1). Incidence of pre-weaning morbidity treatment was recorded by animal care personnel.

Post-weaning Management

Calves were transported via commercial trucking to the Beef Cattle and Sheep Field Laboratory, Urbana, IL for the duration of the finishing period. Calves were vaccinated with the following: Bovishield Gold FP5 L5 HB (Zoetis, Florham Park, NJ), One Shot Ultra 7 (Zoetis), and Pulmo-Guard MpB (AgriLabs, St Joseph, MO). Calves were dewormed with Eprinex pour-on (Merial, Duluth, GA) and tagged with an electronic identification tag (Allflex USA, DFW Airport, TX). Upon entry to the feedlot, calves were adapted to a common, finishing diet (Table

3.3) fed for ad libitum intake over a transition period of 21 d. During the finishing period, calves were split by sex with maternal treatments comingled. Calves were implanted with Component EC (10 mg estradiol benzoate, 100 mg progesterone, 29 mg tylosin 99 tartate; Elanco Animal Health, Greenfield, IN) 8 d post-weaning and received a Compudose 200 implant (25.7 mg estradiol; Elanco Animal Health) 176 d post-weaning.

Initial BW was recorded on 2 consecutive d for evaluation of post-weaning performance 7 d after calves started their final finishing diet (155 ± 9 d of age). Individual feed intake was monitored using the GrowSafe automated feeding system (Model 4000E, GrowSafe Systems Ltd., Airdrie, Alberta, Canada) during the finishing period. Incidence of morbidity treatment during the finishing phase was recorded by animal care staff. Final BW was calculated from HCW using a standard dressing percentage of 63%. Post-weaning performance was excluded for 1 calf born to an HE dam because of mortality.

Beginning on d 141 of the finishing period, backfat was estimated via ultrasound to determine slaughter date. Cattle were slaughtered at a commercial facility in 3 groups. Cattle in the 1st and 2nd slaughter groups were selected for slaughter 20 ± 1 d after a minimum backfat estimation of 0.9 cm. All remaining cattle (n = 20) were slaughtered 21 d after the 2nd slaughter group. Trained personnel recorded slaughter order and HCW was taken on day of slaughter. Backfat, % KPH, LM area, yield grade, and marbling score were taken after a 24 h carcass chill with Video Image Analysis as part of the USDA camera system.

Feed Sampling and Analysis

Individual ingredients used in treatment diets were procured prior to initiation of experiment and stored under roof. Ingredients were sampled after receipt and analyzed for CP, NDF, ADF, fat, Ca, and P, with TDN calculated from ADF by Rock River Laboratory, Inc.

(Watertown, WI). Crude protein, ADF, and fat were analyzed using AOAC (1990) methods 990.03, 973.18, and 920.39, respectively. The method described by Goering and Van Soest (1970) was used for analysis of NDF. Minerals were extracted by acid digestion and analyzed using an Optima 3000 Inductively Coupled Plasma-Optical Emission Spectrometer (Perkin Elmer, Waltham, MA). Calculations for TDN value of hay and cornstalks were based on ADF. A value of 90% TDN for DDGS and corn bran was used when formulating treatments in acknowledgement that calculations for TDN based on ADF concentration underestimate the energy value of corn coproducts. Using this analysis, treatment diets were then formulated before initiation of study. Nutrient values listed in NRC (1996) were used for corn gluten feed in the common post-calving diet. Individual feed ingredients used in the common finishing diet were analyzed by Rock River Laboratory, Inc. for CP, NDF, ADF, and fat using the methods described above. Reported NE_g of the finishing diet was back-calculated from observed animal performance using equations from NRC (1996).

Statistical Analysis

Pen was considered the experimental unit for all response variables. Data concerning cow BW and BCS, calving date, milk production, progeny pre- and post-weaning performance, and carcass characteristics were analyzed using the MIXED procedure of SAS (SAS Inst. Inc., Cary, NC). Data concerning percentage of unassisted births, subsequent reproduction, and incidence of progeny morbidity were analyzed using the GLIMMIX procedure of SAS. The least square means function of SAS was used to separate treatment means. The statistical model included gestational treatment and BW block as fixed effects and treatment pen as a random effect. Calf sex and sire were used as fixed effects for the analysis of calving information, pre-weaning and post-weaning calf performance, and carcass characteristics. For measure of subsequent

reproduction, AI bull was included in the statistical mole as a fixed effect. Treatment effects were considered significant at $P \leq 0.05$ and trends will be discussed at $0.05 < P \leq 0.10$.

Results

Cow Performance

Data concerning cow BW, BCS, calving, milk production, and subsequent reproduction are shown in Table 3.4. There were no differences ($P \geq 0.28$) in initial cow BW or BCS. Surprisingly, post-calving BW or BCW were not different ($P \geq 0.33$). At breeding, cows fed HE were heavier ($P = 0.03$) than those fed REQ; yet, treatment had no effect ($P = 0.37$) on breeding BCS. Loss in cow BW from initial to 24 h post-calving BW tended to be grater ($P = 0.07$) for cows fed REQ relative to HE. Treatment had no effect ($P = 0.80$) on BCS change from initial to 24 h post-calving. Gain in BW from initiation of experiment to breeding was greater ($P < 0.01$) for cow fed HE relative to those fed REQ. From initiation of experiment through breeding, cows fed HE tended ($P = 0.09$) to lose less BCS relative to cows fed REQ.

Calf birth BW was greater ($P = 0.02$) for those born to dams fed HE when compared to those born to cows fed REQ (Table 3.5). Despite this, there were no differences ($P \geq 0.30$) in calving date or percentage of unassisted births. Prepartum dietary energy level had no effect ($P \geq 0.27$) on milk production measured at 65 ± 9 or 120 ± 9 d postpartum. Effect of treatment on AI conception rate was non-significant ($P = 0.34$). It should be noted that increased prepartum dietary energy resulted in a numerical increase of 11 percentage units for AI conception rate for cows fed HE relative to those fed REQ. Overall pregnancy rate was not different ($P = 0.86$) across treatment.

Progeny Performance

Data concerning progeny pre- and post-weaning performance are shown in Table 3.5. Despite differences in calf Birth BW, there were no differences ($P \geq 0.43$) in weaning BW or pre-weaning ADG. When measured at weaning, there were no differences ($P = 0.94$) in ultrasound backfat. Ultrasound marbling score at weaning tended ($P = 0.10$) to be greater for caves born to dams fed HE relative to those born to dams fed REQ. There were no differences ($P = 0.27$) in pre-weaning health of progeny.

There was no difference ($P = 0.20$) in progeny initial feedlot BW, recorded 35 d post-weaning. Maternal dietary energy intake had no effect ($P \geq 0.69$) on progeny final BW or post-weaning ADG. Days on feed, feedlot DMI nor G:F were different ($P \geq 0.24$) across treatment. There were no differences ($P \geq 0.51$) in post-weaning morbidity or percentage of progeny treated 2 or more times for bovine respiratory disease (**BRD**).

Progeny Carcass Characteristics

Data concerning progeny carcass characteristics are shown in Table 3.6. As evidenced by no difference in final BW, HCW was not different ($P = 0.69$). By design, backfat was not different ($P = 0.66$) across treatment. Treatment did not affect ($P \geq 0.84$) KPH percentage or LM area. Prepartum dietary energy intake had no effect ($P \geq 0.60$) on progeny yield grade or marbling scores.

Discussion

Cow Performance

No difference in post-calving BW or BCS was unexpected because the HE ration was formulated to provide 25% greater TDN than the REQ ration. No difference in post-calving BW

may have resulted from differences in fill when BW was recorded 24 h post-calving. Despite no difference in post-calving BW or BCS, the fact that cows fed HE gained more BW, and tended to lose less BCS, through breeding, indicates that energy content of HE was greater that REQ.

One reason to expect cow BW and BCS to be greater for cows fed HE relative to REQ is the greater fat intake of HE cows. Cows fed HE consumed 295% greater fat than cows fed REQ (699 g for HE and 237 g for REQ, Table 3.2), a result of 50% inclusion of corn coproduct in the HE ration. Both Radunz et al. (2010) and Wilson (2012) have observed greater cow BW when either DDGS or a blend of DDGS and corn bran, respectively, were fed as primary ration energy sources relative to cows fed isocaloric amounts of hay. In the experiments conducted by Radunz et al. (2010) and Wilson (2012), cows fed corn coproducts consumed 251% and 189%, respectively, more fat than their hay-fed counterparts. In addition to greater fat concentration, the HE ration contained more digestible fiber, as evidenced by lower NDF and ADF values (Table 3.1).

Overestimation of the energy value of corn bran may explain why less dramatic BW and BCS responses than expected were observed. When incorporating corn coproducts into beef cattle rations, determining accurate feed values has remained a challenge because of their changing nutrient profile as biorefining methods are improved. Due to their unique fiber, protein, and fat composition and the further development of the biorefining process, determining accurate feeding values of corn coproducts has been difficult (Klopfenstein et al., 2008; Jolly et al., 2013). Klopfenstein et al. (2008) and Loy et al. (2008) determined that the feeding value of DDGS is greater than that of corn (88% TDN; NRC 1996) when fed to feedlot cattle (88% to 134.6% TDN) or heifers consuming forage (95.8% to 120% TDN), respectively. The corn bran used in the current experiment (15.5% CP, 75.8% RDP, 31.8% NDF, 11.7% ADF, and 10.7% fat) is

lower in CP that DDGS or CGF, similar in RDP, NDF, and ADF to CGF, and similar in fat to DDGS. Assigning an appropriate feed value to corn bran is challenging given the lack of research in this area. In recognition of the lack of a published TDN value for the corn bran product used in this experiment and that NRC (1996) TDN values for corn coproducts (88% for DDGS, 80% for CGF) typically underestimate their energy value, the authors used a value of 90% TDN for corn bran when formulating treatments. With observed differences in cow performance being less than expected, one can conclude that the true TDN value of corn bran is likely less than 90% TDN.

Greater post-ruminal protein supply for cows fed HE could also lead to the expectation for greater BW gain relative to those fed REQ. Treatment RDP and MP balance was calculated retrospectively using Level 1 of the NRC (1996) model (Table 3.2). Cows fed HE were deficient in RDP balance (-208 g/d for HE and 40 g/d for REQ); yet, had greater MP balance relative to cows fed REQ (291 g/d for HE and 139 g/d for REQ). Cows fed HE may have been able to compensate for the deficiency in RDP, and potentially depressed microbial crude protein synthesis, via increased post-ruminal protein digestion. Excess MP available post-ruminally could also be deaminated and used as an energy source. It should be noted that tabular values were used to estimate ruminal protein degradability and not laboratory analysis.

Despite the possibility of greater RUP intake contributing to increased BW gains for cows fed HE, little evidence exists to confirm this theory. No differences were observed in cow BW or BCS by Bohnert et al. (2002) when cows in late gestation were either supplemented to meet 100% RDP requirement or supplemented with a 60% RUP supplement that provided 80% of RDP requirement. The RDP balances in the experiment conducted by Bohnert et al. (2002) are similar to these in the current experiment as the REQ ration provided 104% of RDP requirement

and the HE ration only provided 81% of RDP requirement. There is evidence that cow BW is not increased by additional RUP when RDP requirement is met through either the basal diet or supplemental RUP (Sletmoen-Olson et al., 2000; Encinias et al., 2005). In the current experiment, both treatments were isonitrogenous and exceeded MP requirements. The REQ and HE treatments provided 121% and 143% of MP requirements; indicating that cows on either treatment were provided above adequate protein supply, regardless of ruminal protein degradability.

Whether additional dietary energy was provided by fat, fiber, or protein, HE represents a greater plane of nutrition than REQ. Considerable evidence exists that links greater maternal plane of nutrition during late gestation and increased calf birth BW. Observed cow performance in the experiments conducted by Radunz et al. (2010) and Wilson (2012) indicate that cows fed corn coproducts as energy sources during late gestation were on a greater plane of nutrition. Radunz et al. (2010) and Wilson (2012) observed greater calf birth BW or a tendency for greater calf birth BW, respectively. Gunn et al. (2014) observed greater calf birth BW when heifers were provided excessive CP during late gestation via a diet consisting of 43% DDGS and 54% cornstalks. An increase in dystocia was also observed by Gunn et al. (2014) when gestating heifers were fed excessive dietary CP. In agreement with the current experiment, Radunz et al. (2010) and Wilson (2012) observed no increases in dystocia with increased calf birth BW when mature cows were used.

It is of note that AI conception rate was numerically 11 percentage units greater for cows fed HE prepartum relative to those fed REQ. This numerical difference in AI conception may be attributed to greater prepartum dietary fat consumed by cows fed HE. In an experiment conducted by Bellows et al. (2001), heifers fed diets containing oilseeds with 3.8% to 5.1% fat

had greater pregnancy rates than heifers fed a control diet containing 2.4% fat. In the current experiment, HE contained 5.7% fat and REQ contained 2.1% fat (Table 3.1). However, with subsequent reproduction only being reported for 6 pens per treatment (82 cows total), more experimental animals would be needed to reach statistical significance. Previous research has shown that BCS, a gauge of long-term energy reserves, is influential on subsequent reproduction; with a minimum BCS at calving of 5 or greater being essential for reproductive success (Richards et al., 1986; Spitzer et al., 1995). The findings of Richards et al. (1986) indicate that additional BCS beyond 5 at calving does not improve pregnancy rate. In the current experiment, in which no differences in overall pregnancy rate were observed, both treatments maintained BCS greater than 5 from initiation of experiment through breeding. Because treatments were applied prepartum, it was expected that there appeared to be no carryover effects of treatment on milk production. In agreement with the current experiment, neither Radunz et al. (2010) nor Wilson (2012) observed differences in milk production when cows were fed rations with high corn coproduct inclusion during late gestation.

Progeny Performance

Greater calf birth BW did not result in greater weaning BW for calves born to dams fed HE. This finding may be particularly concerning for cow/calf producers because additional birth BW with no increase in weaning BW increases risk of dystocia with no offsetting increase in progeny value. In sheep, feeding dams 150% of NRC (1985) requirement 60 pre-breeding and through parturition did not affect weaning BW of progeny relative to progeny born to dams fed to requirement (Long et al., 2010). In contrast to the current experiment, previous research indicates that maternal nutrition does have the potential to affect weaning BW of subsequent progeny. Radunz et al. (2012) observed a trend for greater weaning BW for calves born to dams

fed corn as their primary energy source during late gestation relative those born to dams fed hay or DDGS. Progeny weaning BW was increased when dams were fed elevated levels of dietary fat during late gestation relative to dams fed a low-fat control diet (Bellows et al., 2001).

A trend was observed for greater marbling scores at weaning for progeny born to dams fed HE. The relatively small numerical difference in treatment average marbling scores (16 points) indicates low variation in weaning marbling scores of progeny and are likely of little biological significance. No differences in ultrasound marbling scores at weaning were observed by Radunz et al. (2012) when dams were fed rations using hay or DDGS as energy sources during late gestation.

As evidenced by no effect of treatment on progeny weaning BW, there were no treatment differences in post-weaning performance when progeny were fed a common feedlot diet (Table 3.5). In agreement with the current experiment, Wilson (2012) observed increased cow BW gain when late gestation ration utilized corn coproducts as an energy source; yet, no differences in progeny post-weaning growth, DMI, or efficiency were observed. Radunz et al. (2012) observed a trend for greater days on feed for progeny born to dams fed hay rather than corn coproducts as an energy source. Long et al. (2010) observed greater progeny BW of lambs born to obese dams relative to non-obese when fed a high-energy diet post-weaning. Differences in nutrient status of REQ dams relative to HE dams may not have been significant enough to cause differential programming effects on progeny growth.

Previous research has indicated that maternal nutrition has the ability to impact health of subsequent progeny. In fact, the fetal programming theory is grounded in human cohort studies that observed increased incidence of chronic disease of progeny exposed to maternal nutrient restriction (Barker, 2007). In beef cattle, supplemental CP to cows grazing low quality forages

during late gestation has resulted in decreased percentage of progeny treated for incidence of post-weaning BRD (Larson et al., 2009). Radunz et al. (2012) observed no differences in progeny pre- or post-weaning morbidity or mortality when dams were fed differing energy sources prepartum. In the current experiment, no differences in progeny morbidity were not surprising given the lack of fetal programming effects on other measured response variables. Greater power may also be needed to detect significant differences in progeny health.

Progeny Carcass Characteristics

No differences in carcass characteristics were observed across treatment. Despite a trend for increased marbling score at weaning, progeny born to dams fed HE did not have greater carcass marbling scores. The ability to detect differences in backfat may have been confounded by the method used to select cattle for slaughter. Wilson (2012) observed no difference in carcass characteristics of subsequent progeny whether dams were fed corn coproducts and cornstalks or hay as energy sources during late gestation. Our hypothesis was that increased prepartum dietary energy would increase marbling in subsequent progeny. Previous research has shown the potential for maternal nutrition during late gestation to influence carcass characteristics, specifically indicators of carcass adiposity. Radunz et al. (2011) observed decreased LM area and visceral adiposity of lambs born to dams fed DDGS as an energy source during mid- and late gestation relative to those born to dams fed haylage or corn. Greater marbling scores were observed in calves born to dams fed hay during late gestation relative to calves born to dams fed corn, with calves born to dams fed DDGS being intermediate (Radunz et al., 2012). Larson et al. (2009) observed greater marbling scores in steer progeny born to dams offered supplemental CP during late gestation relative to steers born to unsupplemented dams. After being fed a high

energy diet post-weaning, Long et al. (2010) observed greater adiposity of lambs born to obese dams relative to lambs born to non-obese dams fed to requirement.

Much of the research concerning the fetal programming effects of maternal nutrition in beef cattle production systems has investigated differing global planes of nutrition or fed isocaloric rations of differing nutrient sources. Few studies have investigated supply of specific nutrients (fat, CP, or RDP, etc.) alone. Experimentally, investigating the fetal programing effects of specific nutrients is difficult given feasibility of feeding beef cows purified treatment rations.

Implications

Under the conditions of our current experiment, feeding beef cows late gestation diets formulated to provide 125% of TDN requirement resulted in modest improvement in BW relative to cows fed to TDN requirement. No differences in cow BCS, milk production, or pregnancy rate were observed. Greater prepartum dietary energy did result in greater birth BW of subsequent progeny. However, greater prepartum energy did not affect progeny pre- or post-weaning growth, health, or carcass characteristics.

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Tables

Table 3.1. Diet and nutrient composition of treatment and post-calving diets.

Item	Treatment[1, 2]		Post-calving[2, 3]
	REQ	HE[3]	
Ingredient, % DM			
Ground hay	93	--	--
Ground cornstalks	--	50	50
Dried distillers grains plus solubles	7	--	--
Corn bran[4]	--	50	--
Pelleted corn gluten feed[5]	--	--	50
Analyzed nutrient content, %DM			
DM	89.8	93.5	89.8
TDN[6]	61.8	70.3	65.3
CP	11.0	10.0	14.2
RDP, % CP[7]	81.9	72.4	72.0
RUP, % CP[7]	18.1	27.6	28.0
NDF	61.3	57.0	59.2
ADF	40.1	31.6	32.1
Fat	2.1	5.7	2.4

[1]REQ = limit-fed to provide 100% TDN requirement; HE = limit-fed to provide 125% TDN requirement

[2]Given ad libitum access to trace-mineral salt: Salt = 20.3%, Ca = 16.1%, P = 8.2%, Mg = 2.3% (magnesium oxide), K = 2.3% (potassium chloride), S = 0.2%, Co = 10 mg/kg (cobalt carbonate), I = 48 mg/kg (ethylenediamine dihydriodide), Cu = 1,498 mg/kg (copper sulfate), Fe = 8 mg/kg (ferrous sulfate), Mn = 2,017 mg/kg (manganous sulfate), Se = 30 mg/kg (sodium selenite), Zn = 3026 mg/kg (zinc oxide), vitamin A = 444.7 IU/kg, vitamin D_3 = 88.9 U/kg, vitamin E = 2,223.5 IU/kg

[3]Diet contained 0.14 kg/cow·day^{-1} ground limestone

[4]Dakota Bran (Dakota Gold Research Association, Sioux Falls, SD)

[5]Values for corn gluten feed from NRC (1996)

[6]Values for ground hay and ground cornstalks calculated from ADF, TDN value for dried distillers grains plus solubles and corn bran assumed to be 90%

[7]Values for corn bran provided by Dakota Gold Research Association, other values from NRC

Table 3.2. Dry matter, daily nutrient intake, and evaluation of treatment rations.

	Treatment[1,2]	
Item	REQ	HE
DMI, kg/d	11.1	12.2
TDN, kg/d	6.9	8.6
CP, g/d	1,237	1,220
RDP, g/d[3]	1,013	883
RUP, g/d[3]	224	337
Fat, g/d	237	699
Diet Evaluation[4]		
RDP Balance, g/d	40	-208
RDP, % Requirement	104	81
MP Balance, g/d	139	291
MP, % Requirement	121	143

[1]REQ = limit-fed to provide 100% TDN requirement; HE = limit-fed to provide 125% TDN requirement

[2]Average of BW blocks formulated to meet nutrient requirements of 636 kg and 727 kg cows with 9.1 kg peak milk production

[3]Calculated using NRC (1996) tabular values and values provided by Dakota Gold Research Association (Sioux Falls, SD) as a percentage of crude protein

[4]Diet evaluation using Level 1 of NRC model

Table 3.3. Diet and nutrient composition of common feedlot diet

Item	Inclusion, % DM
Ingredient, % DM	
Distillers grains plus solubles[1]	45
Corn[2]	30
Corn husklage	20
Supplement[3,4]	5
Analyzed nutrient content, % DM	
DM	55.2
CP	16.5
NDF	32.2
ADF	12.4
Fat	5.4
NE_g[5], kcal/kg	1.37

[1]Dried distillers grains plus solubles fed d 1 to 22 of finishing period, modified wet distillers grains plus solubles fed d 23 to 219 of finishing period

[2]Dry cracked corn fed d 1 to 33 of finishing period, high moisture corn fed d 34 to 219 of finishing period

[3] Supplement fed d 1 to 165 of finishing period contained: 64.5% Ground corn, 30.8% Limestone, 2.1% Trace Mineral Salt (85% salt, 0.03% Fe [ferrous sulfate], 0.03% Zn [zinc oxide], 5,710 mg/kg Mn [manganous oxide], 2,290 mg/kg Cu [copper sulfate], 100 mg/kg I [calcium iodate], 86 mg/kg Se [sodium selenite]), 0.3% Rumensin 90 (Monensin 198 g/kg; Elanco Animal Health, Greenfield, IN), 0.2% Vitamin premix (3,306.9 IU/kg vitamin A [retinyl acetate], 330.7 IU/kg vitamin D_3 [cholecalciferol], 44.1 IU/kg vitamin E [DL-α-tocopheryl acetate], 2,205 mg/kg vitamin K, 18 mg/kg vitamin B_{12}, 4,409 mg/kg riboflavin, 12,125 mg/kg D pantothenic acid, 16,535 mg/kg niacin, 143,189 mg/kg choline), 0.2% thiamine, 0.2% Tylan 40 (Tylosin 88 g/kg, Elanco Animal Health), 0.1% copper sulfate.

[4] Supplement fed d 166 to 219 of finishing period contained: 45.9% Ground corn, 50.0% Limestone, 2.0% Trace mineral salt (8.5% Ca [CaCO3], 5% Mg [MgO and MgSO4], 7.6% K [KCl2], 6.7% Cl [KCl2] 10% S [S8, prilled], 0.5% Cu [CuSO4 and Availa-4 (Zinpro Performance Minerals; Zinpro Corp, Eden Prairie, MN)], 2% Fe [FeSO4], 3% Mn [MnSO4 and Availa-4], 3% Zn [ZnSO4 and Availa-4], 278 mg/kg Co [Availa-4], 250 mg/kg I [Ca(IO3)2], 150 mg/kg Se [Na2SeO3], 2,205 KIU/kg VitA [retinyl acetate], 662.5 KIU/kg VitD [cholecalciferol], 22,047.5 IU/kg VitE [DL-α-tocopheryl acetate]), 0.34% Rumensin 90 (Monensin 198 g/kg; Elanco Animal Health), 0.22% Tylan 40 (Tylosin 88 g/kg, Elanco Animal Health).

[5]NE_g value back-calculated from animal performance using NRC (1996)

Table 3.4. Influence of prepartum dietary energy on cow BW, BCS, calving, milk production, and subsequent reproduction.

	Treatment[1]			
Item[2]	REQ	HE	SEM	*P*-value
BW, kg				
Initial	686	681	7	0.65
Post-calving	652	660	8	0.51
Breeding	655	684	10	0.03
Change initial to calving	-34	-22	5	0.07
Change initial to breeding	-31	3	6	< 0.01
BCS				
Initial	6.0	5.9	0.1	0.28
Post-calving	5.7	5.6	0.1	0.33
Breeding	5.8	5.8	0.1	0.37
Change initial to calving	-0.3	-0.3	0.1	0.80
Change initial to breeding	-0.2	-0.1	0.1	0.09
Calving				
Calving date, Julian d	48	47	2	0.78
Unassisted births, %	90	86	--	0.30
Milk production, kg				
65 ± 9 d	5.9	5.8	0.8	0.99
120 ± 9 d	6.0	6.8	0.5	0.27
Subsequent Reproduction[3]				
AI conception, %	41	52	--	0.34
Overall pregnancy, %	72	74	--	0.86

[1]REQ = limit-fed to provide 100% TDN requirement; HE = limit-fed to provide 125% TDN requirement

[2]Cow performance reported for 87 cows (REQ, n = 45; HE, n = 42) , 6 pens per treatment

[3]Subsequent reproduction reported for 82 cows (REQ, n = 44; HE, n = 38) , 6 pens per treatment

Table 3.5. Influence of prepartum dietary energy on calf pre-weaning and post-weaning performance and health.

	Treatment[1]			
Item	REQ	HE	SEM	*P*-value
Pre-weaning[2]				
BW, kg				
Birth	41	44	1	0.02
Weaning[3]	160	164	5	0.43
ADG	0.95	0.97	0.03	0.69
Weaning ultrasound measurements				
12th Rib Fat Thickness, cm	0.31	0.31	0.01	0.94
Marbling Score[4]	303	319	10	0.10
Morbidity, %[5]	0	7	--	0.27
Post-weaning[6]				
BW, kg				
Initial[7]	223	231	6	0.20
Final[8]	524	531	12	0.69
Days on feed	187	187	6	0.97
ADG, kg/d	1.61	1.61	0.04	0.80
DMI, kg/d	8.6	8.8	0.2	0.35
G:F	0.189	0.184	0.004	0.24
Morbidity, %[9]	37	36	--	0.93
Multiple Treatment, %[9,10]	1	8	--	0.51

[1]REQ = dams limit-fed to provide 100% TDN requirement; HE = dams limit-fed to provide 125% TDN requirement

[2]Pre-weaning performance reported for 86 calves (REQ, n = 45; HE, n = 41), 6 pens per treatment

[3]Weaning BW taken on 120 ± 9 d of age

[4]300-399 = Slight, 400-499 = Small, 500-599 = Modest, 600-699 = Moderate, 700-799 = Slightly Abundant

[5]Pre-weaning morbidity reported for 87 calves (REQ, n = 46; HE, n = 41), 6 pens per treatment

[6]Post-weaning performance reported for 85 calves (REQ, n = 45; HE, n = 40), 6 pens per treatment

[7]BW of feedlot progeny taken on 155 ± 9 d of age

[8]HCW/standard dressing percent (63%)

[9]Post-weaning health reported for 86 calves (REQ, n = 45; HE, n = 41), 6 pens per treatment

[10]Calves treated two or more times for bovine respiratory disease

Table 3.6. Influence of prepartum dietary energy on calf carcass characteristics.

	Treatment[1]			
Item[2]	REQ	HE	SEM	*P*-value
HCW, kg	330	333	8	0.69
12th-Rib Fat Thickness, cm	1.2	1.3	0.1	0.66
KPH, %	2.1	2.1	0.1	0.84
LM Area, cm^2	79.0	79.4	1.9	0.88
Yield Grade	3.1	3.2	0.1	0.60
Marbling Score[3]	446	446	19	0.97

[1]REQ = dams limit-fed to provide 100% TDN requirement; HE = dams limit-fed to provide 125% TDN requirement

[2]Carcass characteristics reported for 84 calves (REQ, n = 45; HE, n = 40), 6 pens per treatment

[3]300-399 = Slight, 400-499 = Small, 500-599 = Modest, 600-699 = Moderate, 700-799 = Slightly Abundant

CHAPTER 4

INFLUENCE OF PREPARTUM DIETARY PROTEIN INTAKE ON BEEF COW PERFORMANCE AND CALF GROWTH, CARCASS CHARACTERISTICS, AND PLASMA GLUCOSE AND INSULIN CONCENTRATIONS

Abstract

Two experiments were conducted to investigate the effects of prepartum dietary protein intake on cow performance as well as subsequent progeny growth, carcass characteristics, and plasma glucose and insulin concentrations. Treatments in both experiments were formulated to be isocaloric, and provide 100% (**REQ**) or 129% (**HP**) of CP requirement. Treatments were limit-fed 92 ± 10 or 78 ± 12 d prepartum to calving in Exp. 1 (64 total cows) or 2 (49 total cows), respectively. In both experiments, all cows were fed a common diet postpartum. Cow BW and BCS were recorded at initiation of treatments and within 48 h post-calving. In each experiment, progeny were fed a common post-weaning finishing diet. In Exp. 2, glucose and insulin concentrations were analyzed on a subset of progeny (12 per treatment) 90, 120, 150, 180, 210, and 240 min post-feeding, 2 d before slaughter. Treatment had no effect ($P \geq 0.14$) on cow BW, BCS, milk production, and subsequent reproduction or progeny pre-weaning growth in either experiment. In Exp. 1, post-weaning ADG, final BW, and HCW were decreased ($P \leq 0.01$) for progeny born to HP dams. In Exp. 2, progeny post-weaning growth was not affected ($P \geq 0.24$) by treatment; yet, 12th rib fat thickness, KPH, and YG were greater ($P \leq 0.04$) for progeny born to HP dams. Progeny born to HP dams had decreased ($P \leq 0.01$) glucose and insulin concentrations, and insulin to glucose ratios, indicating greater insulin sensitivity. Although

feeding cows 129% of CP requirement during late gestation did not affect cow performance, progeny post-weaning growth was decreased or carcass adiposity was increased by maternal treatment.

Key words: beef cow, fetal programming, gestational nutrition, prepartum, protein

Introduction

The increased use of corn coproducts in beef cow rations has led to greater opportunity of cow/calf producers overfeeding dietary protein because when rations are balanced to meet energy requirements, the high CP concentration of corn coproducts easily exceeds the relatively low CP requirements of beef cows. Feeding rations with high inclusion of corn coproducts results in acceptable performance of lactating cows (Shike et al., 2009; Braungardt et al., 2010). Shike et al. (2009) and Braungardt et al. (2010) fed rations that contained 76% and 63% dry distillers grains plus solubles (**DDGS**) and were 22.7% and 18.3% CP. In comparison, CP requirements of a 635 kg cow with 9.1 kg of peak milk production range from 6.0% to 10.3% throughout the cow/calf cycle (NRC, 1996). Protein supplementation to cows grazing low quality forage during late gestation has the potential to improve feedlot ADG and marbling scores of subsequent feedlot progeny (Stalker et al., 2006; Larson et al., 2009). The potential fetal programming effects of maternal dietary CP intake need to be further investigated in drylot cow rations which are common in upper Midwest beef production systems.

We hypothesized that increased prepartum dietary protein would improve cow BW and BCS, progeny growth, and marbling scores. We also hypothesized that greater maternal dietary protein would increase post-feeding glucose and insulin concentrations. Objectives were to

evaluate the effects of increased dietary CP during late gestation on cow performance as well as progeny growth, carcass characteristics, and glucose and insulin concentrations.

Materials and Methods

Experimental animals were managed according to the guidelines recommended in the Guide for the Care and Use of Agriculture Animals in Agriculture Research and Teaching (Federation of Animal Science Societies, 2010). All experimental procedures followed were approved by the University of Illinois Institutional Animal Care and Use Committee. Two experiments were conducted to evaluate the effects of increased dietary protein during late gestation on cow performance as well as subsequent progeny pre-weaning and post-weaning growth, carcass characteristics, and post-feeding plasma glucose and insulin concentrations. Cows were maintained at the Beef Cattle and Sheep Field Laboratory in Urbana, IL.

Exp. 1:

Animals, Experimental Design, and Treatments

Spring-calving, mature Angus, Simmental, and Simmental x Angus cows (n = 64; BW = 659 ± 83 kg; age = 4.2 ± 1.9 yr) and their progeny were used in a complete randomized design. Cows were stratified by BW and breed and allotted into pens (12 total pens, 6 pens total per treatment) with 5 or 6 cows per pen. Pens were randomly assigned to 1 of 2 treatments (Table 4.1): limit-fed oatlage and corn silage (**REQ**, n = 6 pens) or limit-fed oatlage, corn silage, and modified wet distillers grains plus solubles (**MDGS**; **HP**, n = 6 pens) 92 ± 10 d before expected calving date. The REQ and HP treatment rations were formulated to provide 100% or 129% of NRC (1996) CP requirement, respectively, and be isocaloric. Treatment rations were balanced for 635 kg cows with 9.1 kg milk at peak milk production. Using the table generator function of NRC (1996), treatment rations were balanced using TDN and CP. Dry matter intake of treatment

rations was increased each 30d of the prepartum feeding period to reflect changing nutrient requirements of cows during late gestation. Treatment rations were evaluated retrospectively with Level 1 of the NRC (1996) model using observed initial BW and BCS, milk production, and calf birth BW, and DMI of each treatment (Table 4.2). Rations were fed in concrete, fence-line bunks as a total mixed ration daily at 0900 h. Cows were provided trace mineral salt, free choice (Table 4.1). Cows remained on treatment rations until calving. Within 48 h after calving, cows were moved to new pens, comingled among treatment groups, and limit-fed a common diet formulated to meet or exceed NRC (1996) requirements. The common post-calving diet was 13% modified distillers grains plus solubles and 87% corn silage (Table 4.1).

Pre-calving and Pre-weaning Management of Cows and Calves

Cows were maintained in 10.36 m x 4.88 m pens with a partially slatted concrete floor with a solid concrete floor creep area that only calves had access to after calving. Both cow and calf areas were equipped with rubber matting. Empty cow BW was recorded and BCS was assigned at the start of the prepartum feeding period. To achieve a 1 d shrunk initial BW, cows were removed from feed and water for 18 h before weighing. Within 48 h after calving, cow BW was recorded and BCS assigned to evaluate cow performance at the end of the treatment period. Thus, post-calving cow BW reflects loss of fetus, placental membranes, and associated fluids. Cow BW, BCS, incidence of dystocia, and milk production were reported for 6 pens per treatment and included data from 43 cows and excluded those who lost calves (REQ, n = 3; HP, n = 1), twinned (REQ, n = 2; HP, n = 0), failed to calve (REQ, n = 2; HP, n = 1), had a uterine prolapse (REQ, n = 0; HP, n = 1), had injured calves before breeding (REQ, n = 1; HP, n = 2), died (REQ, n = 1; HP, n = 2) before weaning their calf, or had heifer or bull calves retained in the breeding herd (REQ, n = 1; HP, n = 4). Incidence of calf loss during parturition was not

related to treatment (P = 0.65). Milk production was estimated via the weigh-suckle-weigh technique (Boggs et al., 1980) at 49 ± 8 d and 112 ± 8 d postpartum. Subsequent reproduction was reported for 6 pens per treatment and included data from 40 cows and excluded 1 HP cow that was culled and 2 REQ cows that died post-weaning and pre-breeding. At rebreeding (49 ± 8 d postpartum), cows were synchronized using a CoSynch + CIDR protocol (Bremer et al., 2004) and were artificially inseminated as a single group. Cow BW was recorded and BCS assigned at time of AI to evaluate lasting effects of treatments. After AI, all cows went to pasture and were exposed to clean-up bulls for 3 subsequent estrous cycles. Conception rates for AI were determined via transrectal ultrasonography at 67 d after insemination. Overall pregnancy rates were determined via transrectal ultrasonography at 123 d after insemination. Cow BW was recorded and BCS assigned at time of 2nd pregnancy check, 172 ± 8 d postpartum. During spring and summer, cow/calf pairs were rotationally grazed through mixed pastures of predominantly bromegrass (*Bromus inermis*) with white clover (*Trifolium repens*) and orchardgrass (*Dactylis glomerata L.*)

Calf BW was recorded within 48 h after birth and at time of early weaning (112 ± 8 d of age) to measure pre-weaning calf ADG. At time of weaning, 12th rib fat thickness (**backfat**) and marbling score were estimated for all calves via compositional ultrasound. Ultrasound measurements were taken with an Aloka 500SV (Wallingford, CT) B-110 mode instrument equipped with a 3.5-MHz general purpose transducer array. Backfat measurements were taken in a transverse orientation between the 12th and 13th ribs approximately 10 cm distal from the midline. Ultrasound images were processed utilizing CPEC ultrasound imaging software (Cattle Performance Enhancement Company LLC., Oakley, KS). Pre-weaning calf performance was reported for 6 pens per treatment and included data from for all steer and non-replacement heifer

calves (n = 43; REQ: n = 22; 11 steers, 11 heifers; HP: n = 21; 9 steers, 12 heifers) weaned by cows placed on treatments, minus twins and those injured or deceased before weaning. Incidence of pre-weaning morbidity treatment was recorded by animal care personnel.

Post-weaning Management

Steer and non-replacement heifer calves were housed in feedlot pens (4.88 m × 4.88 m pens, 8 calves per pen) with concrete slatted-floors covered by rubber matting at the Beef Cattle and Sheep Field Laboratory, Urbana, IL for the duration of the finishing period. Calves were vaccinated with the following: Bovishield Gold FP5 L5 HB (Zoetis, Florham Park, NJ), One Shot Ultra 7 (Zoetis), and Pulmo-Guard MpB (AgriLabs, St Joseph, MO). Calves were dewormed with Eprinex (Merial, Duluth, GA) pour-on and tagged with an electronic identification tag (Allflex USA, DFW Airport, TX). Calves were adapted to a common, finishing diet (Table 4.3) fed for ad libitum intake over a transition period of 18 d. During the finishing period, calves were split by sex with maternal treatments comingled. Calves were implanted with Component EC (10 mg estradiol benzoate, 100 mg progesterone, 29 mg tylosin 99 tartate; Elanco Animal Health, Greenfield, IN) 5 d post-weaning and received a Compudose 200 implant (25.7 mg estradiol; Elanco Animal Health) 110 d post-weaning.

Because transition to a common finishing diet began immediately after weaning, initial BW for measurement of progeny feedlot performance was the BW recorded at weaning. Individual feed intake was monitored using the GrowSafe automated feeding system (Model 4000E, GrowSafe Systems Ltd., Airdrie, Alberta, Canada) during the finishing period. Incidence of morbidity treatment during the finishing phase was recorded by animal care staff. Final BW was calculated from HCW using a standard dressing percentage of 63%. Post-weaning performance was excluded for 1 calf from a cow fed REQ due to mortality.

Beginning on d 220 of the finishing period, backfat was estimated via ultrasound to determine slaughter date. Cattle were selected for slaughter at a commercial facility once it was estimated that final backfat would equal 1.2 cm, in such a way that cattle were shipped in 2 groups. Trained personnel recorded slaughter order and HCW was recorded on day of slaughter. Backfat, % KPH, LM area, yield grade, and marbling score were recorded after a 24 h carcass chill with Video Image Analysis as part of the USDA camera system.

Feed Sampling and Analysis

Individual ingredients used in treatment were procured before initiation of experiment and stored under roof or covered in a bunker silo. Ingredients were sampled after receipt and analyzed for CP, NDF, ADF, fat, Ca, and P with TDN calculated from ADF by Rock River Laboratory, Inc. (Watertown, WI). Crude protein, ADF, and fat were analyzed using AOAC (1990) methods 990.03, 973.18, and 920.39, respectively. The method described by Goering and Van Soest (1970) was used for analysis of NDF. Minerals were extracted by acid digestion and analyzed using an Optima 3000 Inductively Coupled Plasma-Optical Emission Spectrometer (Perkin Elmer, Waltham, MA). Calculations for TDN value of hay and cornstalks were based on ADF. The tabular value of 88% TDN listed in NRC (1996) for DDGS was used for DDGS when formulating treatments. Using this analysis, treatment rations were formulated before initiation of study.

Samples of wet corn gluten feed (**CGF**) and corn husklage fed in the common finishing diet were analyzed by Rock River Laboratory, Inc. for CP, NDF, ADF, and fat using the methods described above. For high moisture corn and ground corn, CP, NDF, ADF, and fat values listed in NRC (1996) were used. Reported NE_g of the finishing diet was back-calculated from observed animal performance using equations from NRC (1996).

Statistical Analysis

Pen was considered the experimental unit for all response variables. Data concerning cow BW and BCS, calving date, milk production, progeny pre- and post-weaning performance, and carcass characteristics were analyzed using the MIXED procedure of SAS (SAS Inst. Inc., Cary, NC). Data concerning percentage of unassisted births, subsequent reproduction, and incidence of progeny morbidity were analyzed using the GLIMMIX procedure of SAS. Because of low incidence of morbidity, raw treatment averages are reported. The least square means function of SAS was used to separate treatment means. The statistical model included gestational treatment as a fixed effect and treatment pen as a random effect. Calf sex and sire were used as fixed effects for the analysis of calving information, pre-weaning and post-weaning calf performance, and carcass characteristics. Treatment effects were considered significant at $P \leq 0.05$ and trends at $0.05 < P \leq 0.10$.

Exp. 2:

Animals, Experimental Design, and Treatments

Spring-calving, mature Angus, Simmental, and Simmental x Angus cows (n = 49; BW = 657 ± 70 kg; age = 4.1 ± 1.8 yr) and their progeny were used in a complete randomized design. Cows were stratified by BW and breed and allotted into pens (10 total pens, 5 pens total per treatment) with 4 or 6 cows per pen. Pens were randomly assigned to 1 of 2 treatments (Table 4.1) that were similar to those of Exp. 1, but with greater inclusion of MDGS due to lower CP of oatlage used in Exp. 2. (REQ, n = 5 pens; HP, n = 5 pens). Treatments began 78 ± 12 d prepartum and continued until calving. Post-calving nutritional management of cows was as in Exp. 1. Treatments were evaluated retrospectively using Level 1 of the NRC (1996) model (Table 4.2).

Pre-calving and Pre-weaning Management of Cows and Calves

Cows and calves were maintained in slatted-floor confinement barns as described in Exp. 1. Collection of cow BW, BCS, and incidence of dystocia was as described for Exp. 1 and reported for 5 pens per treatment and included data from 42 cows and excluded those who lost calves (REQ, n = 2; HP, n = 2), failed to calve (REQ, n = 0; HP, n = 1), had injured calves before breeding (REQ, n = 0; HP, n = 1), or had a heifer calf retained in the breeding herd (REQ, n = 1; HP, n = 0). Incidence of calf loss during parturition was not related to treatment (P = 0.34). Milk production was estimated via the weigh-suckle-weigh technique (Boggs et al., 1980) at 69 ± 11 d postpartum. Subsequent reproduction was reported for 5 pens per treatment and included data from 31 cows and excluded 18 cows that were culled (REQ, n = 9; HP, n = 9) before breeding. Cows were synchronized, artificially inseminated 53 ± 11 d postpartum, BW was recorded, and BCS assigned as described in Exp. 1. Conception rates for AI were determined via transrectal ultrasonography at 46 d after insemination. Overall pregnancy rates were determined via transrectal ultrasonography at 88 d after insemination. During spring and summer, cow/calf pairs were grazed on the same pastures as in Exp. 1. Cow BW was recorded and BCS assigned during late summer, 155 ± 11 d postpartum.

Calf BW was recorded within 48 h after birth and at time of early weaning (121 ± 11 d of age) to measure pre-weaning calf ADG. At time of weaning, backfat and marbling score were estimated via compositional ultrasound as in Exp. 2. Pre-weaning calf performance was reported for 5 pens per treatment and included data from all steer and non-replacement heifer calves (n = 42; REQ: n = 22; 12 steers, 10 heifers; HP: n = 20; 8 steers, 12 heifers) weaned by cows placed on treatments, minus twins and those injured or deceased before weaning. Incidence of pre-weaning morbidity treatment was recorded by animal care personnel.

Post-weaning Management

Steer and non-replacement heifer calves were housed in the same feedlot barns and vaccinated using the same protocol as in Exp. 1. Calves were adapted to a common, finishing diet (Table 4.3) fed for ad libitum intake over a transition period of 28 d with post-weaning management as described in Exp. 1. Calves were implanted with Component EC (10 mg estradiol benzoate, 100 mg progesterone, 29 mg tylosin 99 tartate; Elanco Animal Health) 4 d post-weaning and received a Compudose 200 implant (25.7 mg estradiol; Elanco Animal Health) 160 d post-weaning. Post-weaning performance was excluded for 2 calves born to dams fed HP due to mortality.

Beginning on d 160 of the finishing period, ultrasound backfat measurements were collected at the 12th rib as in Exp. 1 to determine time of slaughter. Cattle were slaughtered as a single group at a commercial facility once it was estimated that average final backfat would equal 1.4 cm. Collection of carcass characteristics was as in Exp. 1.

Blood Sampling and Analysis

Post-feeding plasma glucose and insulin concentrations were analyzed for a subset of calves (n = 24; REQ: n = 12; 6 steers, 6 heifers; HP: n = 12; 6 steers, 6 heifers; 5 pens per treatment) 2 d before slaughter (190 d post-weaning). Cattle were prevented accesses to feed for 17 h. After the 17 h fast, cattle were allowed access to feed in concrete bunks for 45 min. Blood was collected from the jugular vein using 10 mL EDTA coated vacutainer tubes at 90, 120, 150, 180, 210, and 240 min post-feeding. Blood tubes were stored in ice water for not more than 30 min and centrifuged at 4,415 × g for 10 min at 4°C (Sorvall Legend XFR, Thermo Scientific, Waltham, MA). Plasma was aliquoted into two 1.5 mL microcentrifuge tubes and stored at -80°C for subsequent analysis of glucose and insulin concentrations.

Plasma glucose and insulin samples were run using previously validated procedures of Long and Schafer (2013). Glucose concentrations were analyzed colorimetrically in triplicate (Liquid Glucose Hexokinase Reagent, Pointe Scientific Inc., Canton, MI). Mean glucose intra- and interassay CV were 2.1% and 2.3%, respectively. Insulin concentrations were analyzed via previously validated RIA (Long and Schafer, 2013; Siemens Medical Solutions Diagnostics, Los Angeles, CA). Insulin samples were analyzed in 1 single assay with an intra-assay CV were 8.7%.

Feed Sampling and Analysis

Individual ingredient analysis, and ration formulation were conducted as described in Exp. 1. A value of 90% TDN for MDGS was used when formulating treatments in acknowledgement that calculations for TDN based on ADF concentration and the tabular value of 88% found in NRC (1996) underestimate the energy value of corn coproducts. All feed ingredients used in the common finishing diet were procured from single sources and were analyzed by Rock River Laboratory, Inc. using methods described in Exp. 1. Reported NE_g of the finishing diet was back-calculated from observed animal performance using equations from NRC (1996).

Statistical Analysis

Statistical analysis for measures of cow performance and calf pre-weaning and post-weaning growth, and carcass characteristics was conducted as described for Exp. 1. Glucose and insulin concentrations and insulin to glucose ratio were analyzed using the MIXED procedure of SAS. The statistical model included gestational treatment, time of bleed, calf sex, calf sire, and the interaction between gestational treatment and time of bleed as fixed effects. Repeated measures were used for individual calf with a heterogeneous Toeplitz covariance structure used.

This covariance structure yielded the most desirable combination of fit statistics of covariance structures tested (compound symmetry, heterogeneous compound symmetry, unstructured, autoregressive (1), heterogeneous autoregressive (1), Toeplitz, heterogeneous Toeplitz, and variance components). Treatment pen and glucose or insulin run were included as random effects for analysis of glucose concentration. Treatment effects were considered significant at $P \leq 0.05$ and trends at $0.05 < P \leq 0.10$.

Results and Discussion

Exp. 1

Cow Performance

Data concerning cow BW, BCS, calving information, milk production, and subsequent milk production are found in Table 4.4. Initial BW and BCS were not different ($P \geq 0.92$) across treatment. Post-calving BW and BCS were also not different ($P \geq 0.14$). Yet, cows fed HP were numerically 37 kg heavier following calving relative to cows fed REQ. Body weight at breeding was not statistically different ($P = 0.22$); however, cows fed HP remained 29 kg heavier than cows fed REQ. There were no differences ($P \geq 0.43$) in BCS at time of breeding or in BW or BCS during late summer.

Data concerning the effects of elevated prepartum dietary protein intake of drylot diets on BW and BCS are conflicting. Gunn et al. (2014) observed no differences in BW of heifers that were fed late-gestation rations containing corn silage or 43% DDGS and 54% cornstalks that were formulated to be isocaloric and meet or greatly exceed NRC (2000) CP requirement, respectively. Heifers fed to exceed CP requirements also had lower BCS relative to control-fed heifers throughout the experiment conducted by Gunn et al. (2014). In contrast to the experiment

conducted by Gunn et al. (2014), Radunz et al. (2010) observed greater cow BW when cows were limit-fed a ration that contained DDGS as an energy source relative to cows limit-fed rations that contained corn or hay as energy sources. All 3 treatments fed by Radunz et al. (2010) were formulated to be isocaloric, but were not isonitrogenous; thus, the DDGS treatment contained considerably greater dietary CP (20.5% for DDGS, 11.4% for corn, and 8.2% CP for hay treatments).

Numerical differences in cow post-calving and breeding BW may be explained by the 23% greater fat intake by cows fed HP relative to those fed REQ (379 g/d for HP and 308 g/d for REQ). BW differences between treatments may also be attributed to the energy value for MDGS when formulating treatments. The tabular TDN value of 88% provided by NRC (1996), which provides the same TDN value for corn, was used for formulation of treatments. The energy value of distillers grains plus solubles has been demonstrated to be greater than the energy value of corn (Klopfenstein et al., 2008; Loy et al., 2008). In addition to greater dietary CP intake for cows fed HP relative to those fed REQ (Table 4.2), cows fed HP consumed a greater percentage of dietary CP as RUP. Hunter and Magner (1988) observed greater BW gain when lactating cows were fed high RUP supplements. Hunter and Magner (1988) hypothesized that increased BW gain was caused by increased insulin response to greater postruminal AA supply. It may be possible that gestating cows consuming more CP as RUP have improved BW relative to cows provided more CP as RDP. However, differences in ruminal protein degradability of treatments may be partially negated because treatment rations were limit-fed. Scholljegerdes et al. (2005) demonstrated that ruminal degradation of supplemental protein increases with increasing degree of forage restriction.

Treatment did not affect ($P \geq 0.57$) progeny birth BW, percentage of unassisted births, or calving date (Table 4.5). This finding contrasts previous experiments that have evaluated differences in dietary energy source (Loerch, 1996; Radunz et al., 2010) or greater CP intake (Gunn et al., 2014) during late gestation. Loerch (1996) and Radunz et al. (2010) observed greater calf birth BW when limit-fed late gestation rations that used either corn or DDGS as energy sources were compared to their hay-fed counterparts. Neither Loerch (1996) nor Radunz et al. (2010) observed differences in dystocia when comparing late gestation ration types. Gunn et al. (2014) not only observed greater progeny birth BW when heifers were fed excessive CP during late gestation, but also observed an increase in dystocia with excessive CP intake. Increased incidence of dystocia observed by Gunn et al. (2014) coincides with increased gestation length by 2.5 d when heifers were fed excessive CP during late gestation. In agreement with the current experiment, no difference in gestation length was observed by Radunz et al. (2010). The differences in dystocia may be partly attributed to the fact that the current experiment and the experiments conducted by Loerch (1996) and Radunz et al. (2010) used mature cows and the experiment conducted by Gunn et al. (2014) used gestating heifers.

Prepartum treatment did not affect ($P \geq 0.36$) AI conception or overall pregnancy rate. No differences in subsequent reproduction were observed by Radunz et al. (2010) between cows fed DDGS and cows fed corn or hay rations that contained lower dietary CP intake. Greater follicular growth and a decreased anestrous period was observed by Gunn et al. (2014) for heifers fed to exceed CP requirement; however, AI conception or overall pregnancy rate was not different. It should be noted that differences in reproductive function in the experiment conducted by Gunn et al. (2014) cannot be completely linked to excessive prepartum dietary CP because heifers remained on treatments through 114 d postpartum. There is evidence that

subsequent reproduction is not improved when BCS at time of calving of 5 or greater is achieved (Richards et al., 1986; Spitzer et al., 1995). This theory is supported by research that BCS is a gauge of long-term energy reserves (Wagner et al., 1988). In the current experiment, average BCS of both treatments remained greater than 5 from initiation of treatments through late summer. It is acknowledged that with subsequent reproduction only being reported for 6 pens per treatment (39 cows total), more pens and experimental animals would be needed to detect significant differences.

Milk production was not different ($P \geq 0.16$) across treatment, whether measured on 49 ± 8 or 112 ± 8 d postpartum. Because treatments were only applied prepartum and ceased at calving, it was expected that greater prepartum dietary CP intake would have no effect on milk production. In agreement with the current experiment, Radunz et al. (2010) observed no differences in milk production when dams were fed prepartum rations that provided different CP intake.

Progeny Performance

Data concerning progeny pre- and post-weaning performance are found in Table 4.5. Prepartum dietary protein intake had no effect ($P \geq 0.70$) on weaning BW or progeny post-weaning ADG. When measured at time of weaning, backfat or ultrasound marbling scores were not different ($P \geq 0.18$) by treatment. No differences in progeny pre-weaning growth in the current experiment are in contrast with the findings of Gunn et al. (2014), who found that progeny born to dams fed excessive CP prepartum were heavier at weaning with a trend for greater ADG relative to progeny of control-fed dams. Progeny pre-weaning growth and BW differences in the experiment conducted by Gunn et al. (2014) may be explained by greater birth BW of calves born to dams fed excessive CP and the fact the heifers were maintained on

treatments during lactation; however, no differences in milk production or energy corrected milk production were observed. No differences in progeny weaning BW or backfat were observed by Radunz et al. (2012) when dams were fed isocaloric, but not isonitrogenous, rations with either DDGS or hay as energy sources during late gestation.

Crude protein supplementation to cows grazing low quality forages (dormant native range or cornstalks) during late gestation has proven to influence performance of subsequent progeny (Stalker et al., 2006; Larson et al., 2009). Both Stalker et al. (2006) and Larson et al. (2009) observed greater calf weaning BW when dams were provided CP supplementation during late gestation relative to unsupplemented dams. However, direct comparison of experiments that investigated the fetal programming effects of supplemental CP intake of grazing cows to experiments that evaluated beef cow drylot rations can be misleading. Cows grazing low quality forages are often protein deficient when not provided supplemental protein. Supplemental protein then serves to increase forage intake and digestibility, improving energy status (Olson et al., 1999). Cattlemen have greater nutritional control of cows maintained in drylots and the ability to formulate complete rations to meet or exceed both energy and protein requirements of gestating cows. Thus, providing supplemental CP to grazing cows may only meet or slightly exceed protein requirements and drylot rations with high CP concentrations may greatly exceed cow protein requirements if DMI is not controlled.

Feedlot ADG was decreased ($P < 0.01$) for progeny born to dams fed HP relative to progeny born to REQ fed dams. There were no treatment differences ($P = 0.98$) for days on feed (**DOF**). Despite no differences in calf weaning BW, final BW of calves born to dams fed HP was decreased ($P = 0.01$) relative to calves born to dams fed REQ. Feedlot DMI was not different ($P \geq 0.69$) by treatment. Feedlot G:F was not statistically significant ($P = 0.13$); however, it should

be noted that G:F of calves born to HP dams was numerically lower than that of calves born to dams fed REQ (0.167 for HP and 0.182 for REQ). In the experiment conducted by Radunz et al. (2012), maternal nutrition had no effect on progeny final BW, feedlot ADG, DMI, or G:F; but, a trend for fewer DOF was observed for calves born to dams fed DDGS relative to progeny born to dams fed hay. In the current experiment, no differences in DOF were observed because treatments were equally represented in each slaughter group that were sent 28 d apart. Larson et al. (2009) observed trends for steer progeny born to CP supplemented dams to have greater final BW, feedlot ADG and DMI. In contrast, Stalker et al. (2006) observed no differences in progeny feedlot ADG or DMI whether dams were provided supplemental CP or unsupplemented. As previously mentioned, supplemental CP to grazing cows may not illicit similar effects on cow nutritional status, and resulting progeny, as when drylot-fed cows are provided excess dietary CP. Under the conditions of our experiment, feeding cows rations that provided 129% of CP requirement decreased growth potential and gain efficiency of progeny when fed a high-energy feedlot diet.

There were no differences ($P \geq 0.25$) in either pre- or post-weaning progeny morbidity. It is acknowledged that statistical power in this experiment is insufficient to detect statistical differences in binomial data, such as percentage of progeny receiving morbidity treatment. There is evidence that maternal nutrition during gestation has the potential to affect health of subsequent progeny. Larson et al. (2009) observed no difference in percentage of progeny treated for morbidity from birth to weaning; yet, steers born to CP supplemented dams required less treatment for morbidity from weaning to slaughter. Stalker et al. (2006) observed greater percentage of calf crop weaned when dams were supplemented with CP during late gestation; however, this was not linked to differences in passive immunity as no differences in IgG transfer

were detected. In agreements with the current experiment, Radunz et al. (2012) observed no differences in progeny health from birth to slaughter.

Progeny Carcass Characteristics

Data concerning progeny carcass characteristics are found in Table 4.6. Treatments resulted in reduced ($P = 0.01$) HCW of progeny when dams were fed HP during late gestation relative to those born to REQ dams. There were no differences ($P \geq 0.12$) in carcass backfat, KPH, LM area, YG, or marbling score. Reduced final BW of calves born to dams fed HP is a direct reflection of reduced HCW because final BW was calculated from HCW using a standard dressing percentage of 63%. No differences in backfat were expected because cattle were selected for slaughter once it was estimated that backfat would equal 1.2 cm. It is of note that marbling scores were numerically greater for calves born to dams fed HP relative to those fed REQ (589 for HP and 542 for REQ). A 47 point difference in marbling score approaches a one half difference in USDA grade, which is of biological significance. However any increase in marbling score is offset by the 28 kg reduction in HCW for progeny born to HP dams. No differences in HCW, backfat, LM area, KPH, yield grade, or marbling score were observed by Radunz et al. (2012), whether dams of progeny were fed DDGS or hay during late gestation. Stalker et al. (2006) observed no effect of dam supplementation on carcass characteristics of steer progeny. Larson et al. (2009) observed a trend for greater HCW and greater marbling scores when dams were offered CP supplement. It was posed by Larson et al. (2009) that marbling differences may be an indirect effect of improved feedlot health of steer progeny born to dams offered prepartum CP supplement.

Exp. 2

Cow Performance

Data concerning cow BW, BCS, calving information, milk production, and subsequent milk production are found in Table 4.7. Initial cow BW and BCS were not different ($P \geq 0.51$). Prepartum dietary protein intake had no effect ($P \geq 0.96$) on either post-calving cow BW or BCS. Treatment also had no effect ($P \geq 0.53$) on BW or BCS at time of breeding or late summer. In contrast to Exp. 1, numerical differences in cow post-calving BW were not observed. The results of Exp. 2 agree with the findings of Gunn et al. (2014), in which no differences in BW were observed when heifers were fed excessive dietary CP during late gestation. Lower numerical differences in cow BW in Exp. 2 may be the result of the greater TDN value used for MDGS when formulating treatment rations. As in Exp. 1, dietary protein intake did not affect ($P \geq 0.30$) calf birth BW (Table 4.8), percentage of unassisted births, or calving date. When measured on 69 ± 11 d postpartum, milk production was not different ($P = 0.86$) across treatment. As previously mentioned, the observation of no increase in progeny birth BW when dams were fed to exceed CP requirement is in contrast to previous research (Radunz et al., 2010; Gunn et al., 2014).

There were no differences ($P \geq 0.15$) in either AI conception or overall pregnancy rates. It should be noted that there was a numerical difference for AI conception with cows fed HP having a 28% lower conception rate. This in contrast to Exp. 1, in which, no statistical or notable numerical difference in AI conception were observed. It has been determined that excessive dietary protein intake, indicated by BUN, negatively affects uterine environment and decreases fertility (Butler, 1998). However, reduction in fertility when distillers grains are included in cow rations at moderate levels has not been documented (Gunn et al., 2014). As previously stated,

both Exp. 1 and 2 would require greater number of experimental animals to detect differences in subsequent reproduction.

Progeny Performance

Data concerning progeny pre- and post-weaning performance are found in Table 4.8. As with Exp. 1, prepartum dietary protein did not affect progeny pre-weaning performance or compositional ultrasound measurements. There were no differences ($P \geq 0.58$) in calf weaning BW or pre-weaning ADG. At time of weaning, there were no differences ($P \geq 0.23$) in backfat or ultrasound marbling score. The observation that prepartum CP intake had no effect on pre-weaning performance is in agreement with Radunz et al. (2012). As previously mentioned, increased weaning BW when dams were supplemented CP during late gestation (Stalker et al., 2006; Larson et al., 2009). However, many comparisons between range cow supplementation experiments to drylot feeding experiments are confounded by production system.

In contrast to Exp. 1, progeny feedlot ADG and final BW were not affected ($P \geq 0.33$) by prepartum protein intake. Feedlot DMI nor G:F were different ($P \geq 0.24$) across treatment. Neither pre- nor post-weaning morbidity were affected ($P \geq 0.49$) by maternal nutrition. As in Exp. 2, Radunz et al. (2012) observed no effects of maternal nutrition on progeny final BW, feedlot ADG, DMI, of G:F when dams were fed rations that provided the exceeded CP requirement. Differences in post-weaning performance in Exp. 1 and 2 may be attributed to greater NE_g of the common feedlot diet and lower final BW of calves in Exp. 2. In Exp. 2, cattle, regardless of treatment, consumed a higher energy feedlot diet, experienced greater post-weaning ADG, and finished at lower final BW. In comparison, cattle in Exp. 1 had lower feedlot ADG and spent more DOF (269 d in Exp. 1 and 191 d in Exp. 2); thus programmed differences in gain potential may have had longer to manifest.

Progeny Carcass Characteristics

Data concerning progeny carcass characteristics are found in Table 4.9. There were no differences ($P \geq 0.33$) in HCW, LM area or marbling score by maternal treatment. Feeding cows HP during late gestation did result in greater ($P < 0.01$) carcass backfat, and greater ($P = 0.04$) KPH of progeny relative to progeny born to cows fed REQ. Greater backfat and KPH also resulted in greater ($P = 0.01$) YG for calves born to dams fed HP. These finding indicate that greater prepartum dietary protein intake increased carcass adiposity with little corresponding increase in HCW (10 kg, $P = 0.33$) and no difference in LM area ($P = 0.78$); resulting in greater YG. In Exp. 1, cattle were selected for slaughter on backfat was estimated to equal 1.2 cm, with cattle being slaughtered in 2 groups. In Exp. 2, cattle were slaughtered a single group once it was estimated that backfat was equal to 1.4 cm. Differences in endpoint determination may have contributed to differences in carcass back fat between to two experiments. Progeny born to REQ-fed dams may have had decreased potential for lean gain and had greater opportunity to deposit backfat in Exp. 2 relative to Exp. 1. While the results of Exp. 1 and 2 are contrasting, feeding cows 129% of protein requirement during late gestation detrimentally affected progeny carcass characteristics. These results are in contrast to the work of Radunz et al. (2012) who observed no differences in progeny carcass characteristics when dams were fed to meet or exceed CP requirement. Larson et al. (2009) also observed no differences in progeny carcass characteristics when dams were provided supplemental CP during late gestation.

Progeny Glucose and Insulin Concentrations

Data concerning progeny post-feeding glucose concentration, insulin concentration, and glucose to insulin ratio are found in Figure 4.1. Calves born to dams fed REQ had greater ($P < 0.01$) post-feeding plasma glucose concentrations relative to calves born to dams fed HP. There

was a trend ($P = 0.09$) for an interaction between treatment and time of bleed for plasma glucose concentration; however, the fixed effect of time of bleed was not significant ($P = 0.48$). The effects of treatment and time of bleed were significant ($P \leq 0.01$) for post-feeding plasma insulin concentrations. There was an interaction ($P = 0.03$) between treatment and time of bleed for plasma insulin concentrations; with calves born to REQ fed dams having greater insulin concentrations at 120, 150, 180, and 210 min post-feeding. For insulin to glucose ratio, the effects of treatment and time of bleed were significant ($P \leq 0.01$); with calves born to REQ fed dams having greater insulin to glucose ratios and the ratios for both treatments decreasing over time. There was no interaction ($P = 0.25$) between prepartum protein intake and time of bleed for insulin to glucose ratio. Fixed effects of calf sex and sire were not significant ($P \geq 0.20$) for plasma glucose or insulin concentrations and insulin to glucose ratios. The combination of progeny born to REQ fed dams having greater post-feeding glucose and insulin concentrations when measured 2 d before slaughter indicate greater hyperglycemia and insulin resistance relative to progeny born to HP fed dams. Greater insulin to glucose ratio for calves born to dams fed REQ confirms that more units of insulin were secreted to facilitate glucose uptake. These findings are counter to our hypothesis of greater glucose and insulin concentrations for calves born to dams fed HP. It is acknowledged that our methods did not include a measurement of fasted, baseline glucose or insulin concentrations. This does limit inference space regarding plasma glucose and insulin concentrations to only 90 to 210 min post-feeding, but it is clear that prepartum dietary protein intake did affect glucose and insulin concentrations from 90 to 210 min post-feeding.

Previous research concerning the effects of prepartum dietary protein intake on plasma glucose and insulin concentration is limited. During glucose tolerance tests, Radunz et al. (2012)

observed greater initial insulin response with no subsequent increase in glucose clearance rate in progeny born to dams fed DDGS during late gestation relative to progeny born to hay-fed dams. The findings of Radunz et al. (2012) infer that progeny born to dams fed DDGS, with greater prepartum protein intake, were more insulin resistant during the finishing period. In the current experiment, initial insulin response was not measured, but the results of the current experiment appear to contrast with those of Radunz et al. (2012) as progeny born to HP dams were more insulin sensitive 90 to 210 min post-feeding. Much of the work evaluating the fetal programming effects of maternal nutrition on subsequent progeny has investigated maternal nutrient restriction or maternal obesity. Research conducted in sheep has shown that both maternal nutrient restriction during early to mid-gestation or maternal obesity results in greater insulin resistance in progeny when compared to progeny born to control-fed dams (Ford et al., 2007; Long et al., 2010b). In an experiment conducted by Long et al. (2010c), initial insulin response and glucose clearance after glucose bolus infusion was greater for progeny born to dams restricted to 55% of NRC (1996) requirements 32 to 115 d of gestation when compared to progeny born to dams fed 100% of NRC (1996) requirements. It is interesting that the glucose and insulin results of the current experiment have some similarities to a nutrient restriction model. It may be that in the current experiment, post-feeding initial insulin response was greater in calves born to dams fed HP, glucose clearance was greater, and plasma glucose concentrations were lower in progeny of HP dams by 90 min post-feeding. This theory is supported by the finding of Long et al. (2010a) that expression of GLUT4, the primary insulin-dependent intracellular glucose transporter, tended to be greater in skeletal muscle of progeny born to nutrient restricted dams relative to dams fed to requirement. Greater GLUT4 expression could facilitate greater glucose uptake in response to circulating insulin.

Implications

Providing 129% of crude protein requirements during late gestation did not affect cow BW, BCS, calf birth BW, milk production, or subsequent reproduction. Feeding cows 129% of crude protein requirements during late gestation had no effect on progeny pre-weaning growth. Excessive prepartum dietary protein has the potential to negatively impact progeny post-weaning ADG and HCW or increase carcass backfat and yield grade. Greater prepartum dietary protein did affect post-feeding plasma glucose and insulin concentrations and insulin to glucose ratios. These data indicate that when cow/calf producers formulate drylot beef cow rations, greatly exceeding cow protein requirements can have unforeseen consequences on the performance of subsequent progeny. However, greater number of experiments investigating the fetal programming effects of maternal dietary protein intake on subsequent progeny is warranted to confirm the findings of our experiments.

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Tables and Figures

Table 4.1. Diet and nutrient composition of treatment and post-calving diets.

	Exp. 1[1,2]		Exp. 2[1,2]		Post-calving[2]	
Item	REQ	HP	REQ	HP[3]	Exp. 1	Exp. 2
Ingredient, % DM						
Oatlage	67	54	54	41	--	--
Corn silage	33	26	27	20	87	87
Modified distillers grains plus solubles	--	20	19	39	13	13
Analyzed nutrient content, %DM						
DM	29.6	33.4	35.0	38.3	33.9	47.7
TDN[4]	61.7	67.0	66.1	72.0	71.8	75.6
CP	9.3	13.0	9.9	13.8	9.3	8.9
RDP, % CP[5]	82.4	71.3	71.9	60.8	70.5	70.5
RUP, % CP[5]	17.6	28.7	28.1	39.2	29.5	29.5
NDF	54.8	52.6	54.5	51.9	42.5	34.4
ADF	36.5	32.6	34.2	30.0	24.9	18.8
Fat	2.9	3.9	3.3	4.4	3.5	3.0

[1]REQ = limit-fed to provide 100% CP requirement; HP = limit-fed to provide 129% CP requirement

[2]Given ad libitum access to trace-mineral salt: 69.8% Salt, 4.6% Ca (Ca_2PO_4 and $CaCO_3$), 2.58% P (dicalcium phosphate), 0.2% Mg (MgO), 0.02% K (Ca_2PO_4 and $CaCO_3$), 0.3% S (Ca_2PO_4 and $CaCO_3$), 1.34 % Fe ($FeSO_4$), 1.1% Zn (ZnO), 1.3 mg/kg Co (Ca_2PO_4), 112 mg/kg I ($C_2H_{10}I_2N_2$), 3,419 mg/kg Cu (Cu_2SO_4), 2,190 mg/kg Mn ($MnSO_4$), 32 mg/kg Se (Na_2SeO_3), 6,640 IU/kg vitamin A, 664 IU/kg vitamin D_3, 89 IU/kg vitamin E

[3]Diet contained 0.1 kg/cow·day^{-1} ground limestone

[4]TDN values for oatlage and corn silages calculated from ADF. TDN value of 88% for modified distillers grains plus solubles used in Yr 1. TDN value of 90% for modified distillers grains plus solubles used in Yr 2.

[7]Values from NRC (1996)

Table 4.2. Dry matter, daily nutrient intake, and evaluation of treatment rations.

	Exp. 1[1,2]		Exp. 2[1,2]	
Item	REQ	HP	REQ	HP
DMI, kg/d	10.6	9.7	9.9	9.2
TDN, kg/d	6.5	6.5	6.6	6.6
CP, g/d	979	1,262	985	1,267
RDP, g/d[3]	806	900	708	771
RUP, g/d[3]	173	362	277	496
Fat, g/d	308	379	323	402
Diet evaluation[4]				
RDP balance, g/d	-34	-101	-309	-324
RDP, % requirement	96	88	64	62
MP balance, g/d	28	314	228	468
MP, % requirement	104	148	134	170

[1]REQ = limit-fed to provide 100% CP requirement; HP = limit-fed to provide 129% CP requirement

[2]Formulated to meet nutrient requirements of 636 kg cows with 9.1 kg peak milk production

[3]Calculated using NRC (1996) tabular values as a percentage of crude protein

[4]Diet evaluation using Level 1 of NRC (1996) model

Table 4.3. Diet and nutrient composition of common feedlot diet

Item	Exp. 1	Exp. 2
Ingredient, % DM		
Distillers grains plus solubles[1]	--	45.0
Corn Gluten Feed	38.5	--
Corn[2]	33.5	30.0
Corn husklage	20.0	20.0
Supplement[3,4,5]	8.0	5.0
Analyzed nutrient content, % DM		
DM	53.5	54.4
CP	14.9	16.4
NDF	22.4	32.4
ADF	10.8	12.5
Fat	4.0	5.4
NE_g[6], kcal/kg	1.36	1.59

[1]Exp. 2: dried distillers grains plus solubles fed d 1 to 13 of finishing period, modified wet distillers grains plus solubles fed d 14 to 191 of finishing period

[2]Exp. 2: dry cracked corn fed d 1 to 25 of finishing period, high moisture corn fed d 26 to 191 of finishing period

[3] Exp. 1 supplement: 81.22% Ground corn, 15.0% Limestone, 1.0% Trace Mineral Salt (85% salt, 0.03% Fe [$FeSO_4$], 0.03% Zn [ZnO], 5,710 mg/kg Mn [MnO], 2,290 mg/kg Cu [$CuSO_4$], 100 mg/kg I [$Ca(IO_3)_2$], 86 mg/kg Se [Na_2SeO_3]), 0.84% Urea, 0.3% Rumensin 90 (Monensin 198 g/kg; Elanco Animal Health, Greenfield, IN), 0.1% Vitamin premix (3,306.9 kIU/kg vitamin A [retinyl acetate], 330.7 kIU/kg vitamin D_3 [cholecalciferol], 44.1 kIU/kg vitamin E [DL-α-tocopheryl acetate]), 0.1% thiamine, 0.09% Tylan 40 (Tylosin 88 g/kg, Elanco Animal Health), 0.05% copper sulfate.

[4] Exp. 2: supplement fed d 1 to 158 of finishing period contained: 64.5% Ground corn, 30.8% Limestone, 2.1% Trace Mineral Salt (85% salt, 0.03% Fe [$FeSO_4$], 0.03% Zn [ZnO], 5,710 mg/kg Mn [MnO], 2,290 mg/kg Cu [$CuSO_4$], 100 mg/kg I [$Ca(IO_3)_2$], 86 mg/kg Se [Na_2SeO_3]), 0.3% Rumensin 90 (Monensin 198 g/kg; Elanco Animal Health), 0.2% Vitamin premix (3,306.9 kIU/kg vitamin A [retinyl acetate], k330.7 IU/kg vitamin D_3 [cholecalciferol], 44.1 kIU/kg vitamin E [DL-α-tocopheryl acetate]), 0.2% thiamine, 0.2% Tylan 40 (Tylosin 88 g/kg, Elanco Animal Health), 0.1% copper sulfate.

[5] Exp. 2: supplement fed d 159 to 191 of finishing period contained: 45.9% Ground corn, 50.0% Limestone, 2.0% Trace mineral salt (8.5% Ca [$CaCO_3$], 5% Mg [MgO and $MgSO_4$], 7.6% K [KCl_2], 6.7% Cl [KCl_2] 10% S [S_8, prilled], 0.5% Cu [$CuSO_4$ and Availa-4 (Zinpro Performance Minerals; Zinpro Corp, Eden Prairie, MN)], 2% Fe [$FeSO_4$], 3% Mn [$MnSO_4$ and Availa-4], 3% Zn [$ZnSO_4$ and Availa-4], 278 mg/kg Co [Availa-4], 250 mg/kg I [$Ca(IO_3)_2$], 150 mg/kg Se [Na_2SeO_3], 2,205 KIU/kg VitA [retinyl acetate], 662.5 KIU/kg VitD [cholecalciferol], 22,047.5 IU/kg VitE [DL-α-tocopheryl acetate]), 0.34% Rumensin 90 (Monensin 198 g/kg; Elanco Animal Health), 0.22% Tylan 40 (Tylosin 88g/kg, Elanco Animal Health).

[6]NE_g value back-calculated from animal performance using NRC (1996)

Table 4.4. Influence of prepartum dietary protein intake on cow BW, BCS, calving, milk production, and subsequent reproduction (Exp. 1).

	Treatment[1]			
Item[2]	REQ	HP	SEM	*P*-value
BW, kg				
Initial	658	660	15	0.92
Post-calving	685	722	17	0.14
Breeding	635	664	16	0.22
Late summer	698	704	16	0.78
BCS				
Initial	5.9	5.9	0.1	0.97
Post-calving	5.8	5.9	0.1	0.71
Breeding	5.8	5.8	0.1	0.43
Late summer	5.9	5.8	0.1	0.79
Calving				
Calving date, Julian d	69	71	3	0.57
Unassisted births, %	91	95	--	0.58
Milk production, kg				
49 ± 8 d	7.0	8.1	0.5	0.16
112 ± 8 d	11.2	11.6	1.2	0.82
Subsequent reproduction[3]				
AI conception, %	58	61	--	0.84
Overall pregnancy, %	95	86	--	0.36

[1]REQ = limit-fed to provide 100% CP requirement; HP = limit-fed to provide 129% CP requirement

[2]Cow performance reported for 43 cows (REQ, n = 22; HP, n = 21) , 6 pens per treatment

[3]Subsequent reproduction reported for 39 cows (REQ, n = 19; HP, n = 21) , 6 pens per treatment

Table 4.5. Influence of prepartum dietary protein intake on calf pre-weaning and post-weaning performance and health (Exp. 1).

	Treatment[1]			
Item	REQ	HP	SEM	*P*-value
Pre-weaning[2]				
BW, kg				
Birth	38	37	2	0.65
Weaning[3]	158	157	7	0.90
ADG	1.07	1.09	0.04	0.70
Weaning ultrasound measurements				
12th Rib fat thickness, cm	0.33	0.34	0.01	0.18
Marbling score[4]	326	338	15	0.47
Morbidity, %	5	10	--	0.53
Post-weaning[6]				
BW, kg				
Initial[7]	161	159	6	0.70
Final[8]	580	534	16	0.01
Days on feed	269	269	3	0.98
ADG, kg/d	1.55	1.39	0.05	< 0.01
DMI, kg/d	8.4	8.3	0.4	0.69
G:F	0.182	0.167	0.007	0.13
Morbidity, %	10	0	--	0.25

[1]REQ = dams limit-fed to provide 100% CP requirement; HP = dams limit-fed to provide 129% CP requirement

[2]Pre-weaning performance and morbidity reported for 43 calves (REQ, n = 22; HP, n = 21), 6 pens per treatment

[3]Weaning BW recorded on 112 ± 8 d of age

[4]400-499 = Small, 500-599 = Modest, 600-699 = Moderate, 700-799 = Slightly Abundant

[6]Post-weaning performance and morbidity reported for 42 calves (REQ, n = 21; HP, n = 21), 6 pens per treatment

[7]BW of progeny recorded on 112 ± 8 d of age

[8]HCW/standard dressing percent (63%)

Table 4.6. Influence of prepartum dietary protein intake on calf carcass characteristics (Exp. 1).

	Treatment[1]			
Item[2]	REQ	HP	SEM	*P*-value
HCW, kg	365	337	10	0.01
12th-rib fat thickness, cm	1.3	1.2	0.1	0.41
KPH, %	2.1	2.2	0.1	0.12
LM area, cm^2	83.9	81.9	2.6	0.41
Yield grade	3.2	2.9	0.2	0.14
Marbling score[3]	542	589	35	0.25

[1]REQ = dams limit-fed to provide 100% CP requirement; HP = dams limit-fed to provide 129% CP requirement

[2]Carcass characteristics reported for 42 calves (REQ, n = 21; HP, n = 21), 6 pens per treatment

[3]400-499 = Small, 500-599 = Modest, 600-699 = Moderate, 700-799 = Slightly Abundant

Table 4.7. Influence of prepartum dietary protein intake on cow BW, BCS, calving, milk production, and subsequent reproduction (Exp. 2).

	Treatment[1]			
Item[2]	REQ	HP	SEM	*P*-value
BW, kg				
Initial	661	664	17	0.90
Post-calving	692	691	18	0.96
Breeding	686	677	17	0.70
Late summer	665	653	15	0.53
BCS				
Initial	5.7	5.9	0.2	0.51
Post-calving	6.1	6.1	0.2	0.96
Breeding	5.8	5.9	0.1	0.75
Late summer	5.7	5.6	0.2	0.75
Calving				
Calving date, Julian d	65	62	3	0.36
Unassisted births, %	100	95	--	0.30
Milk production, kg				
69 ± 11 d	10.7	11.0	1.2	0.86
Subsequent reproduction[3]				
AI conception, %	67	39	--	0.15
Overall pregnancy, %	87	80	--	0.64

[1]REQ = limit-fed to provide 100% CP requirement; HP = limit-fed to provide 129% CP requirement

[2]Cow performance reported for 42 cows (REQ, n = 22; HP, n = 20) , 10 pens per treatment

[3]Subsequent reproduction reported for 28 cows (REQ, n = 15; HP, n = 13) , 10 pens per treatment

Table 4.8. Influence of prepartum dietary protein intake on calf pre-weaning and post-weaning performance and health (Exp. 2).

	Treatment[1]			
Item	REQ	HP	SEM	*P*-value
Pre-weaning[2]				
BW, kg				
Birth	39	39	1	0.69
Weaning[3]	169	168	8	0.89
ADG	1.06	1.02	0.05	0.58
Weaning ultrasound measurements				
12th Rib fat thickness, cm	0.32	0.31	0.01	0.70
Marbling score[4]	383	401	12	0.23
Morbidity, %	8	14	--	0.53
Post-weaning[6]				
BW, kg				
Initial[7]	168	170	8	0.88
Final[8]	517	533	12	0.33
ADG, kg/d	1.58	1.65	0.04	0.58
DMI, kg/d	8.1	8.1	0.2	0.91
G:F	0.198	0.207	0.006	0.24
Morbidity, %	5	0	--	0.49

[1]REQ = dams limit-fed to provide 100% CP requirement; HP = dams limit-fed to provide 129% CP requirement

[2]Pre-weaning performance and morbidity reported for 42 calves (REQ, n = 22; HP, n = 20), 5 pens per treatment

[3]Weaning BW recorded on 121 ± 11 d of age

[4]400-499 = Small, 500-599 = Modest, 600-699 = Moderate, 700-799 = Slightly Abundant

[6]Post-weaning performance and morbidity reported for 40 calves (REQ, n = 22; HP, n = 18), 5 pens per treatment

[7]BW of progeny recorded on 151 ± 11 d of age

[8]HCW/standard dressing percent (63%)

Table 4.9. Influence of prepartum dietary protein intake on calf carcass characteristics (Exp. 2).

	Treatment[1]			
Item[2]	REQ	HP	SEM	*P*-value
HCW, kg	325	335	8	0.33
12th-rib fat thickness, cm	1.2	1.6	0.1	< 0.01
KPH, %	2.1	2.2	0.1	0.04
LM area, cm^2	76.8	76.1	2.6	0.77
Yield grade	3.1	3.7	0.2	0.01
Marbling ccore[3]	453	481	28	0.45

[1]REQ = dams limit-fed to provide 100% CP requirement; HP = dams limit-fed to provide 129% CP requirement

[2]Carcass characteristics reported for 40 calves (REQ, n = 22; HP, n = 18), 5 pens per treatment

[3]400-499 = Small, 500-599 = Modest, 600-699 = Moderate, 700-799 = Slightly Abundant

Figure 4.1. Effects of treatment on post-feeding glucose and insulin concentrations and post-feeding insulin to glucose ration when measured 2 d before slaughter.

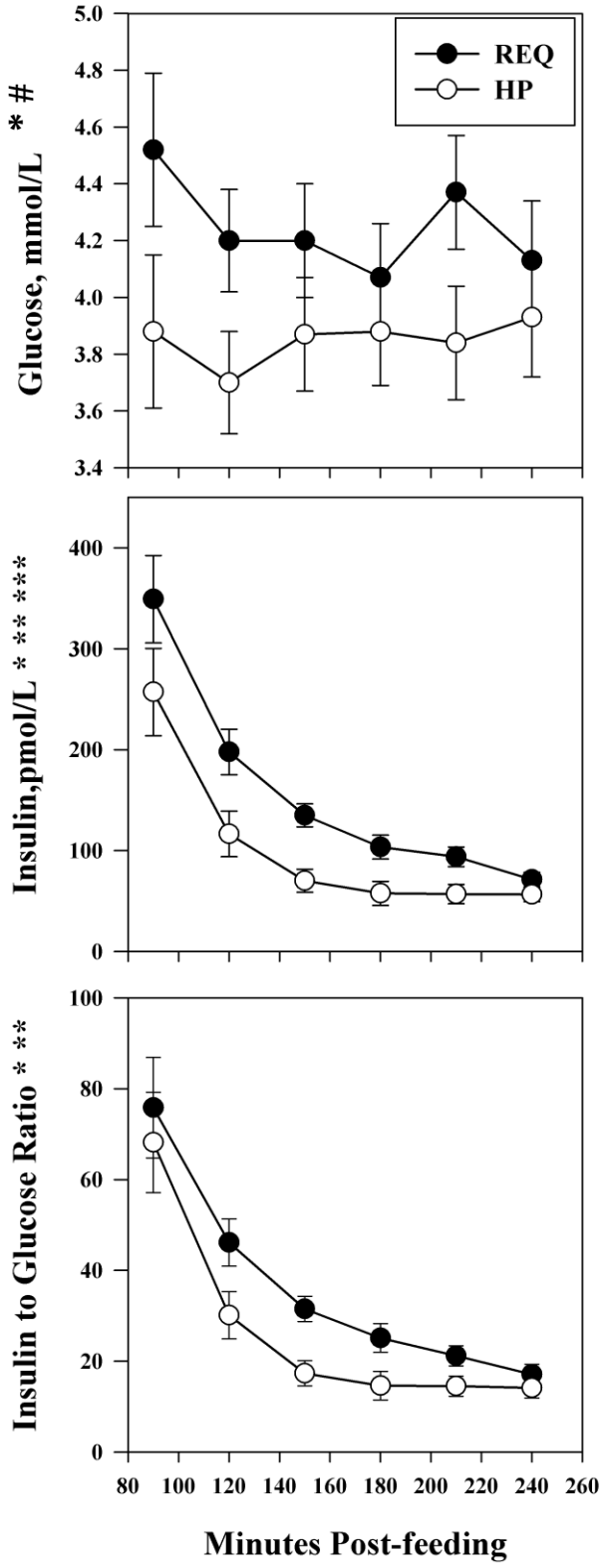

Figure 4.1 (cont.). Effects of treatment, dams limit-fed to provide 100% CP requirement (REQ) or dams limit-fed to provide 129% CP requirement (HP), on post-feeding glucose and insulin concentrations and post-feeding insulin to glucose ratio when measured 2 d before slaughter. Dams were fed treatment rations 92 ± 10 d prepartum through calving. Plasma was collected from a subset of progeny (n = 24; REQ: n = 12; 6 steers, 6 heifers; HP: n = 12; 6 steers, 6 heifers; 5 pens per treatment), via jugular venipuncture, 90, 120, 150, 180, 210, and 240 min post-feeding. **Notes: *** Treatments differ by $P < 0.01$, **Time of bleed differs by $P \leq 0.05$, *** Treatment by time of bleed interaction $P = 0.03$, # Treatment by time of bleed interaction $P = 0.09$.

CHAPTER 5

EFFECTS OF MATERNAL PLANE OF NUTRITION DURING MID-GESTATION ON BEEF COW PERFORMANCE AND CALF GROWTH AND FEED EFFICIENCY, METHANE PRODUCTION, GLUCOSE TOLERANCE, CARCASS CHARACTERISTICS, AND GENE EXPRESSION

Abstract

Objectives were to investigate the effects of divergent plane of nutrition during mid-gestation on cow performance and progeny growth, feed efficiency, methane production, glucose tolerance, carcass characteristics, and gene expression in LM. Mature cows (n = 3 pens per treatment, 35 total) were limit-fed for 3 planes of nutrition from 196 ± 14 to 114 ± 14 d prepartum: 100% energy and protein requirement (**REQ**), 70% requirement (**70%REQ**), or 130% requirement (**130%REQ**). Calves (27 total) were weaned at 198 ± 14 d of age and transitioned to a common finishing diet. Methane emissions were collected over 24 h at 303 ± 14 d of age. An intravenous glucose tolerance test was conducted at 318 ± 14 d of age. Biopsies of progeny LM were taken 99 ± 14, 197 ± 14, and 392 ± 14 d of age for later analysis of gene expression via qPCR. All calves were slaughtered at 404 ± 14 d of age at an average backfat of 1.3 cm. Cow ADG during mid-gestation was greatest ($P < 0.01$) for 130%REQ, least for 70%REQ, with REQ intermediate. Transition ADG was greatest ($P < 0.01$) for 70%REQ progeny, least for REQ progeny, with 130%REQ progeny intermediate. Finishing G:F tended ($P = 0.06$) to be decreased for REQ progeny relative to 70%REQ and 130%REQ progeny. Ultrasound 12th rib fat thickness at 392 ± 14 d of age was greater ($P = 0.02$) for REQ progeny

relative to 70%REQ and 130%REQ progeny. Treatment had no effect ($P \geq 0.21$) on progeny RFI or 24 h methane emissions; but, REQ progeny tended ($P = 0.06$) to have decreased RG relative to 70%REQ and 130%REQ progeny. Treatment had no effect ($P \geq 0.12$) on progeny glucose and insulin concentrations, AUC, glucose clearance rate, or insulin to glucose ratio. Progeny of REQ dams had greater ($P = 0.04$) HCW than 70%REQ progeny, with 130%REQ intermediate and not different from either. Treatment had no effect ($P \geq 0.27$) on other carcass characteristics. Treatment had not effect ($P \geq 0.24$) on expression of *FABP4*, *MYOD1*, *FASN*, *SCD*, *SLC2A4*, *YY1*, *PAX7*, *MEF2C*, *MYOG*, *PPARG*, *MYH2*, and *MYH7*. Expression of all target genes, except MYH7, changed ($P \leq 0.03$) as progeny d of age increased. There was a treatment by d of age interaction ($P = 0.04$) for expression of *MYH1*, in which expression of *MYH1* was least in progeny born to 70%REQ dams at 392 ± 14 d of age relative to REQ and 130% progeny. There were treatment by progeny sex by d of age interactions ($P \leq 0.01$) for expression of *SLC2A4*, *YY1*, and *MYH7*, in which expression of *SLC2A4*and *YY1* was least for heifers born to 70%REQ dams. For heifers, abundance of *MYH7* mRNA at 392 ± 14 d of age was greatest for progeny born to 130%REQ dams, least for those born to 70%REQ dams, with REQ progeny intermediate and different from both. For steers, *MYH7* expression at 197 ± 14 d of age was greater for progeny born to REQ dams relative to progeny born to 70%REQ or 130%REQ dams. Treatments were successful in diverging cow BW and BCS. Differing mid-gestation plane of nutrition affected transition period ADG and HCW; yet, did not dramatically impact methane production, insulin resistance, or gene expression in LM.

Key words: carcass characteristics, feed efficiency, fetal programming, gene expression, glucose tolerance, methane

Introduction

Observations of calf effects in beef cow nutrition experiments have been reported for decades (Corah et al., 1975); but, the number experiments designed to evaluate potential fetal programming effects over the life cycle of progeny is limited. Mid-gestation is a vital time for the development of fetal skeletal muscle and adipose tissue (Du et al., 2010). Maternal plane of nutrition has been demonstrated to elicit lasting effects on progeny growth and carcass characteristics in ruminants (Underwood et al., 2010; Funston et al., 2010a). The work of Ford et al. (2007) and Long et al. (2010b) investigated the fetal programming effects of either restricting ewes to 50% of nutrient requirement or overfeeding ewes to 150% of nutrient requirement, respectively, during gestation. It was our goal to investigate a narrower range of maternal nutrient restriction or overfeeding, 70% or 130% of nutrient requirement, which may be more applicable to beef production systems. We hypothesized that maternal nutrient restriction during mid-gestation would decrease calf final BW, increase feed efficiency, decrease methane production, decrease insulin sensitivity, and increase carcass adiposity relative to progeny of dams fed to requirement. We also hypothesized that maternal overnutrition would decrease calf growth, decrease feed efficiency, increase methane production, increase insulin sensitivity, and increase carcass adiposity relative to progeny of dams fed to requirement. It was hypothesized that phenotypic differences of progeny would coincide with differential expression of adipogenic, muscle regulatory, and muscle fiber type genes across treatments. Our objectives were to evaluate the effects of divergent plane of nutrition during mid-gestation on cow performance and progeny growth, feed efficiency, methane production, glucose tolerance, carcass characteristics, and gene expression.

Materials and Methods

Animals, Experimental Design, and Treatments

Experimental animals were managed according to the guidelines recommended in the Guide for the Care and Use of Agriculture Animals in Agriculture Research and Teaching (Federation of Animal Science Societies, 2010). All experimental procedures followed were approved by the University of Illinois Institutional Animal Care and Use Committee. Multiparous Angus, and Simmental x Angus cows (n = 35; BW = 601 ± 71 kg; age = 4.8 ± 2.1 yr) and their progeny were used in a complete randomized design to evaluate the effects of maternal plane of nutrition during mid-gestation on cow performance as well as calf pre-weaning and post-weaning growth, feed efficiency, methane production, glucose tolerance, and carcass characteristics. Cows were maintained at the Beef Cattle and Sheep Field Laboratory in Urbana, IL.

Angus and Simmental x Angus cows were bred via AI to a single Simmental or Simmental x Angus bull, respectively, and then exposed to clean-up bulls of the same breed; thus, all progeny were Simmental x Angus with 6 sires represented. Fetuses were sexed via rectal ultrasonography 83 d post-AI. One wk before allotment, all cows were fed a common diet formulated to meet 100% NRC (1996) energy and protein requirements (Table 5.1) to equalize fill. Cows were stratified by BW, breed, calf sire, and calf sex and then allotted into pens (9 total pens, 3 pens per treatment) with 3 or 4 cows per pen. Pens were randomly assigned to 1 of 3 maternal planes of nutrition formulated to provide (Table 5.1): 100% energy and protein requirement (**REQ**, n = 3 pens, 11 cows), 70% requirement (**70%REQ**, n = 3 pens, 12 cows), or 130% requirement (**130%REQ**, n = 3 pens, 10 cows). Cows were limit-fed a common total mixed ration and DMI was adjusted for nutritional plane. Treatment rations were fed 196 ± 14 d

to 114 ± 14 d prepartum. Treatment rations were balanced using Level 1 of the NRC model. Model parameters included: initial cow BW and BCS, 9.1 kg milk at peak milk production, 36.2 kg calf birth BW, and suggested values or defaults for other parameters. Cows were provided a trace mineral (Table 5.1) salt, free choice. At 113 ± 14 d prepartum, cows were fed a common ration (Table 5.1) formulated to provide 100% NRC energy requirements. One day after calving, cows were moved to new pens, comingled among treatment groups, and remained on the common post-treatment ration.

Pre-calving and Pre-weaning Management of Cows and Calves

Cows were maintained in 10.36 m x 4.88 m pens with a partially slatted concrete floor with a solid concrete floor creep area that only calves had access to after calving. Both cow and calf areas were equipped with rubber matting. Cow BW was recorded on 2 consecutive d and BCS was assigned at the initiation and end of the prepartum feeding period. Pre-calving cow BW was recorded on 2 consecutive d and BCS assigned at 7 ± 7 d before calving.

Post-feeding plasma glucose, insulin, NEFA, and blood urea nitrogen (**BUN**) concentrations were analyzed on all cows at 1 d before initiation of the treatment period and at the end of the treatment period. Plasma progesterone concentrations were also analyzed to indirectly evaluate gravid uterine mass (Sullivan et al., 2009) 1 d before initiation of the treatment period, 160 ± 14 d prepartum, and at the end of the treatment period. Blood was collected from the jugular vein using EDTA coated vacutainer tubes before feeding, 3, 6, and 9 h post-feeding. At each bleed time, four 10 mL vacutainer tubes were filled (1 additional tube was collected pre-feeding for progesterone analysis). Blood tubes were stored in ice water for a maximum of 30 min and centrifuged at 3,147 × g for 10 min at 10°C. Plasma was aliquoted into four 1.5 mL microcentrifuge tubes and stored at -80°C for subsequent analysis. Before analysis,

plasma was pooled by pen; only including plasma from cows that progeny's data were reported through the conclusion of the experiment (n = 27).

Cow BW, BCS, and milk production were reported for 3 pens per treatment and included data from 30 cows and excluded cows that lost calves before weaning (REQ, n = 1; 70%REQ, n = 0; 130%REQ, n = 2), one 70%REQ cow that aborted pre-term, and one 70%REQ cow who was culled before calving due to temperament. Cow performance data is included for 1 REQ cow that died 123 d post-calving, but before weaning. Milk production was estimated utilizing the weigh-suckle-weigh technique (Boggs et al., 1980) at 99 ± 14 d and 199 ± 14 d postpartum. During spring and summer, cow/calf pairs were rotated through mixed pastures of predominantly bromegrass (*Bromus inermis*) with white clover (*Trifolium repens*) and orchardgrass (*Dactylis glomerata L.*)

Calf BW was recorded within 48 h after birth and on 2 consecutive d at 100 ± 14 d of age and weaning (198 ± 14 d of age) to measure pre-weaning growth performance. Pre-weaning calf performance was reported for 3 pens per treatment and included data from all calves (n = 27; REQ: n = 9; 3 steers, 6 heifers; 70%REQ: n = 10; 7 steers, 3 heifers; 130%REQ: n = 8; 4 steers, 4 heifers) weaned by cows placed on treatments excluding 2 heifers due to poor growth (BW more than 2 standard deviations below group average BW at weaning; REQ, n = 1; 70%REQ, n = 0; 130%REQ, n = 1). On 100 ± 14 d of age and at weaning (198 ± 14 d of age), 12th rib backfat thickness (**backfat**) and marbling score were estimated via ultrasound to measure body composition. Ultrasound measurements were taken with an Aloka 500SV (Wallingford, CT) B-110 mode instrument equipped with a 3.5-MHz general purpose transducer array. Images were taken in a transverse orientation between the 12th and 13th ribs approximately 10 cm distal from

the midline. Ultrasound images were processed utilizing CPEC ultrasound imaging software (Cattle Performance Enhancement Company LLC., Oakley, KS).

Post-weaning Management

Calves were housed in slatted-floor, feedlot barns at the Beef Cattle and Sheep Field Laboratory, Urbana, IL for the duration of the finishing period. Calves were vaccinated with the following: Bovishield Gold FP5 L5 HB (Zoetis, Florham Park, NJ), One Shot Ultra 7 (Zoetis), and Pulmo-Guard MpB (AgriLabs, St Joseph, MO). Calves were dewormed with Eprinex pour-on (Merial, Duluth, GA) and tagged with an electronic identification tag (Allflex USA, DFW Airport, TX). Upon entry to the feedlot, calves were adapted to a common, finishing diet fed for ad libitum intake over a transition period of 30 d (Table 5.2). Calves were implanted with a Compudose 200 implant (25.7 mg estradiol; Elanco Animal Health, Greenfield, IN) 30 d post-weaning.

During the transition period, calves were halter broken before enteric methane collection and an intravenous glucose tolerance test (GTT) that was conducted during the finishing period, described later. Calf BW was recorded at the end of the 30 d transition period. Individual feed intake was monitored using the GrowSafe automated feeding system (Model 4000E, GrowSafe Systems Ltd., Airdrie, Alberta, Canada) during the finishing period. Calf BW was recorded as well as ultrasound backfat and marbling scores taken at 288 ± 14 d of age. Final BW was recorded 13 d before slaughter on 2 consecutive d.

Beginning on d 170 of the finishing period, ultrasound backfat measurements were taken to determine slaughter date. Cattle were slaughtered as a single group at 404 ± 14 d of age at a commercial facility once it was estimated that average final backfat would equal 1.3 cm. Trained personnel recorded slaughter order and HCW was taken on day of slaughter. Backfat, % KPH,

LM area, yield grade, and marbling score were taken after a 24 h carcass chill with Video Image Analysis as part of the USDA camera.

Longissimus muscle samples were collected at the first lumbar vertebrae 1 d post-slaughter. Muscle samples were then deboned, trimmed, and a 2.54 cm thick steak sliced for subsequent analysis of Warner-Bratzler Shear Force (WBSF). Steaks were aged for 14 d, cooked to an internal temperature of 70°C with a thermocouple, and WBSF determined using an HD*Plus*/100 texture analyzer (Texture Technologies Corp, Hamilton, MA). The average shear values of 6 cores from each steak were used to calculate WBSF. Remaining *Longissimus* muscle was ground via processor and analyzed for intramuscular fat (IMF) percentage (using Ankom Technology method 2; Ankom XT10 Fat Analyzer, Ankom Technology, Macedon, NY).

Feed Efficiency

The following measures of feed efficiency were evaluated during the finishing period: residual feed intake (RFI) and residual gain (RG). Calf BW was collected on 2 consecutive d 30 post-weaning (d 0 of efficiency evaluation) and 13 d before slaughter (d 163 of efficiency evaluation). Calves were also weighed on d 32, 58, 87, 113, and 140 of the efficiency evaluation period. For each calf, BW was regressed on d of efficiency evaluation period. Intercept and regressed ADG (slope of the regression equation) was then used to calculate mid-test BW, d 82, for each calf. Mid-test metabolic BW (MMW) of each calf was calculated as mid-test $BW^{0.75}$. The residual from the regression of DMI (of the finishing period) on regressed ADG, MMW, and carcass BF was considered RFI. The residual from the regression of ADG (regressed ADG from each calf) on DMI, MMW, and carcass BF was considered RG. Thus, desirable values for RFI and RG are negative and positive, respectively.

Methane Collection

Enteric methane emissions were measured over a 5 d period that began at 303 ± 14 d of age using the University of Illinois Ruminant Emission Measurement System (REMS). Calculation of methane emissions using the REMS system has previously been described by Segers (2013). The REMS system is comprised of 6 positively pressured, environmentally controlled Plexiglas chambers with canvas hoods, and an infrared photoacoustic multi-gas technology (IR-PAS, INNOVA 1412, California Analytical, Inc., Orange, CA) that measured methane. A solenoid valve multiplexer sampled 10 consecutive gas samples from each chamber to measure gas emissions at a given time. While in REMS chambers, cattle were restrained using a neck stanchion, but were able to stand and lay down. Chambers were fitted with canvas hoods that were fitted around the animal's neck to contain all gases expired by the animal. Each REMS chamber was equipped with a feed bin and automatic water cup. Gas emissions were measured every 50.52 min; resulting in 28 total measurements per chamber over a 23 h 27 min period. Methane emissions over the 23 h 27 min collection period were normalized to 24 h.

Calves were acclimated to REMS chambers with access to feed and water 11 d before methane collection for a period of 24 h. One d before methane collection, calves were allotted as pairs to a new pen equipped with the GrowSafe automated feeding system to measure DMI 24 h before methane collection. On each morning of methane collection, calves were offered ad libitum access to feed for 3 h. At 3 h post-feeding, cattle were removed from their pen and placed in REMS chambers within 30 min. Cattle were the offered ad libitum access to feed and water for the duration of the methane collection period. At the end of methane collection, cattle were returned to their original feedlot period.

Glucose Tolerance Test

A GTT was conducted on each calf during a 2 d period that began at 318 ± 14 d of age. Calves were removed from feed 24 h before the GTT. Approximately 16 h before the GTT, cattle were restrained in a squeeze chute (Flying W Livestock Equipment, Watonga, OK) and aseptic procedure was used to insert a 40 cm indwelling venous catheter (Tygon Tubing, Saint-Gobain, Valley Forge, PA) via a 3.81 cm 12 gauge needle. Half the length of the catheter was inserted into the animal and then fitted with a hub for blood draw using a syringe. To prevent clotting overnight, catheters were flushed with 2 mL of heparin stock solution (1,000 ug/mL). Cattle were then housed in individual pens between catheterization and the GTT. Calf BW was recorded to determine glucose bolus size and catheters checked 45 min before GTT. Cattle were then tied in stanchions for 45 min before GTT to reduce stress of animal handling before GTT. Blood (10 mL, stored in EDTA coated tube) was collected via catheter 5 and 2 min before glucose infusion to determine baseline glucose and insulin concentrations. Before each blood sample, 4 mL of blood was drawn via syringe to clear the catheter and then discarded. To prevent clotting, catheters were flushed with 2 ml of sterile heparinized saline (9 g/L of NaCl) after collection of each blood sample. Glucose bolus (50% dextrose solution) was administered at a rate of 0.25 g glucose·kg^{-1} BW. In order to ensure that no dextrose solution remained in the catheter, 5 ml of saline solution was flushed through the catheter after dextrose infusion. Blood samples were then collected 5, 10, 15, 20, 30, 60, 90, and 120 min post-glucose infusion. Blood tubes were stored in ice water for a maximum of 30 min and centrifuged (Sorvall Legend XFR, Thermo Scientific, Waltham, MA) at 4,415 × g for 10 min at 4°C. Plasma was aliquoted into two 1.5 mL microcentrifuge tubes and stored at -80°C for subsequent analysis of glucose and insulin concentrations. After GTT, calves were returned to their original feedlot pen. Plasma glucose and insulin concentrations at 5 and 2 min pre-infusion of glucose bolus were averaged to determine

baseline concentrations. Glucose area under the curve (**AUC**) and insulin AUC were calculated using the positive incremental method described by Cardoso et al. (2011). Insulin to glucose ratio was calculated using the AUC values for insulin and glucose. Glucose clearance rates were calculated from 5 to 20 min and 20 to 120 min post-infusion using the method described by Bernhard et al. (2012). Glucose half-life was also calculated from 5 to 20 min and 20 to 120 min post-infusion as described by Bernhard et al. (2012).

Blood Analysis

Plasma samples from cows and their progeny were analyzed for glucose concentration via a colorimetric procedure using a Glucose Liquicolor kit (Procedure No. 1070, Stanbio Laboratory, Boerne, TX). Methods for glucose analysis were previously described by Shoup (2014). Plasma samples from cows and their progeny were analyzed for insulin concentration via a Bovine Insulin ELISA kit (Mercodia, Inc., Winston Salem, NC). Glucose and insulin absorbance were measured at 500 nm and 450 nm, respectively, using a plate reader (Synergy HT, BioTek, Winooski, VT). Results for glucose analysis were deemed acceptable if the coefficient of variation (CV) within duplicates was at or below 5%. Results for insulin analysis were deemed acceptable if the CV within duplicates was at or below 10%. All insulin samples were run within 5 d with 1 pooled-sample control used with each ELISA kit. Plasma NEFA and BUN concentrations were analyzed using an Olympus AU680 Chemistry-Immuno Analyzer (Olympus Corporation, Center Valley, PA). Standard used for NEFA analysis was NEFA-HR (2) (Levels 1 and 2, Wako Chemicals, Richmond, VA). Standard used for BUN analysis was Lyphochek Assayed Chemistry Control (Levels 1 and 2; Bio Rad Laboratories, Hercules, CA). Plasma progesterone concentrations were analyzed using a chemiluminescent enzyme immunoassay (Immulite 1000; Siemens Medical Solutions Diagnostics, Los Angeles, CA).

For GTT, plasma glucose and insulin concentrations were analyzed as described previously for cow plasma. Results for glucose analysis were deemed acceptable if the CV within duplicates was at or below 5%. Results for insulin analysis were deemed acceptable if the CV within duplicates was at or below 10%. All insulin samples were run within 14 d with 1 pooled-sample control used with each ELISA kit.

Insulin and glucose concentrations were converted to the SI units pmol/L and mmol/L, respectively, in order to quantify activity of insulin and glucose. The traditional insulin unit of ng/mL was converted to pmol/L using the molecular weight of bovine insulin, 5734 g/mol, reported by Darby et al. (2001); resulting in a conversion rate of 1 ng/mL = 174.398 pmol/L. The traditional glucose unit of mg/dl was converted to mmol/L using the conversion of 1 mg/dl = 0.05551 mmol/L (Young, 1987).

Muscle Biopsies

Biopsy samples were analyzed for differential gene expression in LM of progeny. Cattle were biopsied on 2 consecutive d at 99 ± 14 d, 197 ± 14 d, and 392 ± 14 d of age (13 d prior to slaughter). Longissimus muscle biopsies were conducted using the procedure described by Graugnard et al. (2010) with the following modifications: 10 ml Lidocaine-HCL were administered per animal; first biopsy site was 5 cm cranial to the ilium, with subsequent biopsies 5 cm cranial to the previous site; incisions were closed with tissue adhesive (Vetbond, 3M Company, St. Paul, MN) and covered with an aerosol bandage (Alushield, Neogen Corporation, Lansing, MI). Tissue samples were immediately frozen in liquid nitrogen and stored at -80°C for subsequent RNA extraction.

On each d calves were biopsied, blood was collected from the jugular vein using EDTA coated vacutainer tubes for later analysis of plasma adiponectin concentration. Blood tubes were

stored in ice water for a maximum of 30 min and centrifuged at 4,415 × g for 10 min at 4°C (Sorvall Legend XFR, Thermo Scientific). Plasma was aliquoted into four 1.5 ml microcentrifuge tubes and stored at -80°C for subsequent analysis. Plasma adiponectin concentrations were analyzed via RIA (HADP-61HK, EMD Millipore, Billerica, MA) procedure previously described by Raddatz, (2008). The sensitivity of the assay was 1.6 ng/mL. The intra-assay CV for low (9.9 ng/mL) and high (55.2 ng/mL) concentrations were 10.2% and 13.4%, respectively.

RNA Extraction, Evaluation, and RT-qPCR

Biopsy tissue was weighed (0.08 to 0.12 g) and RNA extracted using QIAzol Lysis Reagent (Qiagen, Hilden, Germany). Genomic DNA was removed from RNA by use of DNase from RNeasy Mini Kit columns (Qiagen). Concentration of extracted RNA was measured with a NanoDrop ND-1000 spectrophotometer (NanoDrop Technologies, Wilmington, DE). Quality of RNA was assessed using a 2100 Bioanalyzer (Agilent Technologies Inc., Santa Clara, CA) to calculate a RNA integrity value (RIN) for each sample. Values for RIN range from 1 to 10 (low to high quality) based on the area of 18S and 28S rRNA area and the height of the 28S rRNA peak. Extracted RNA had a mean RIN value of 7.9 ± 0.33. A portion of RNA was diluted to 100 mg/L using DNase/RNase free water prior to reverse transcription.

Complementary DNA (cDNA) was synthesized using 100 ng RNA, 1 μg dT18 (Operon Biotechnologies, Huntsville, AL), 1 μL 10 mmol/L dNTP mix (Invitrogen Corp., Carlsbad, CA), 1 μL random primers (Invitrogen Corp.), and 10 μL DNase/RNase free water. The mixture was incubated at 65 °C for 5 min and placed on ice for 3 min. Six μL of master mix containing 4.5 μL 5X First-Strand Buffer, 1 μL 0.1 M DTT, 0.25 μL (50 U) of SuperScriptTM III RT (Invitrogen Corp.), and 0.25 μL of RNase Inhibitor (10 U, Promega, WI). The reaction was carried out in an Eppendorf Mastercycler Gradient (Eppendorf Corp., Hamburg, Germany) using the following temperature

program: 25°C for 5 min, 50°C for 60 min and 70°C for 15 min. Resulting cDNA was then diluted 1:4 with DNase/RNase free water.

Quantitative PCR (qPCR) was performed using 4 µL diluted cDNA combined with 6 µL of a mixture composed of 5 µL 1 × SYBR Green master mix (Applied Biosystems, Foster City, CA), 0.4 µL each of 10 µM forward and reverse primers, and 0.2 µL DNase/RNase free water in a MicroAmp™ Optical 384-Well Reaction Plate (Applied Biosystems, Foster City, CA). Samples were run in triplicate and a 6 point relative standard curve plus the non-template control (NTC) were used (User Bulletin #2, Applied Biosystems). The reactions were carried out in an ABI Prism 7900 HT SDS instrument (Applied Biosystems) using the following conditions: 2 min 97 at 50°C, 10 min at 95°C, 40 cycles of 15 s at 95°C (denaturation) and 1 min at 60°C (annealing + extension). The presence of a single PCR product was verified by the dissociation protocol using incremental temperatures to 95°C for 15 s plus 65°C for 15 s. Data were calculated with the 7900 HT Sequence Detection Systems Software (version 2.2.1, Applied Biosystems). The final data were normalized using the geometric mean of the genes UXT, MTG1 and RPS15A, which are considered as internal control genes due to their stability, and lack of variation in muscle tissue.

Feed Sampling and Analysis

For initial treatment ration formulation, individual ingredients used in treatment rations were sampled and analyzed for CP, NDF, ADF, fat, Ca, and P with TDN calculated from ADF by Rock River Laboratory, Inc. (Watertown, WI). Crude protein, ADF, and fat were analyzed using AOAC (1990) methods 990.03, 973.18, and 920.39, respectively. The method described by Goering and Van Soest (1970) was used for analysis of NDF. Minerals were extracted by acid digestion and analyzed using an Optima 3000 Inductively Coupled Plasma-Optical Emission Spectrometer (Perkin Elmer, Waltham, MA). Calculations for TDN value of hay and cornstalks were based on ADF.

Over the course of the experiment, individual feed ingredients were sampled every 2 wk, dried in a 55°C forced air oven for 3 d and then ground with a Wiley mill (1-mm screen, Arthur H. Thomas, Philadelphia, PA), and composited at the conclusion of the experiment. Feed samples were analyzed for NDF and ADF (using Ankom Technology method 5 and 6, respectively; Ankom^{200} Fiber Analyzer, Ankom Technology), fat (using Ankom Technology method 2; Ankom XT10 Fat Analyzer, Ankom Technology), CP (Leco TruMac, LECO Corporation, St. Joseph, MI), and ash (600° C for 2 h ; Thermolyne muffle oven Model F30420C, Thermo Scientific). Energy value used for DDGS in common post-treatment ration was 120% TDN as published by Loy et al. (2008). Reported NEg of the finishing diet was back-calculated from observed animal performance using equations from NRC (1996).

Statistical Analysis

Pen was considered the experimental unit for all response variables concerning cow performance, plasma metabolite and hormone concentrations, as well as progeny performance, efficiency, glucose and insulin kinetics, carcass characteristics and gene expression. Data were analyzed using the MIXED procedure of SAS (9.3; SAS Inst. Inc., Cary, NC); with the exception of the CORR procedure of SAS that was used to correlate gene expression to cow and progeny response variables. The least square means function of SAS was used to separate treatment means. For measures of cow BW, BCS, plasma metabolite and hormone concentrations, and milk production, the statistical model included gestational plane of nutrition as a fixed effect and treatment pen as a random effect. For measures of calving date, calf birth BW, measures of calf pre- and post-weaning performance, carcass characteristics, plasma glucose and insulin concentrations, measures of feed efficiency, methane emissions, and gene expression, the statistical model included gestational plane of nutrition, calf sex, and calf sire as fixed effects and

treatment pen as a random effect. Data concerning relative mRNA abundance were transformed using a logarithmic ($\log_{10} x$) function to improve data normality. A logarithmic transformation provided the most normally distributed residuals relative to a squared or square root transformation when tested with a Shapiro-Wilk test. For cow plasma metabolite and hormone concentrations, repeated measures, with compound symmetry covariance structure, were used for time of blood collection for glucose and insulin concentrations and day of blood collection for BUN, NEFA, and progesterone concentrations. For plasma glucose and insulin concentrations during intravenous GTT, repeated measures, with a Toeplitz covariance structure, were used for time of blood collection. For progeny plasma adiponectin concentrations, repeated measures, with an unstructured covariance structure, were used for day of blood collection. For gene expression in LM of progeny, repeated measures, with an autoregressive (1) covariance structure, were used for day of biopsy. The selected covariance structure for each parameter yielded the most desirable combination of fit statistics of covariance structures tested (compound symmetry, unstructured, autoregressive (1), Toeplitz, and variance components). Baseline glucose and insulin concentration was used as a covariate for analysis of glucose AUC and insulin AUC, respectively. Treatment effects were considered significant at $P \leq 0.05$ and trends at $0.05 < P \leq 0.10$.

Results and Discussion

Cow Performance and blood components

Initial cow BW, BCS, and ultrasound backfat were not different ($P \geq 0.26$) across treatments. Cow BW at 160 ± 14 and 114 ± 14 d prepartum was greatest ($P < 0.01$) for cows fed 130%REQ, least for cows fed 70%REQ, and intermediate for those fed REQ (Figure 5.1).

Differences in prepartum plane of nutrition were also supported by cows fed 70% REQ having decreased ($P < 0.01$) BCS and ultrasound backfat (Figure 5.1) at 114 ± 14 d prepartum, the day which maternal treatments ceased. Thus, cow ADG during mid-gestation was greater ($P < 0.01$) for cows fed REQ and 130%REQ when compared to those fed 70%REQ (Table 5.5). These performance responses for cow BW and BCS were expected because cows were fed treatment rations during mid-gestation formulated to diverge cow BW and BCS. It is of note that mid-gestation cow ADG for cows fed REQ and 130%REQ were not different from one another. This may be explained by the greater DMI of 130%REQ cows relative to those fed REQ. Greater DMI would result in greater passage rate and lower digestibility per unit of DMI (Scholljegerdes et al., 2004).

After realimentation to a common plane of nutrition formulated to meet nutrient requirements, cow ADG during late gestation was not different ($P = 0.15$) by treatment; yet cow BW 7 ± 7 d pre-calving was not different. The fact that pre-calving BW was not different was unexpected. However, it can be reasoned that cows fed 70%REQ that had been nutrient restricted during mid-gestation were susceptible to experience compensatory gain when placed on a higher plane of nutrition during late gestation. It was our objective to evaluate the fetal programming effects of divergent plane of nutrition only during mid-gestation.

Maternal plane of nutrition during mid-gestation tended to affect ($P = 0.08$) progeny birth BW. Birth BW was greater for progeny born to 70%REQ and 130%REQ relative to those born to REQ fed dams. Greater birth BW of 130%REQ progeny may be attributed to greater cow ADG during mid-gestation; and greater birth BW of 70%REQ progeny may be attributed to numerically greater cow ADG during late gestation. Several experiments have demonstrated the potential for prepartum nutrition to increase progeny birth BW (Radunz et al., 2010; Wilson,

2012; Gunn et al., 2014). In the experiments conducted by Radunz et al. (2010) and Wilson, (2012), cow BW gain was improved when cows were fed rations that contained corn coproducts as energy sources relative to those fed hay during late gestation. In the experiment conducted by Gunn et al. (2014), heifers were fed rations that easily exceeded CP requirement during late gestation. The majority of fetal programing experiments conducted in practical beef production systems have focused on late gestation because late gestation is a time of rapid fetal growth (Du et al., 2010; Funston et al., 2010a). However, the majority of skeletal muscle differentiation occurs during mid-gestation; thus, nutrient restriction during mid-gestation can negatively affect muscle fiber number (Du et al., 2010). In contrast to the previously discussed experiments, Long et al. (2010b) observed no differences in lamb birth BW when ewes were fed to 150% of NRC (1985) requirements throughout pregnancy relative to control-fed ewes. Ford et al. (2007) observed no differences in lamb birth BW regardless of whether dams were fed 50% or 100% of NRC (1985) requirements during mid- to late gestation.

Prepartum plane of nutrition during mid-gestation had no effect ($P \geq 0.23$) on calving date or milk production when measured at 100 ± 14 and 198 ± 14 d postpartum (Table 5.5). Because maternal treatments ceased 114 ± 14 d prepartum, no differences in milk production were expected. When comparing rations that differed in energy source during mid- to late gestation, Radunz et al. (2010) observed no differences in gestation length or milk production. Stalker et al. (2006) observed no difference in calving date when cows that were grazed on low-quality forage during late gestation were provided supplemental CP or not offered supplement. In, contrast, Gunn et al. (2014) observed longer gestation length when heifers were fed late gestation rations that exceeded CP requirement. The effects of prepartum nutrition on gestation length are not understood.

Maternal plane of nutrition had no effect ($P = 0.67$) on cow plasma glucose concentrations when measured before feeding and 3, 6, and 9 h post-feeding at the start of the treatment period (196 ± 14 d prepartum) or at the conclusion of the treatment period (114 ± 14 d prepartum; Figure 5.2). It is of note that there was an interaction ($P = 0.05$) between day prepartum and time of bleed for cow glucose concentrations. Glucose concentrations were decreased at 114 ± 14 d prepartum relative to 196 ± 14 d prepartum; however, the magnitude of the difference between the two days varied by time of bleed, especially at 6 h post-feeding. Also when measured before feeding and 3, 6, and 9 h post-feeding on 196 ± 14 and 114 ± 14 d prepartum, cow plasma insulin concentrations were not different ($P = 0.99$) across treatments (Figure 5.2).

Radunz et al. (2010) observed no differences in pre- or post-feeding plasma glucose concentrations when cows were fed either DDGS, corn, or hay as energy sources during mid- to late gestation. No differences in plasma glucose concentrations may be attributed to the fact that glucose concentrations are typically tightly regulated. Radunz et al. (2010) also observed no effect of prepartum energy source on plasma insulin concentrations. However, cows fed DDGS, did have greater insulin concentrations at 3 h post-feeding. Radunz et al. (2010) hypothesized that the greater dietary fat of DDGS initiated a greater post-feeding insulin response. In the current experiment, all cows were fed a common diet with DMI adjusted to achieve desired prepartum plane of nutrition. Thus, post-feeding insulin concentrations would not be affected by dietary source of energy.

Cow plasma BUN and NEFA concentrations were analyzed before feeding 196 ± 14 and 114 ± 14 d prepartum (Figures 5.3). Maternal plane of nutrition had no effect ($P = 0.23$) on plasma BUN concentrations; yet, there tended to be an interaction ($P = 0.10$) between maternal

plane of nutrition and d prepartum, as differences in BUN concentrations at 114 ± 14 d were greater than 196 ± 14 d prepartum. Lower BUN concentrations at 114 ± 14 d relative to 196 ± 14 d prepartum may be a reflection of the lower dietary protein concentration of the common diet fed during mid-gestation relative to the corn silage and MDGS diet fed before initiation of the experiment. At 114 ± 14 d prepartum, greater BUN concentration for cows fed 130%REQ relative to cows fed 70%REQ are a result of the divergent planes of nutrition during mid-gestation. Maternal plane of nutrition tended to affect (P = 0.10) plasma NEFA concentrations. At 114 ± 14 d prepartum, NEFA concentrations were greater for cows fed 70%REQ relative to those fed REQ and 130%REQ. Greater NEFA concentrations for cows fed 70%REQ confirms that these cows were in more negative energy balance relative to cows fed to 100% or 130% of requirement.

When analyzed 196 ± 14, 160 ± 14, and 114 ± 14 d prepartum, treatment had no effect (P = 0.98) on cow plasma progesterone concentrations and there was no interaction (P = 0.86) between treatment and d prepartum (Figure 5.3). Circulating progesterone concentrations during mid- and late gestation have been associated with placental weight and progeny birth BW (Sullivan et al., 2009). Radunz et al. (2010) observed that cows fed DDGS had greater plasma progesterone concentrations at 210 d of gestation; these same DDGS-fed cows also gave birth to heavier calves. The current experiment is in contrast to the findings of Radunz et al. (2010) as no differences in plasma progesterone concentrations were observed. Again, differences in blood components between the current experiment and the one conducted by Radunz et al. (2010) may stem from the fact that energy sources were similar across treatments in the current experiment.

Progeny Performance and Efficiency

Data concerning progeny BW, ADG, DMI, G:F, and compositional ultrasound are found in Table 5.6. There were no differences ($P \geq 0.27$) in progeny weaning BW or pre-weaning ADG. In agreement with the current experiment, Long et al. (2010b) observed no differences in lamb BW through 19 mo of age when dams were fed 100% or 150% of nutrient requirements throughout gestation. In contrast to the current experiment, lambs born to dams restricted to 50% of requirement were heavier at weaning when compared to lambs born to requirement-fed dams (Ford et al., 2007).

When measured at 100 ± 14 d age, ultrasound backfat tended ($P = 0.09$) to be greater in progeny born to REQ-fed dams relative to those from 70%REQ and 130%REQ dams. It is of note that differences in backfat at 100 ± 14 d age were less than 0.10 mm and may not be of biological significance. Also, at 100 ± 14 d age, ultrasound marbling score tended to be greater ($P = 0.09$) for progeny from 70%REQ dams relative to those from REQ and 130%REQ dams. This difference in marbling score for 70%REQ progeny at weaning (49 points greater than REQ and 72 points greater than 130%REQ) was decreased by time of weaning, and thus weaning ultrasound marbling scores were not different ($P = 0.81$) across treatments. At time of weaning, ultrasound backfat was also not different ($P = 0.19$) across treatments.

During the 30 d transition period, progeny ADG was greatest ($P < 0.01$) for progeny born to dams fed 70%REQ, least for progeny from REQ dams, with progeny from REQ dams intermediate and different from both. Finishing ADG tended ($P = 0.10$) to be greater for progeny from REQ and 130%REQ dams when compared to those from 70%REQ dams. Finishing F:G tended to be greater ($P = 0.10$) for progeny from 70%REQ and 130%REQ dams relative to those born to REQ fed dams. Decreased finishing F:G for calves born to dams fed REQ may be attributed to the fact that they consumed numerically greater DMI during the finishing period

than progeny born to 70%REQ and 130% dams (0.5 kg greater DMI than 70%REQ and 0.7 kg greater DMI than 130%REQ). However, finishing DMI was not different ($P = 0.34$) across treatments. Progeny BW at 298 ± 14 d of age and final BW were not different ($P \geq 0.22$). Ultrasound backfat at 298 ± 14 d of age was greatest ($P = 0.02$) for progeny from REQ dams relative to those from 70%REQ and 130%REQ dams. In contrast, Long et al. (2010b) observed greater adiposity and decreased lean tissue when evaluating body composition of lambs born to obese dams. Ultrasound marbling score at 298 ± 14 d of age was not different ($P = 0.18$); however, as with 100 ± 14 d age, marbling score for progeny from 70%REQ dams was numerically greater than progeny from REQ and 130%REQ dams (85 points higher than REQ and 86 points higher than 130%REQ). While physiologically significant, these differences may not have been statistically different due to the high standard errors (25 to 36 points) associated with measurement of marbling score via ultrasound.

To our knowledge, no previous fetal programming research has reported progeny performance during the transition period separate from finishing period performance. It is hypothesized that decreased transition ADG of progeny born to REQ-fed dams allowed for improved compensatory growth through the finishing period. Likewise, greater transition period ADG by progeny from 70%REQ dams may have led to decreased finishing ADG through the finishing period. It is of note that finishing F:G was similar for progeny born to 70%REQ and 130%REQ dams, with both being greater than progeny from REQ dams. This leads to the conclusion that maternal nutrient restriction and overfeeding represent similar models for fetal development.

Data concerning progeny RFI, RG, and methane emissions are found in Table 5.7. Maternal plane of nutrition had no effect ($P = 0.21$) on progeny RFI. There was a trend ($P =$

0.06) for progeny from REQ dams to have the lowest, least desirable RG relative to progeny from dams fed 70% REQ or 130%REQ. Lower RG for progeny from REQ dams coincides with these progeny having the lowest finishing G:F. It is of note that progeny born to 130%REQ dams had the most desirable combination of RFI and RG: lowest RFI and greatest RG.

Data concerning the fetal programing effects on feed efficiency of subsequent progeny is limited to experiments that have evaluated the effects of dam CP supplementation during late gestation on DMI, ADG, and RFI of subsequent heifer progeny developed on forage diets (Martin et al., 2007; Funston et al., 2010b). The work of Martin et al. (2007) and Funston et al. (2010b) indicates that maternal nutrient restriction during late gestation can result in heifer progeny that are more efficient later in life (greater F:G and lower RFI). However, Stalker et al. (2006) and Larson et al. (2009) observed no differences in feedlot efficiency of steer mates to the heifers used by Martin et al. (2007) and Funston et al. (2010b), respectively. Funston et al. (2010b) posed that that high rate of gain of steers fed feedlot diets may mask any fetally programmed feed efficiency differences expressed by heifers managed for lower rates of gain.

Maternal plane of nutrition had no effect ($P = 0.77$) on 24 h methane emissions. Decreasing enteric methane emissions is of interest in improving the sustainability and decreasing the carbon footprint of beef production. Total methane production could be decreased by simply selecting for animals that consume less DMI, thus lowering available rumen substrate for fermentation. However, selecting for lower daily methane emissions alone has the potential to negatively affect animal productivity. As a result, identifying animals that emit less methane per unit of feed intake is desirable. To quantify this, 24 h methane emissions were expressed per unit of DMI for: average DMI during the entire finishing period, DMI consumed by cattle while in the methane collection chamber, total DMI on d of methane collection (DMI consumed during

the 3 h period following feeding on the d of collection and entry into the collection chamber and additional feed intake while in the methane collection chamber), and average DMI consumed during the 3 d before methane collection. There were no treatment differences ($P \geq 0.11$) in measures of DMI; thus, no differences ($P \geq 0.21$) in methane per unit of feed intake were observed. Collection chamber DMI and total DMI on d of methane collection were substantially decreased relative to either average finishing DMI or average DMI the 3 d before methane collection. As a result, methane emissions expressed per unit of collection chamber DMI or total collection d DMI were greater, with 2 to 5 times greater standard errors, than when expressed over unit of average finishing DMI or previous 3 d DMI. Thus, expressing methane emissions over unit of average finishing DMI or average DMI 3 d prior to collection may provide a more reliable method to estimate methane emissions per unit of feed intake. To our knowledge, no previous research has attempted to correlate dam maternal plane of nutrition during mid-gestation and methane emissions of subsequent progeny. Nkrumah et al. (2006) and Hegarty et al. (2007) found that more feed efficient cattle produce less methane. However, cattle in these two experiments were selected for high and low feed efficiency, and thus, factors such as voluntary DMI may confound measures of methane production. The work of Freetly and Brown-Brandl (2013) correlated methane emissions across a population of cattle that varied in feed efficiency. Freetly and Brown-Brandl (2013) concluded that selection programs aimed at solely reducing methane emissions may decrease feed efficiency and increase days on feed to achieve desired endpoints, possibly increasing methane production over the life on the animal.

Progeny glucose tolerance

Data concerning plasma glucose and insulin concentrations from the GTT are shown in Figure 5.4. Maternal plane of nutrition during mid-gestation had no effect ($P = 0.95$) on glucose

concentrations during GTT. Maternal treatment also had no effect ($P = 0.78$) on insulin concentrations during GTT. There were no interactions ($P \geq 0.60$) between treatment and time of post-infusion for either glucose or insulin concentrations. Data concerning glucose and insulin kinetics during GTT are found in Table 5.8. Treatment did not affect ($P \geq 0.50$) glucose AUC, baseline glucose concentrations, or maximum glucose concentrations following infusion of glucose bolus. There were no differences ($P \geq 0.16$) in glucose clearance rate when calculated from 5 to 20 min post-infusion and 20 to 120 min post-infusion. Glucose clearance rate was calculated before and after 20 min post-infusion because this time point represented a substantial change in slope when glucose concentrations were plotted in Figure 5.4. There were also no differences ($P \geq 0.64$) in glucose half-life when calculated from 5 to 20 min and 20 to 120 min. Glucose half-life represents the amount of time required for glucose to decease by one half. There were also no differences ($P \geq 0.12$) in insulin AUC or baseline or maximum insulin concentrations. No differences ($P = 0.90$) in insulin to glucose ratio were observed.

Ford et al. (2007) evaluated the effects of maternal nutrient restriction during early gestation on progeny glucose tolerance by nutrient restricting ewes to 50% of NRC (1985) requirement. When GTT was conducted in lambs at 63 d of age, glucose and insulin AUC were greater in lambs born to nutrient restricted dams. When GTT was conducted in lambs at 250 d of age, glucose AUC remained greater in lambs born to nutrient restricted dams; yet, insulin AUC was decreased in progeny of nutrient restricted dams because of decreased initial insulin response. The reduction in initial insulin secretion may be due to β-cell deterioration following hyperinsulinemia earlier in life (Ford et al., 2007). Long et al. (2010b) investigated the effects of maternal obesity on glucose tolerance of subsequent progeny by overfeeding ewes 150% of NRC (1985) requirement throughout gestation. Lambs born to obese dams displayed similar glucose

and insulin homeostasis to lambs born to nutrient restricted dams (Long et al., 2010b). Greater glucose and insulin AUC with increased d on finishing diet was observed by Radunz et al. (2012). However, Radunz et al. (2012) observed greater initial insulin response with increased d on feed. In the current experiment, nutrient restriction or overfeeding during mid-gestation did not affect progeny glucose tolerance, or glucose and insulin kinetics. Also in the current experiment, a single GTT was conducted during the middle of the finishing period. Thus, no inferences can be made about the effect of d of age on progeny glucose tolerance. Gardner et al. (2005) determined that for instance of nutrient restriction during early or late gestation, nutrient restriction during late gestation had a more distinct effect on glucose and insulin metabolism than during early gestation.

Adiponectin is an insulin-sensitizing protein secreted by adipose tissue (Moisá et al., 2013b). Moisá et al. (2013b) also states that adiponectin promotes adipocyte differentiation and increases lipid accumulation in adipocytes. Maternal plane of nutrition had no effect ($P = 0.23$, data not shown) on plasma adiponectin concentrations when analyzed at time of LM biopsy (99 ± 14, 197 ± 14, and 392 ± 14 d of age; data not shown). There was also no interaction ($P = 0.18$) between maternal plane of nutrition and d of age for adiponectin concentrations. Plasma adiponectin concentrations did increase ($P = 0.04$) with d of age; which may be associated with greater adipose tissue mass with greater days on feed.

Progeny carcass characteristics

Data concerning progeny carcass characteristics are found in Table 5.9. Hot carcass weight was greater ($P = 0.04$) for progeny born to dams fed REQ relative to those from 70%REQ dams, with those from 130%REQ dams being intermediate. It is of note that progeny of REQ dams were numerically heavier throughout the finishing period. Despite progeny from REQ

dams having greater ultrasound backfat at 298 ± 14 d of age, carcass backfat was not different ($P = 0.44$). No differences ($P \geq 0.37$) were detected for KPH, LM area, yield grade, or marbling score. Prepartum plane of nutrition during mid-gestation had no effect ($P \geq 0.27$) on cook yield, WBSF, or intramuscular fat percentage of loin samples. It has been demonstrated that consumers consider steaks with WBSF values less than 5.5 kg to be tender (Platter et al., 2003), thus carcasses from all 3 treatments would be considered tender (WBSF shear force values of 2.52, 2.96, and 2.95 for 70%REQ, REQ, and 130%REQ, respectively). Also of note, progeny from 70%REQ dams tended to have greater ultrasound marbling at 100 ± 14 d of age and had numerically greater carcass marbling scores and intramuscular fat percentages of loin sample. It is acknowledged that power was not adequate to detect statistical differences in marbling; but, these numerical differences may represent biological significance. Much of the previous research that has investigated extreme maternal nutrient restriction of overfeeding has reported limited carcass data of subsequent progeny. Lambs born to ewes restricted to 50% of requirement during early gestation had greater HCW and kidney and pelvic fat (Ford et al., 2007). Underwood et al. (2010) observed greater HCW, backfat, and intramuscular fat of steers born to dams grazed on higher-quality, improved pastures during mid-gestation. The findings of Underwood et al. (2010) agree with the numerical differences observed for HCW and backfat between progeny born to 70%REQ and REQ-fed dams in the current experiment. More research needs to be done to determine the effects of maternal plane of nutrition during different stages of gestation on the carcass characteristics of subsequent progeny.

Gene expression

Data concerning abundance of mRNA for select genes is found in Figures 5.5 to 5.11. Expression of *FABP4*, *MYOD1*, *FASN*, *SCD*, *SLC2A4*, *YY1*, *PAX7*, *MEF2C*, *MYOG*, *PPARG*,

MYH2, and *MYH7* were not different ($P \geq 0.24$) by treatment. Expression of *PPARG* was of interest because of its role as a master regulator of adipocyte differentiation (Moisá et al., 2013b). The *PPARG* network also includes *SCD*, *FASN*, *FABP4*, and *SLC2A4* (Moisá et al., 2013b); and thus, expression of these genes in progeny LM were evaluated via qPCR in the current experiment. The synthesis of palmitate from acetyl-CoA and malonyl CoA is catalyzed by *FASN*, which encode the rate-limiting steps in fatty acid synthesis (Long et al., 2012). The function of *FABP4* is to facilitate delivery of long-chain fatty acids nuclear receptors in the adipocyte (Long et al., 2010a). The function of *SCD* is to desaturase a portion of stearic acid, with greater activity observed as days on a finishing diet increase (Moisá et al., 2013b). The primary insulin-sensitive glucose transporter, *GLUT4*, is encoded by *SLC2A4* (Moisá et al., 2013b). The expression of these genes in the *PPARG* network were observed to be greater in LM of beef steers that were early-weaned and placed on a high energy diet relative to those that were normal-weaned. In current experiment, no treatment differences in *PPARG*, *SCD*, *FASN*, *FABP4*, and *SLC2A4* expression may be because all dams were maintained as a single contemporary group and fed for maintenance after treatments ceased 114 ± 14 d prepartum. Maternal plane of nutrition during mid-gestation may not have elicited significant differences in expression of adipogenic gene targets because adipocyte development begins during mid-gestation, but continues through late gestation and 200 d of age (Wertz et al., 2002; Du et al., 2010; Meteer et al., 2013). Determination of degree of expression for *FABP4* may have been confounded that *FABBP4* expression is greater in adipose tissue, not muscle (Long et al., 2012). Thus level of expression of *FABP4* in LM may have varied with the percentage of intramuscular fat of LM. There was a treatment by progeny sex by d of age interaction ($P = 0.01$) for expression of *SCL2A4* (Figure 5.6) and *YY1*. At 99 ± 14 and 197 ± 14 d of age, abundance of

SLC2A4 mRNA was not different; however, at 392 ± 14 d of age, heifer progeny born to 70%REQ dams had decreased expression of *SLC2A4*. The treatment by sex interaction for expression of *SLC2A4* in LM may serve to explain differences in growth observed between steer and heifer progeny. With progeny of dams fed 70%REQ, greater *SLC2A4* expression by steers may facilitate greater uptake of glucose into muscle, and possibly the greater propensity for heifers to deposit subcutaneous adipose tissue relative to steers. However, in the current experiment, no treatment by progeny sex effects were observed for BW, LM area, or backfat.

Mid-gestation is a period of muscle cell differentiation from a group of pluripotent cells not previously dedicated to a certain cell type (Du et al., 2010). Du et al. (2010) also states the skeletal muscle cells mature by d 210 of gestation in beef cattle. Several genes known to affect muscle differentiation are: *MYOD1*, *MYOG*, *YY1*, *PAX7*, and *MEF2C* (Luo et al., 2013). Expression of *MYOD1* is related to regulation of several muscle specific microRNAs. Muscle specific micoRNAs serve to inhibit expression of muscle regulatory factors that either promote or inhibit muscle differentiation. Using samples of LM from progeny of the current experiment, McCann et al. (2015) found differences in muscle specific microRNAs when cows were reclassified by ADG during the treatment period. When expressed, *MYOG* triggers myoblasts, in the second stage of muscle differentiation, to differentiate into myotubes, the second phase of differentiation (Luo et al., 2013). Luo et al. (2013) also states that *PAX7* inhibits cell apoptosis in order to maintain a pool of satellite cells for proliferation; thus, muscle differentiation is delayed unless *PAX7* is inhibited. In non-ruminants, *YY1* is a transcription factor with an inhibitory role in muscle gene transcription and indirectly targets *PPARG* (Luo et al., 2013; Moisá et al., 2013a). The role of *MEF2C* is to serve as a promotor for skeletal muscle differentiation (Luo et al., 2013). There was a treatment by progeny sex by d of age interaction ($P = 0.01$) for

expression of *YY1* (Figure 5.9). At 99 ± 14 and 197 ± 14 d of age, abundance of *YY1* mRNA was not different; however, at 392 ± 14 d of age, heifer progeny born to 70%REQ dams had decreased expression of *YY1*. There was a progeny sex by d of age interaction ($P = 0.04$) for expression of *MEF2C.* At 99 ± 14 and 197 ± 14 d of age, *MEF2C* expression was not different between sexes; however, at 392 ± 14 d of age, abundance of *MEF2C* mRNA was greater in LM of steer progeny relative to heifer progeny. Few treatment differences in genes associated with skeletal muscle differentiation may be a reflection of timing of treatments, maternal planes of nutrition not being divergent enough to affect change, or other muscle regulatory factors, such as microRNAs.

There was an interaction ($P = 0.04$) between maternal plane of nutrition and day of age for *MYH1* mRNA abundance (Figure 5.10). Expression of *MYH1* was not different at 99 ± 14 and 197 ± 14 d of age; however, expression of *MYH1* was decreased at 392 ± 14 d of age in LM of 70%REQ progeny relative to REQ and 130% progeny. Main effect of treatment and day of age for expression of *MYH7* was not significant ($P \geq 0.25$); but, there was a treatment by day of age interaction ($P = 0.04$) for abundance of *MYH7* mRNA (Figure 5.11). There was a treatment by progeny sex by d of age interaction for expression of *MYH7* ($P < 0.01$; Figure 5.11). For heifers, abundance of *MYH7* at 99 ± 14 and 197 ± 14 d of age was not different; however, at 392 ± 14 d of age, progeny born to 130%REQ dams had greater expression of *MYH7* than progeny born to 70%REQ dams, with those born to REQ dams intermediate and different from both. For steers, abundance of *MYH7* at 99 ± 14 and 392 ± 14 d of age was not different; however, at 197 ± 14 d of age, progeny born to REQ dams had greater expression of *MYH7* relative to progeny born to 70%REQ or 130%REQ dams.

The genes *MYH1*, *MYH2*, and *MYH7* are associated with the myosin heavy chains IIx, IIa, and I, respectively, in skeletal muscle (Clark et al., 2011). When ewes were restricted to 50% of NRC (1985) requirements during mid-gestation, percentage of IIx and I muscle fiber types were unchanged in 8 mo old lambs relative to lambs born to requirement-fed dams (Zhu et al., 2006). However, percentage of IIa fibers was decreased and percentage of IIb fibers increased in lambs born to nutrient restricted dams. Expression of genes encoding the myosin heavy chain for type IIb fibers were not analyzed via qPCR in the current experiment and has not been detected in previously published research (Underwod et al. 2010). Underwood et al. (2010) observed no difference in ratio of type I to type II muscle fiber types when dams were grazed on pastures of differing forage quality during mid-gestation.

Despite few treatment difference in the genes targeted in the current experiment, there were significant differences ($P \leq 0.03$) in mRNA abundance of all analyzed genes, except for *MYH7*, as progeny d of age increased. Expression of *PPARG*, *FASN*, and *FABP4* decreased from 99 ± 14 to 197 ± 14 d of age and then was greatest at 392 ± 14 d of age (Figure 5.5). Expression of *SCD* was constant from 99 ± 14 to 197 ± 14 d of age and then increased during the finishing period (Figure 5.5). Expression of *SLC2A4* decreased a d of finishing period decreased as d of the finishing period increased. Expression of *MYOD1* and *YY1* were greatest at 197 ± 14 d of age and was similar at 99 ± 14 to 392 ± 14 d of age; Figures 5.7 and 5.9, respectively. Expression of *MYOG*, *MEF2C*, and *PAX7* were decreased as d of age increased (Figure 5.7). Expression of *MYH1* and *MYH2* increased and decreased from 197 ± 14 to 392 ± 14 d of age, respectively (Figure 5.10). These changes in expression of genes associated with the *PPARG* network over time may be associated with increased adipogenesis before weaning and later during the finishing period as deposition of adipose tissues increases substantially. Decreased expression of

SLC2A4 during the finishing period may also coincide with decreased insulin response and glucose uptake in LM and greater increase in subcutaneous adipose tissue. The expression pattern over time of *MYOD1*, *MYOG*, *MEF2C*, *YY1*, and *PAX7* indicate that regulation of muscle cell differentiation substantially declines after 197 ± 14 d of age.

Type I muscle fiber types are known to be more insulin sensitive that type II muscle fiber types (Zhu et al., 2006). It was the author's hypothesis that in the current experiment, maternal plane of nutrition would influence muscle fiber type in progeny LM, and thus, affect insulin sensitivity of progeny. Maternal plane of nutrition did result in several differences in muscle fiber type of progeny LM; however, muscle fiber type appears to be more dramatically influenced by d of age. It is accepted that insulin resistance increases as d on a high-energy diet increase (Ford et al., 2007; Radunz et al., 2012). Greater insulin resistance observed in other experiments may be correlated with the observed increase in highly glycolytic type IIx muscle fibers and decrease in type IIa fibers types, which more closely resemble insulin-sensitive type I muscle fibers.

Because dam plane of nutrition during mid-gestation had few effects on gene expression in progeny LM, values for abundance of mRNA for all 3 biopsy dates were correlated to the following observed phenotypic outcomes: cow ADG during mid-gestation and progeny birth BW, RFI, RG, methane production, glucose and insulin AUC, HCW, carcass backfat, carcass LM area, carcass marbling score, and WBSF. Pearson correlation coefficients for mRNA abundance at 99 ± 14, 197 ± 14, and 392 ± 14 d of age are found in Figures 5.12, 5.13, and 5.14, respectively. Correlation of gene expression with progeny birth BW, HCW, backfat, LM area was greatest at 99 ± 14 d of age. Generally, Adipogenic genes (*FASN* and *SCD*) were negatively correlated with progeny birth BW, HCW, and LM area. Also at 99 ± 14 d of age, factors that

affect muscle fiber differentiation (*YY1*, *Pax7*, and *MEF2C*) were negatively correlated with backfat. These data indicate that epigenetic regulation of potential growth rate and body lean and adipose composition may be most active at a young age, before most beef animals are weaned. These findings may provide support to the theory of developmental programming and that early calf nutrition serves to affect muscle and adipocyte differentiation. It should be acknowledged that phenotypic variables, such as HCW, are the sum of activity of many complex gene networks. Thus the effects of mRNA abundance for a specific gene may not directly affect observed phenotypic variables. In the current experiment, IGF-1 and growth hormone, which are known to have great influence of mammalian growth, were not analyzed. At 197 ± 14 d of age, *FASN*, *SCD*, and *PPARG* were negatively correlated with progeny RFI; but were positively correlated with RFI at 392 ± 14 d of age. Also at 392 ± 14 d of age, *SLC2A4* and *YY1* were positively correlated with RFI. Expression of genes associated with measure of feed efficiency is complex and fluid over time. The contributions of these genes to RFI are not understood, but may serve to provide future genes of interest when further investigating epigenetic control of feed efficiency.

Implications

Feeding cows to 70%, 100%, or 130% of requirement during mid-gestation resulted in greater BW of overfed cows and decreased BW and BCS of nutrient restricted cows at 114 ± 14 d prepartum, when treatments ceased. When realimented to common ration during late gestation, cow BW and BCS were not different at 7 ± 7 d prepartum. However diverging plane of nutrition during mid-gestation did impart lifelong effects on progeny ADG, feed efficiency, and HCW. However, restricting cows to 70% or overfeeding cows to 130% of nutrient requirements during

mid-gestation did not impart as dramatic of effects on insulin sensitivity or treatment differences in gene expression as observed in experiments that have nutrient restricted or overfed dams to a greater degree.

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Tables and Figures

Table 5.1. Composition and nutrient density of treatment and post-calving diets.

Item	Treatment Diet[1,3]	Common Diet[2,4]
Ingredient, % DM		
Corn silage	52.8	87.0
Alfalfa haylage	23.6	--
Soy hulls	23.6	--
Modified wet distillers grains with solubles		13.0
Analyzed nutrient content, %DM		
DM	47.0	32.6
CP	11.6	11.8
NDF	47.0	43.7
ADF	34.3	22.7
Fat	2.2	2.9

[1] Cows were fed the treatment diet 196 ± 14 d to 114 ± 14 d prepartum and received the following DMI: 5.2 kg for cows fed to 70% of NRC (1996) requirement (70%REQ), 7.4 kg for cows fed to 100% of NRC requirement (REQ), and 9.7 kg for cows fed to 130% of NRC requirement (130%REQ)

[2] Cows were fed 8.5 kg DMI during late gestation and 9.5 kg DMI postpartum of the common diet

[3] Given ad libitum access to trace-mineral salt: 42.2% Salt, 10.5% Ca (monocalcium phosphate), 11.2% P (monocalcium phosphate), 0.53% Mg (MgO and MgSO4), 0.80% K (KCl2), 1.06% S (S8, prilled), 0.21 % Fe (FeSO4), 0.32% Zn [ZnSO4 and Availa-4 (Zinpro Performance Minerals; Zinpro Corp, Eden Prairie, MN)], 4.3 mg/kg Co (Availa-4), 100. mg/kg I (Ca(IO3)2), 532.2 mg/kg Cu (Availa-4), 3,193.4 mg/kg Mn (MnSO4 and Availa-4), 16 mg/kg Se (Na2SeO3), 165,941 IU/kg vitamin A, 37,884 IU/kg vitamin D_3, 1,858 IU/kg vitamin E

[4]Given ad libitum access to trace-mineral salt: 69.8% Salt, 4.6% Ca (dicalcium phosphate and CaCO3), 2.58% P (dicalcium phosphate), 0.2% Mg (MgO and MgSO4), 0.02% K (KCl2), 0.3% S (S8, prilled), 1.34 % Fe (FeSO4), 1.1% Zn (ZnSO4 and Availa-4), 1.3 mg/kg Co (Availa-4), 112 mg/kg I (Ca(IO3)2), 3,419 mg/kg Cu (Availa-4), 2,190 mg/kg Mn (MnSO4 and Availa-4), 32 mg/kg Se (Na2SeO3), 6,640 IU/kg vitamin A, 664 IU/kg vitamin D_3, 89 IU/kg vitamin E

Table 5.2. Composition and nutrient density of common feedlot diet

Item	
Ingredient, % DM	
Modified wet distillers grains with solubles	45
Cracked corn	25
Corn Silage	20
Supplement[1]	10
Analyzed nutrient content, % DM	
DM	59.7
CP	18.0
NDF	28.2
ADF	20.0
Fat	4.8
NE_g[2], kcal/kg	1.23

[1] Supplement contained: 72.8% Ground corn, 25.0% Limestone, 1.0% Trace mineral salt (8.5% Ca [CaCO3], 5% Mg [MgO and MgSO4], 7.6% K [KCl2], 6.7% Cl [KCl2] 10% S [S8, prilled], 0.5% Cu [CuSO4 and Availa-4 (Zinpro Performance Minerals; Zinpro Corp, Eden Prairie, MN)], 2% Fe [FeSO4], 3% Mn [MnSO4 and Availa-4], 3% Zn [ZnSO4 and Availa-4], 278 mg/kg Co [Availa-4], 250 mg/kg I [Ca(IO3)2], 150 mg/kg Se [Na2SeO3], 2,205 KIU/kg VitA [retinyl acetate], 662.5 KIU/kg VitD [cholecalciferol], 22,047.5 IU/kg VitE [DL-α-tocopheryl acetate]), 0.75% Liquid fat, 0.17% Rumensin 90 (Monensin 198 g/kg; Elanco Animal Health, Greenfield, IN), 0.11% Tylan 40 (Tylosin 88 g/kg, Elanco Animal Health).

[2] NE_g value back-calculated from animal performance using NRC (1996)

Table 5.3. Gene ID, GenBank accession number, sequence and amplicon size of primers used to analyze gene expression by qPCR.

Accession #	Gene	Direction[1]	Primer sequence (5' to 3')	bp[2]
NM_001037471.2	*UXT*	F	TGTGGCCCTTGGATATGGTT	101
		R	GGTTGTCGCTGAGCTCTGTG	
NM_001025327.2	*MTG1*	F	CTTGGAATCCGAGGAGCCA	101
		R	CCTGGGATCACCAGAGCTGT	
NM_001037443.2	*RPS15A*	F	GAATGGTGCGCATGAATGTC	101
		R	GACTTTGGAGCACGGCCTAA	
NM_174314.2	*FABP4*	F	TGGTGCTGGAATGTGTCATGA	101
		R	TGGAGTTCGATGCAAACGTC	
NM_001040478.2	*MYOD1*	F	CCCAAAGATTGCGCTTAAGTG	101
		R	GGCGGAAACACAACAGTTCCT	
NM_001012669.1	*FASN*	F	ACCTCGTGAAGGCTGTGACTCA	92
		R	TGAGTCGAGGCCAAGGTCTGGAA	
NM_173959.4	*SCD*	F	CCAAATATCGGTGGGAGTCG	101
		R	ACAGCGAAGGGCTCACTTCTC	
NM_174604.1	*SLC2A4*	F	CCTTGGTCCTTGGCGTATTC	102
		R	TGTAGCTCTGTTCAATCACCTTCTG	
NM_001098081.1	*YY1*	F	ACGACACCAACTGGTCCATACTG	100
		R	CACATGTGTGCGCAAATTGA	
XM_002685738.4	*PAX7*	F	AGATCGAGGAGTACAAGAGGGA	111
		R	TCACTAAACCTGAGGGCACG	
NM_001046113.1	*MEF2C*	F	CAGTCATTGGCTACCCCAGT	152
		R	GCGGTGTTAAAGCCAGAGAG	
NM_001111325.1	*MYOG*	F	TACCGAGGCGGGGGC	120
		R	CAGATGATCCCCTGGGTTGG	
NM_181024.2	*PPARG*	F	CCAAATATCGGTGGGAGTCG	101
		R	ACAGCGAAGGGCTCACTCTC	
NM_174117.1	*MYH1*	F	AGGTGAATTCTCACGCCAGC	136
		R	CAGGGCACTCTTGCCTTTA	
NM_001166227.1	*MYH2*	F	GCTTGCAAGATGAATCTGGTG	146
		R	GGCATTCTTGGCCTTA	
NM_174727.1	*MYH7*	F	TTCCGGCAGAGGTATCGAAT	128
		R	TGGCCCGAACTTATACTGGTTTGTG	

[1]Primer direction

[2]amplicon size in base pairs (bp)

Table 5.4. Indicators of qPCR performance.

Gene	Median Ct[1]	Median Δct[2]	Slope[3]	(R^2)[4]	Efficiency[5]	Relative mRNA abundance[6]
UXT	24.757	1.737	-3.166	0.987	2.07	0.283
MTG1	23.572	0.572	-3.276	0.994	2.02	0.669
RPS15A	20.885	-2.123	-3.244	0.997	2.03	4.512
FABP4	22.186	-0.791	-3.117	0.994	2.09	1.794
MYOD1	23.332	0.227	-3.131	0.996	2.09	0.846
FASN	23.834	0.995	-3.414	0.995	1.96	0.511
SCD	21.878	-1.053	-3.295	0.995	2.01	2.087
SLC2A4	22.752	-0.214	-3.100	0.988	2.10	1.172
YY1	23.548	0.593	-3.362	0.994	1.98	0.666
PAX7	31.073	8.166	-3.229	0.989	2.04	0.003
MEF2C	21.248	-1.775	-3.222	0.993	2.04	3.555
MYOG	26.398	3.333	-3.347	0.978	1.99	0.101
PPARG	28.697	5.700	-3.251	0.988	2.03	0.018
MYH1	16.020	-6.996	-3.272	0.995	2.02	137.395
MYH2	14.617	-8.319	-3.236	0.992	2.04	372.465
MYH7	16.918	-6.032	-3.148	0.991	2.08	82.491

[1]Calculated considering all time points and all calves

[2]Calculated as $\mathrm{Ct\ gene} - \mathrm{geametricic\ mean\ of\ Ct\ internal\ control\ genes}$, for each time point and each calf

[3]Slope of the standard curve

[4]Coefficient of determination of the standard curve

[5]Calculated as $10^{(-1/\mathrm{Slope})}$

[6]Calculated as $1/\mathrm{Efficiency}^{\mathrm{Median\ \Delta ct}}$

Table 5.5. Effects of maternal plane of nutrition during mid-gestation on cow ADG, calving date, and milk production.

	Treatment[1]				
Item[2]	70%REQ	REQ	130%REQ	SEM	*P*-value
ADG, kg/d					
Mid-gestation	0.09[b]	0.76[a]	1.05[a]	0.11	<0.01
Late gestation	1.19	0.94	0.82	0.13	0.15
Overall	0.72[b]	0.87[a]	0.93[a]	0.05	0.02
Calving date, Julian d	115	118	115	2	0.67
Milk production, kg/d					
100 ± 14 d	7.6	11.0	11.1	1.8	0.23
198 ± 14 d	8.7	10.6	10.2	1.0	0.36

[1]70%REQ = cows fed to 70% of NRC (1996) requirement, REQ = cows fed to 100% of NRC requirement, 130%REQ = cows fed to 130% of NRC requirement; treatments were applied from 196 ± 14 d to 114 ± 14 d prepartum

[2]Cow ADG, calving date, and milk production reported for 30 cows (70%REQ = 10, REQ = 11, 130%REQ = 9), 3 pens per treatment

Table 5.6. Effects of maternal plane of nutrition during mid-gestation on progeny pre-weaning, transition, and finishing performance.

	Treatment[1]				
Item[2]	70%REQ	REQ	130%REQ	SEM	*P*-value
BW, kg					
Birth	41	35	39	1	0.08
100 ± 14 d	147	149	140	6	0.59
Weaning[3]	230	245	231	9	0.44
End of Transition[4]	284	293	281	11	0.74
298 ± 14 d	388	401	379	12	0.47
Final BW[5]	526	556	535	14	0.22
ADG, kg/d					
Pre-weaning	0.96	1.06	0.99	0.04	0.27
Transition	1.77[a]	1.50[c]	1.62[b]	0.04	<0.01
Finishing	1.46	1.56	1.55	0.03	0.10
DMI, kg/d					
Transition	8.5	8.4	8.4	0.4	0.99
Finishing	11.1	11.6	10.9	0.3	0.34
G:F					
Transition	0.198	0.183	0.186	0.006	0.18
Finishing	0.140	0.128	0.140	0.004	0.06
Ultrasound measurements					
Backfat[6], cm					
100 ± 14 d	0.32	0.41	0.33	0.03	0.09
Weaning[3]	0.30	0.38	0.36	0.03	0.19
298 ± 14 d	0.68[b]	0.83[a]	0.71[b]	0.34	0.02
Marbling score[7]					
100 ± 14 d	490	441	418	25	0.09
Weaning[3]	382	359	352	36	0.81
298 ± 14 d	456	371	370	35	0.18

[1]70%REQ = dams fed to 70% of NRC (1996) requirement, REQ = dams fed to 100% of NRC requirement, 130%REQ = dams fed to 130% of NRC requirement; treatments were applied from 196 ± 14 d to 114 ± 14 d prepartum

[2]Progeny pre-weaning, transition, and post-weaning performance reported for 27 calves (70%REQ = 10, REQ = 9, 130%REQ = 8), 3 pens per treatment

[3]Weaning BW taken on 198 ± 14 d of age

[4]BW of feedlot progeny taken 30 d post-weaning

[5]Final BW was recorded 13 d before slaughter on 2 consecutive d

[6]12th rib fat thickness

[7]400-499 = Small, 500-599 = Modest, 600-699 = Moderate, 700-799 = Slightly Abundant

Table 5.7. Effects of maternal plane of nutrition during mid-gestation on measures of progeny efficiency and methane production.

	Treatment[1]				
Item[2]	70%REQ	REQ	130%REQ	SEM	*P*-value
RFI, kg	0.09	0.06	-0.22	0.13	0.21
RG, kg	0.01	-0.10	0.05	0.04	0.06
24 h methane emissions, g	102.8	91.8	101.7	11.7	0.77
DMI, kg					
Finishing[3]	11.1	11.6	10.9	0.3	0.34
Collection Chamber[4]	3.8	2.6	3.3	0.4	0.11
D of collection[5]	5.6	4.9	5.9	0.5	0.41
Previous 3 d[6]	10.2	10.9	9.7		0.62
Methane per unit DMI, g/kg					
Finishing DMI	9.3	7.9	9.3	0.9	0.45
Collection Chamber DMI	27.1	35.3	30.8	5.1	0.21
D of collection DMI	18.4	18.7	17.2	2.2	0.86
Previous 3 d DMI	10.1	8.4	10.5	1.3	0.50

[1]70%REQ = dams fed to 70% of NRC (1996) requirement, REQ = dams fed to 100% of NRC requirement, 130%REQ = dams fed to 130% of NRC requirement; treatments were applied from 196 ± 14 d to 114 ± 14 d prepartum

[2]Progeny RFI, RG, and methane production reported for 27 calves (70%REQ = 10, REQ = 9, 130%REQ = 8), 3 pens per treatment

[3]Average DMI during the entire finishing period

[4]DMI consumed by cattle while in the methane collection chamber

[5]Total DMI on d of methane collection: DMI consumed during a 3 h period before entry into the collection chamber and DMI consumed in the collection chamber

[6]Average DMI consumed during the 3 d before methane collection

Table 5.8. Effects of maternal plane of nutrition during mid-gestation on glucose and insulin kinetics of subsequent progeny after an intravenous glucose tolerance test.

	Treatment[1]				
Item[2]	70%REQ	REQ	130%REQ	SEM	*P*-value
Glucose					
AUC[3]	386	302	402	61	0.50
Baseline, mmol/L	5.10	5.48	4.88	0.35	0.50
Maximum conc., mmol/L	13.91	14.44	13.72	0.74	0.78
Clearance Rate, %/min					
5 to 20 min post-infusion	2.46	1.93	2.01	0.22	0.16
20 to 120 min post-infusion	0.44	0.41	0.49	0.07	0.74
Half-life, min					
5 to 20 min post-infusion	33.83	39.46	38.09	5.79	0.67
20 to 120 min post-infusion	172.47	190.60	150.18	29.77	0.64
Insulin					
AUC[3]	37,171	34,489	53,972	6,457	0.12
Baseline, pmol	142.22	139.51	107.25	23.02	0.42
Maximum conc., pmol/L	1,155.94	1,095.60	1,383.13	302.44	0.71
Insulin to glucose ratio[4]	129	119	140	32	0.90

[1]70%REQ = dams fed to 70% of NRC (1996) requirement, REQ = dams fed to 100% of NRC requirement, 130%REQ = dams fed to 130% of NRC requirement; treatments were applied from 196 ± 14 d to 114 ± 14 d prepartum

[2]Progeny glucose and insulin kinetics reported for 26 calves (70%REQ = 10, REQ = 8, 130%REQ = 8), 3 pens per treatment

[3]Area under the curve

[4]Ratio of glucose AUC to insulin AUC

Table 5.9. Effects of maternal plane of nutrition during mid-gestation on progeny carcass characteristics.

	Treatment[1]				
Item[2]	70%REQ	REQ	130%REQ	SEM	*P*-value
HCW, kg	333[b]	360[a]	339[ab]	8	0.04
Backfat, cm[3]	1.27	1.39	1.23	0.10	0.44
KPH, %	2.2	2.0	2.2	0.1	0.37
LM area, cm^2	83.8	87.5	84.7	2.9	0.63
Yield grade	2.9	3.1	3.0	0.2	0.91
Marbling score[4]	457	427	419	31	0.65
Cook Yield, %	78.7	78.6	77.3	1.1	0.54
WBSF[5], kg	2.52	2.96	2.95	0.21	0.27
Intramuscular fat, %	6.05	4.98	5.23	0.91	0.68

[1]70%REQ = dams fed to 70% of NRC (1996) requirement, REQ = dams fed to 100% of NRC requirement, 130%REQ = dams fed to 130% of NRC requirement; treatments were applied from 196 ± 14 d to 114 ± 14 d prepartum

[2]Progeny carcass characteristics reported for 27 calves (70%REQ = 10, REQ = 9, 130%REQ = 8), 3 pens per treatment

[3]12^{th} rib fat thickness, cm

[4]400-499 = Small, 500-599 = Modest, 600-699 = Moderate, 700-799 = Slightly Abundant

[5]Warner-Bratzler Shear Force

Figure 5.1. Effects of maternal plane of nutrition during mid-gestation on cow BW, BCS, and 12th rib backfat thickness.

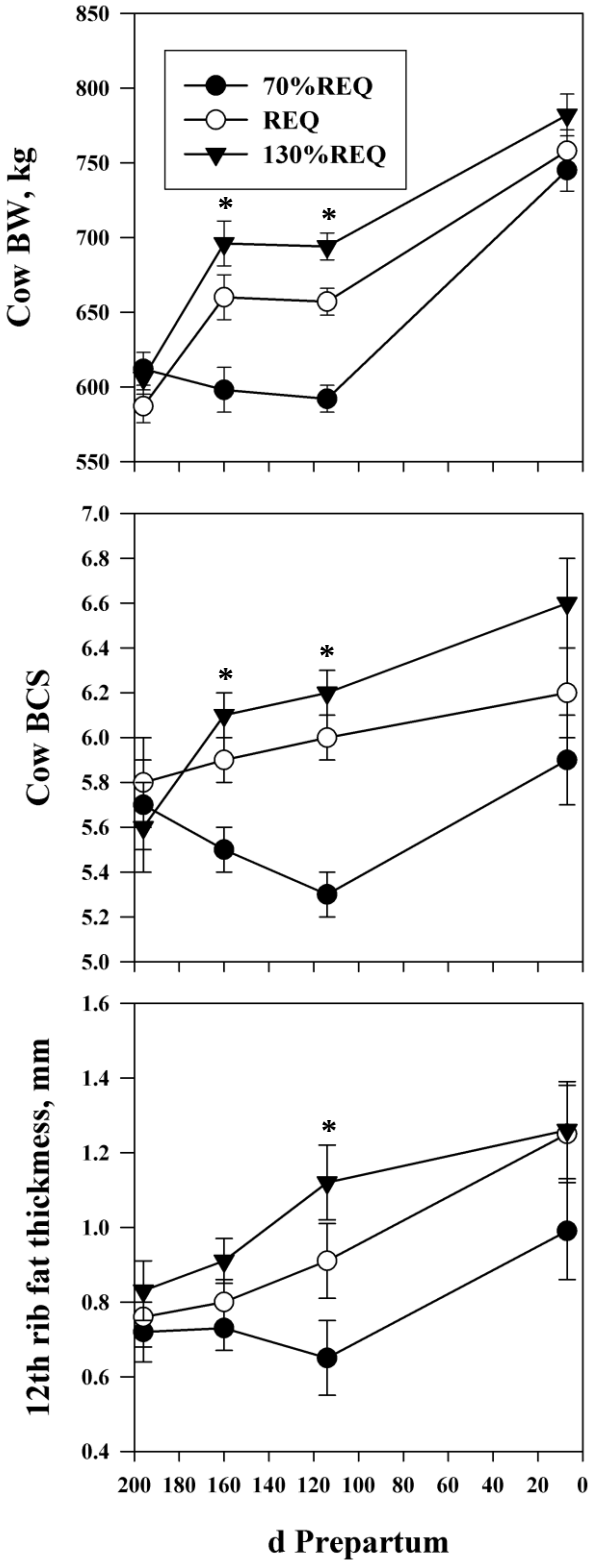

Figure 5.1 (cont.). Effects of maternal plane of nutrition during mid-gestation on cow BW, BCS, and 12th rib backfat thickness when recorded 196 ± 14 d, 160 ± 14 d, 114 ± 14 d, and 7 ± 7 d prepartum. Cows (n = 3 pens per treatment, 30 cows total) were limit-fed to provide 700% NRC (1996) requirement (70%REQ), 100% NRC requirement (REQ), or 130% NRC requirement (130%REQ). **Notes:** within d, differences in Treatment marked with * differ $P \leq 0.05$.

Figure 5.2. Effects of maternal plane of nutrition during mid-gestation on cow plasma glucose and insulin concentrations.

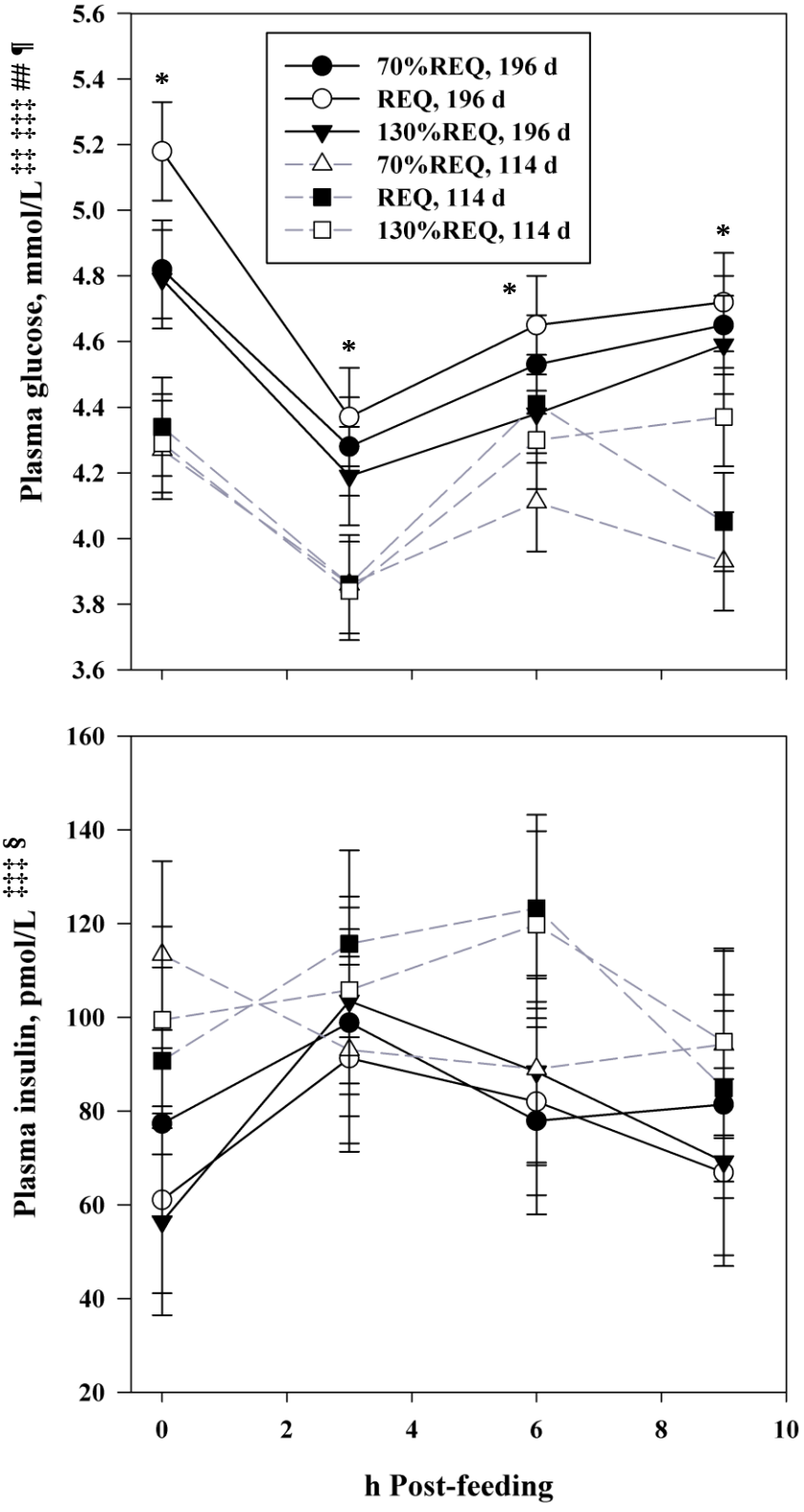

Figure 5.2 (cont.). Effects of maternal plane of nutrition during mid-gestation on cow plasma glucose and insulin concentrations 0, 3, 6, and 9 h post-feeding. Glucose concentrations were analyzed 196 ± 14 d and 114 ± 14 d prepartum. Cows (n = 3 pens per treatment, 30 cows total) were limit-fed to provide 70% NRC (1996) requirement (70%REQ), 100% NRC requirement (REQ), or 130% NRC requirement (130%REQ). **Notes:** within d, differences in Treatment marked with * differ $P \leq 0.05$, ‡‡ Time of bleed $P \leq 0.01$, **§** Time of bleed $P = 0.06$, ## Treatment by d prepartum interaction $P = 0.09$, ¶ d prepartum by time of bleed interaction $P = 0.05$, ‡‡‡ d prepartum $P < 0.01$.

Figure 5.3. Effects of maternal plane of nutrition during mid-gestation on cow plasma blood urea nitrogen, NEFA, and progesterone concentrations.

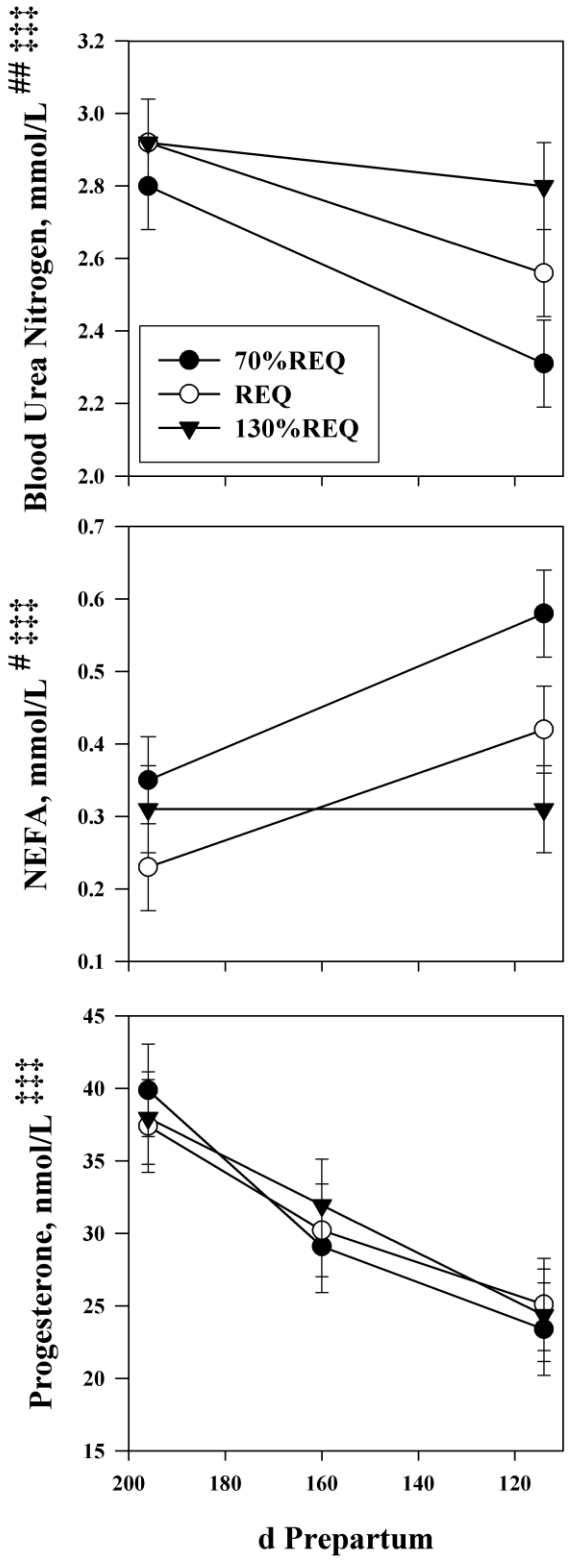

Figure 5.3 (cont.). Effects of maternal plane of nutrition during mid-gestation on cow plasma blood urea nitrogen (**BUN**), NEFA, and progesterone concentrations when analyzed before feeding. Blood was analyzed 196 ± 14 d and 114 ± 14 d prepartum. Cows (n = 3 pens per treatment, 30 cows total) were limit-fed to provide 70% NRC (1996) requirement (70%REQ), 100% NRC requirement (REQ), 130% NRC requirement (130%REQ). **Notes:** # Treatment $P = 0.10$, ## Treatment by d prepartum interaction $P = 0.10$, ¶ d prepartum by time of bleed interaction $P = 0.05$, ‡‡‡ d prepartum $P \leq 0.02$.

Figure 5.4. Effects of maternal plane of nutrition during mid-gestation on plasma glucose and insulin concentrations of subsequent progeny after an intravenous glucose tolerance test.

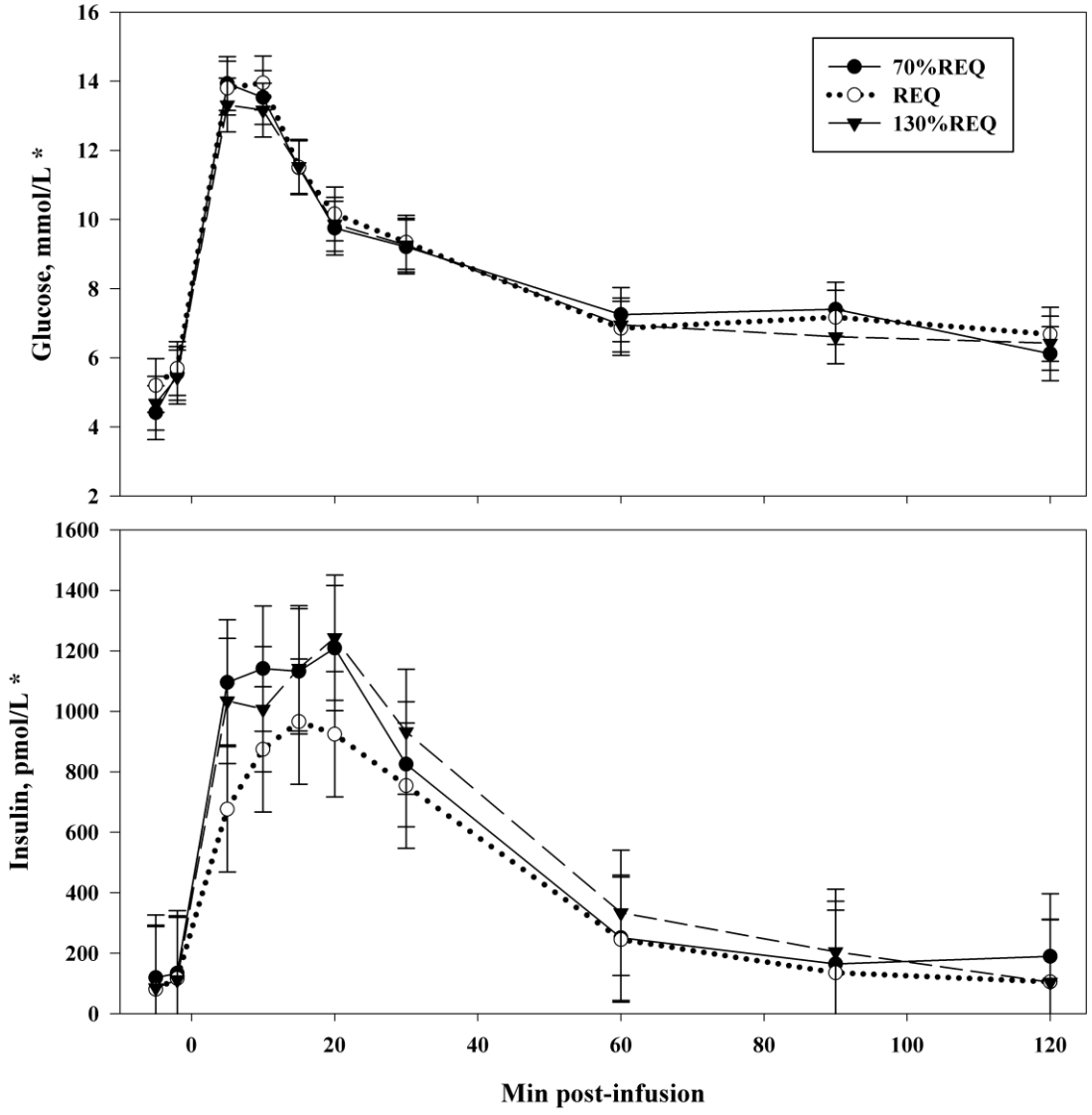

Figure 5.4. Effects of maternal plane of nutrition on plasma glucose and insulin concentrations following intravenous glucose tolerance test conducted on318 ± 14 d of age. Dams were limit-fed to provide 70% NRC (1996) requirement (70%REQ), 100% NRC requirement (REQ), or 130% NRC requirement (130%REQ). **Notes: *** Time of bleed $P < 0.01$.

Figure 5.5. Expression of *PPARG*, *FASN*, *FABP4*, and *SCD* mRNA in LM of progeny born to dams fed differing maternal planes of nutrition during mid-gestation.

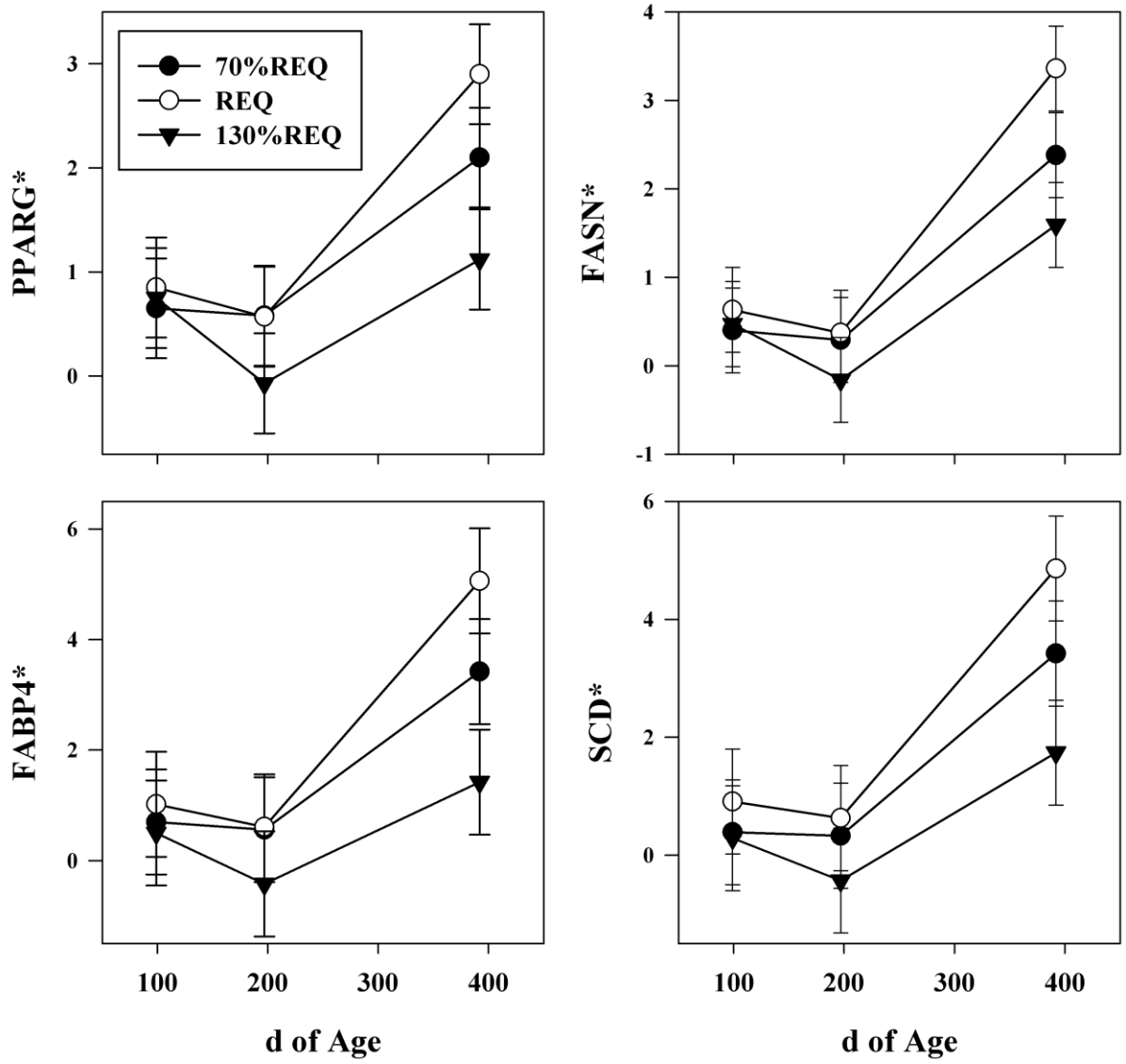

Figure 5.5. Expression of *PPARG*, *FASN*, *FABP4*, and *SCD* mRNA in LM of progeny born to dams fed differing maternal planes of nutrition during mid-gestation. Dams were limit-fed to provide 70% NRC (1996) requirement (70%REQ), 100% NRC requirement (REQ), or 130% NRC requirement (130%REQ). **Notes: *** d of age $P \leq 0.01$.

Figure 5.6. Expression of *SLC2A4* in LM of progeny born to dams fed differing maternal planes of nutrition during mid-gestation.

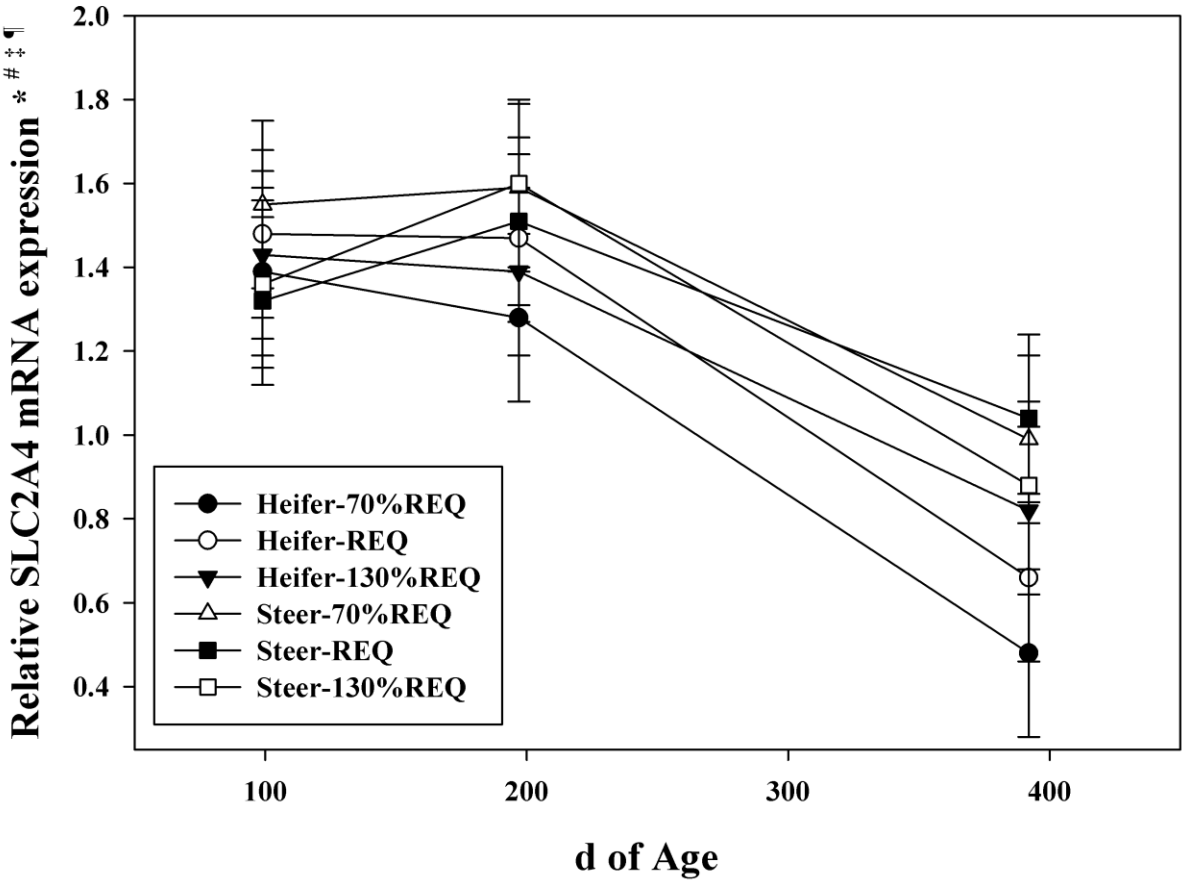

Figure 5.6. Expression of *SLC2A4* in LM of progeny born to dams fed differing maternal planes of nutrition during mid-gestation. Dams were limit-fed to provide 70% NRC (1996) requirement (70%REQ), 100% NRC requirement (REQ), or 130% NRC requirement (130%REQ). **Notes: *** d of age $P \leq 0.01$, # Sex by d of age interaction $P \leq 0.01$, ‡ Treatment by progeny sex interaction $P = 0.04$, ¶ Treatment by progeny sex by d of age interaction $P = 0.01$.

Figure 5.7. Expression of *MYOD1*, *FASN*, *MYOG*, *MEF2C*, and *PAX7* mRNA in LM of progeny born to dams fed differing maternal planes of nutrition during mid-gestation.

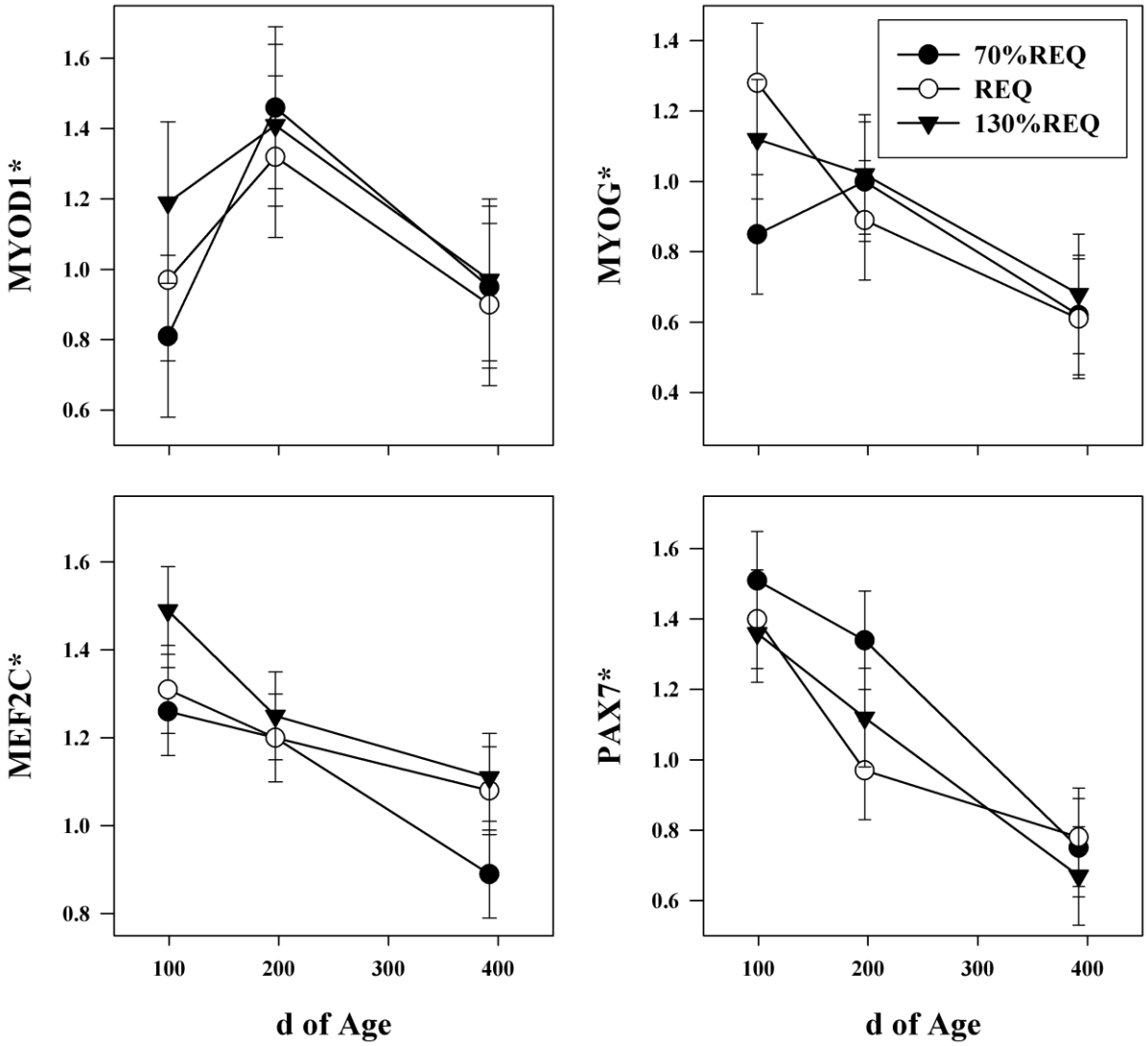

Figure 5.7. Expression of *MYOD1*, *FASN*, *MYOG*, *MEF2C*, and *PAX7* mRNA in LM of progeny born to dams fed differing maternal planes of nutrition during mid-gestation. Dams were limit-fed to provide 70% NRC (1996) requirement (70%REQ), 100% NRC requirement (REQ), or 130% NRC requirement (130%REQ). **Notes: *** d of age $P \leq 0.01$.

Figure 5.8. Expression of *MEF2C* in LM of heifer and steer progeny born to dams fed differing maternal planes of nutrition during mid-gestation.

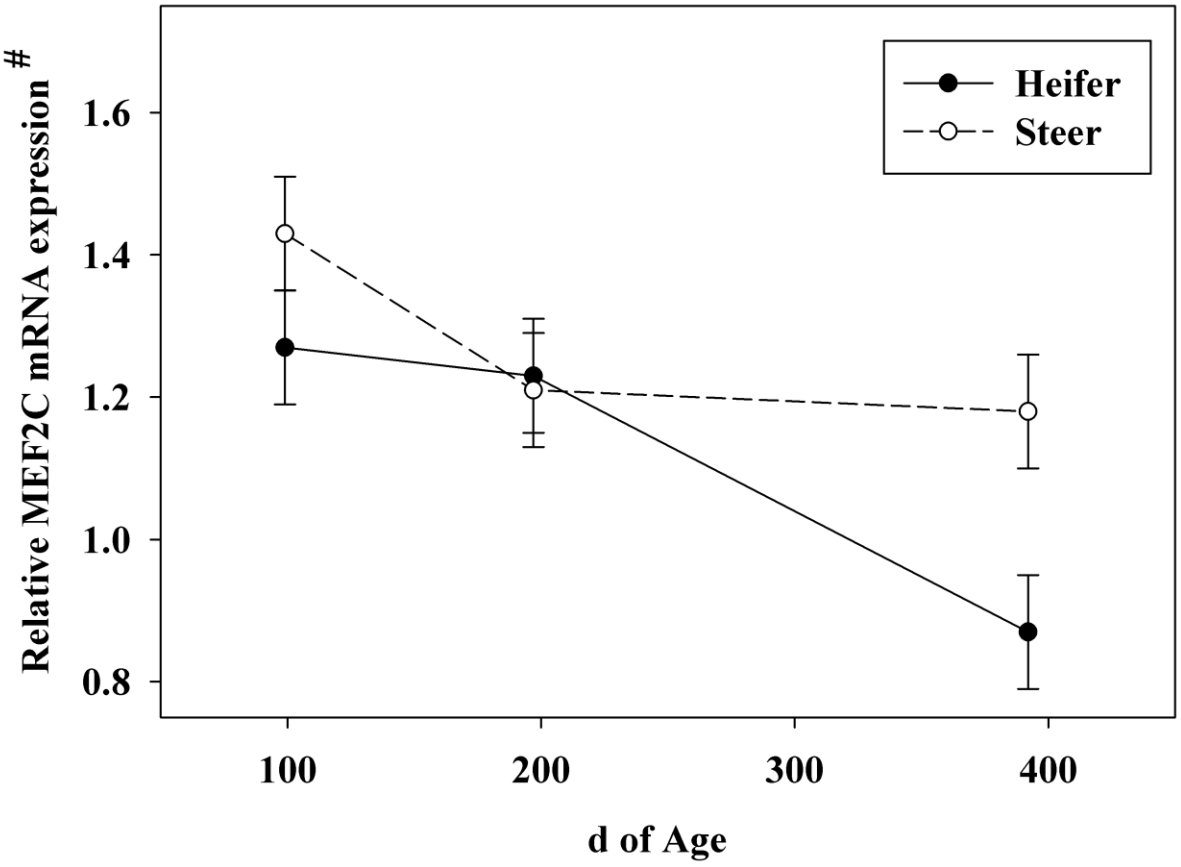

Figure 5.8. Expression of *MEF2C* in LM of heifer and steer progeny born to dams fed differing maternal planes of nutrition during mid-gestation. Dams were limit-fed to provide 70% NRC (1996) requirement (70%REQ), 100% NRC requirement (REQ), or 130% NRC requirement (130%REQ). **Notes: #** Sex by d of age interaction $P = 0.04$.

Figure 5.9. Expression of *YY1* in LM of progeny born to dams fed differing maternal planes of nutrition during mid-gestation.

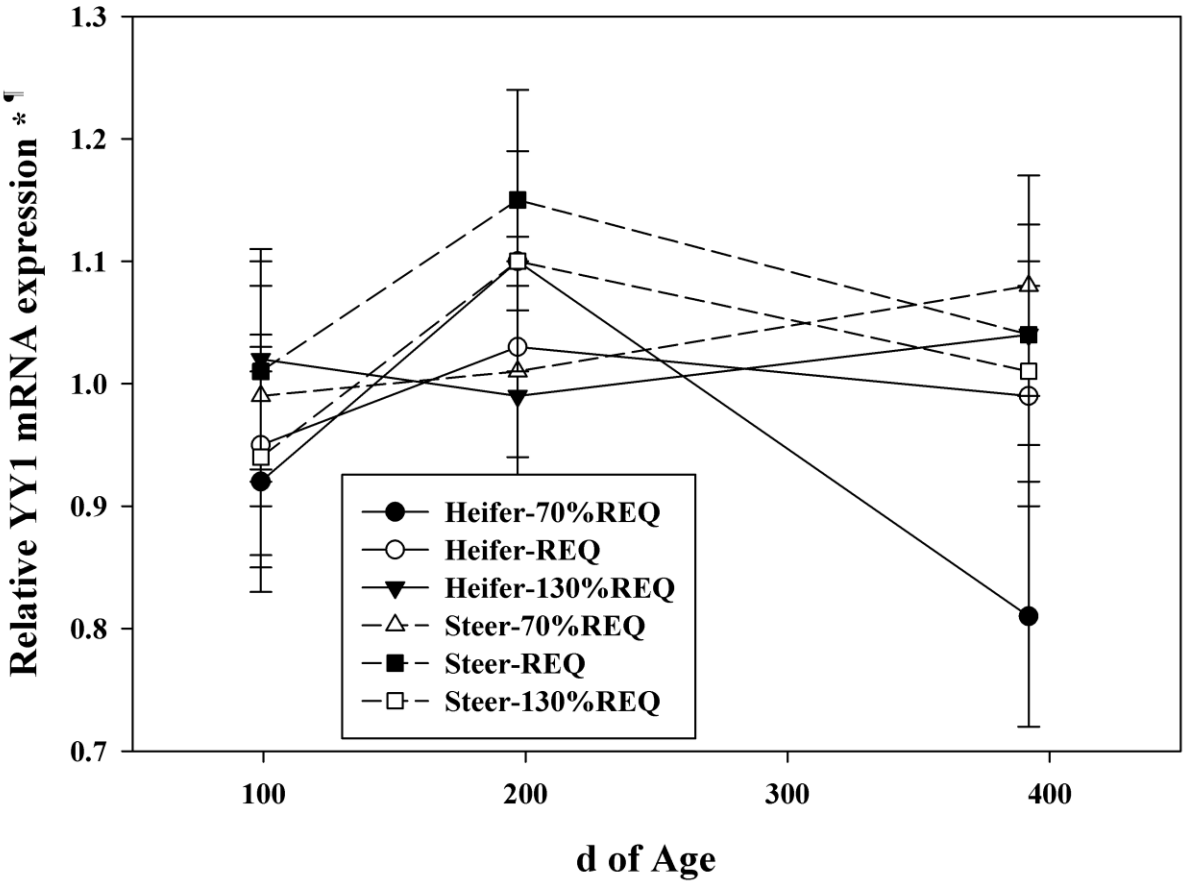

Figure 5.8. Expression of *YY1*in LM of progeny born to dams fed differing maternal planes of nutrition during mid-gestation. Dams were limit-fed to provide 70% NRC (1996) requirement (70%REQ), 100% NRC requirement (REQ), or 130% NRC requirement (130%REQ). **Notes: *** d of age $P = 0.03$, ¶ Treatment by progeny sex by d of age interaction $P = 0.01$.

Figure 5.10. Expression of *MYH1* and *MYH2* mRNA in LM of progeny born to dams fed differing maternal planes of nutrition during mid-gestation.

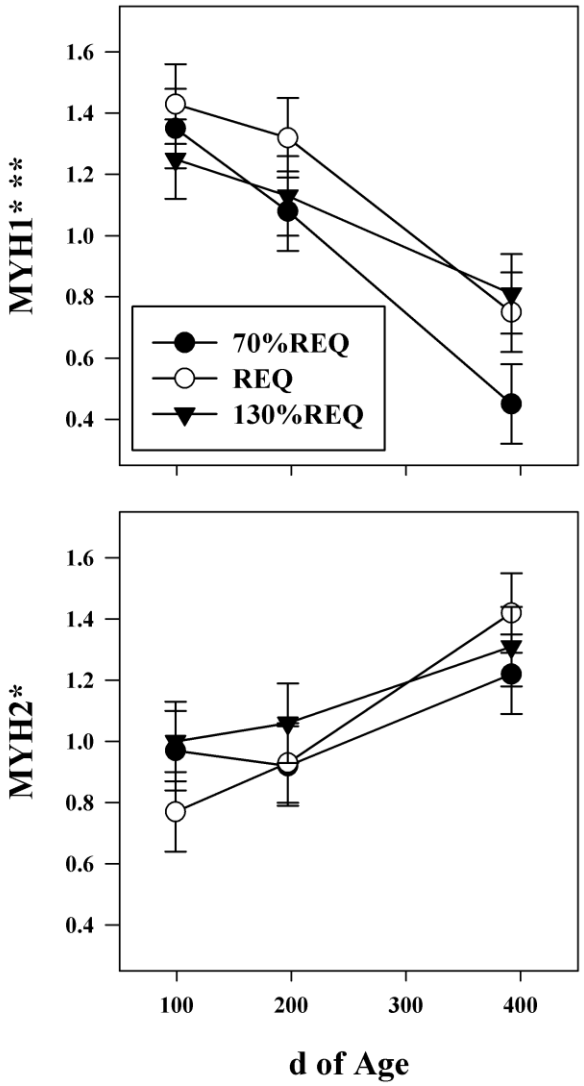

Figure 5.10. Expression of *MYH1* and *MYH2* mRNA in LM of progeny born to dams fed differing maternal planes of nutrition during mid-gestation. Dams were limit-fed to provide 70% NRC (1996) requirement (70%REQ), 100% NRC requirement (REQ), or 130% NRC requirement (130%REQ). **Notes: *** d of age $P \leq 0.01$, **** Treatment by d of age interaction $P = 0.04$.

Figure 5.11. Expression of *MYH7* mRNA in LM of progeny born to dams fed differing maternal planes of nutrition during mid-gestation.

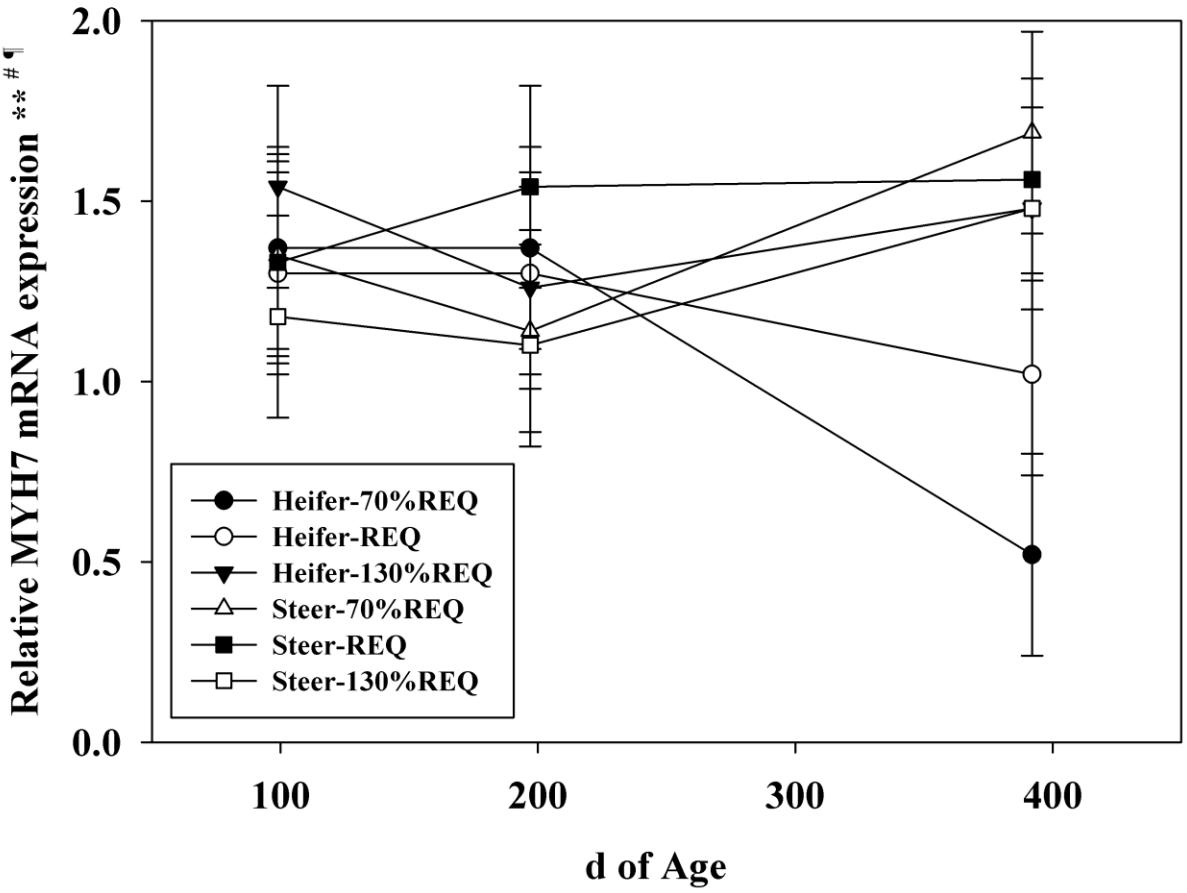

Figure 5.11. Expression of *MYH7* in LM of progeny born to dams fed differing maternal planes of nutrition during mid-gestation. Dams were limit-fed to provide 70% NRC (1996) requirement (70%REQ), 100% NRC requirement (REQ), or 130% NRC requirement (130%REQ). **Notes: **** Treatment by d of age interaction $P = 0.04$, # progeny sex by d of age interaction $P < 0.01$, ¶ Treatment by progeny sex by d of age interaction $P < 0.01$.

Figure 5.12. Correlation between gene expression in progeny LM at 99 ± 14 d of age and cow and progeny response variables.

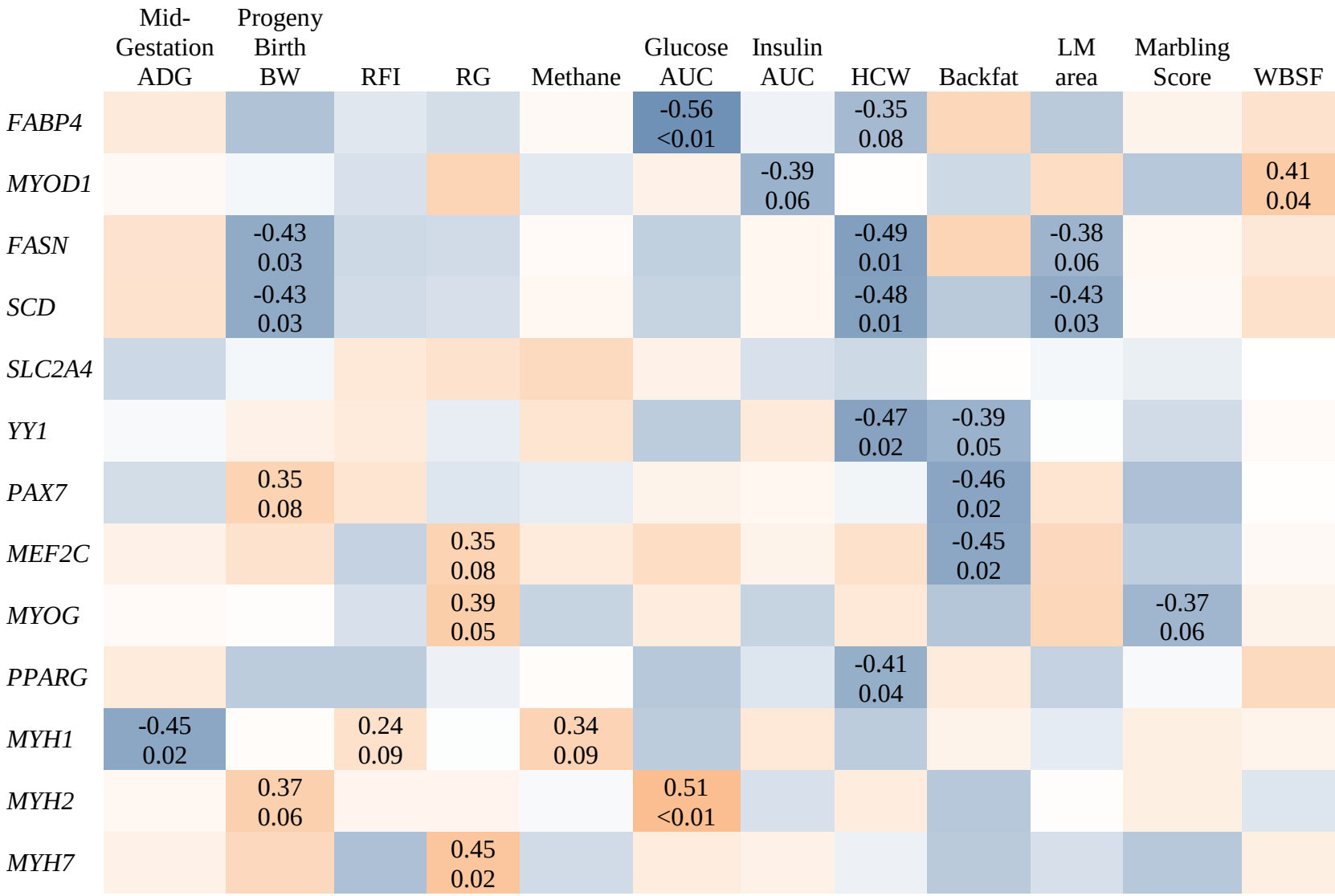

Figure 5.13. Correlation between gene expression in progeny LM at 197 ± 14 d of age and cow and progeny response variables.

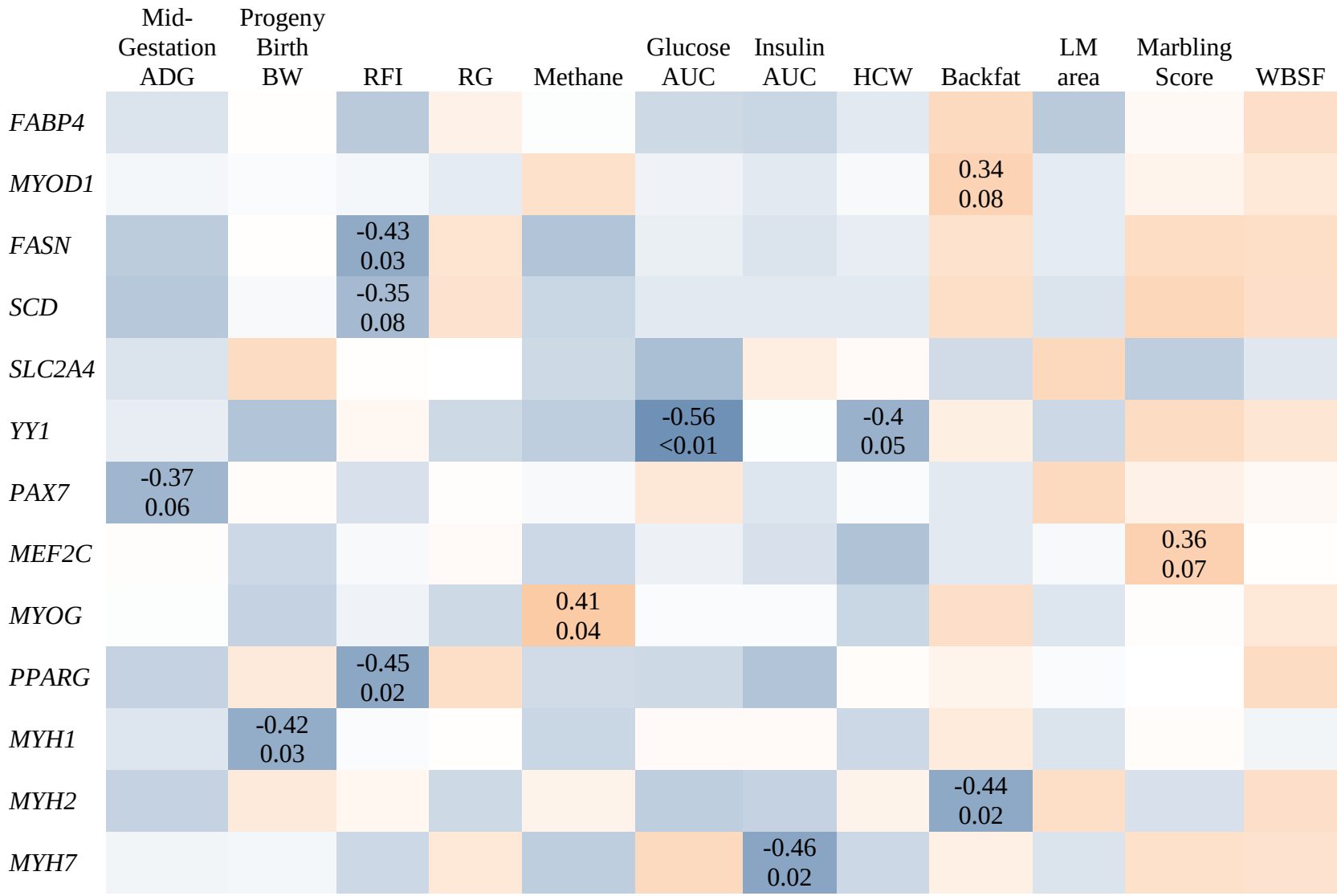

Figure 5.14. Correlation between gene expression in progeny LM at 392 ± 14 d of age and cow and progeny response variables.

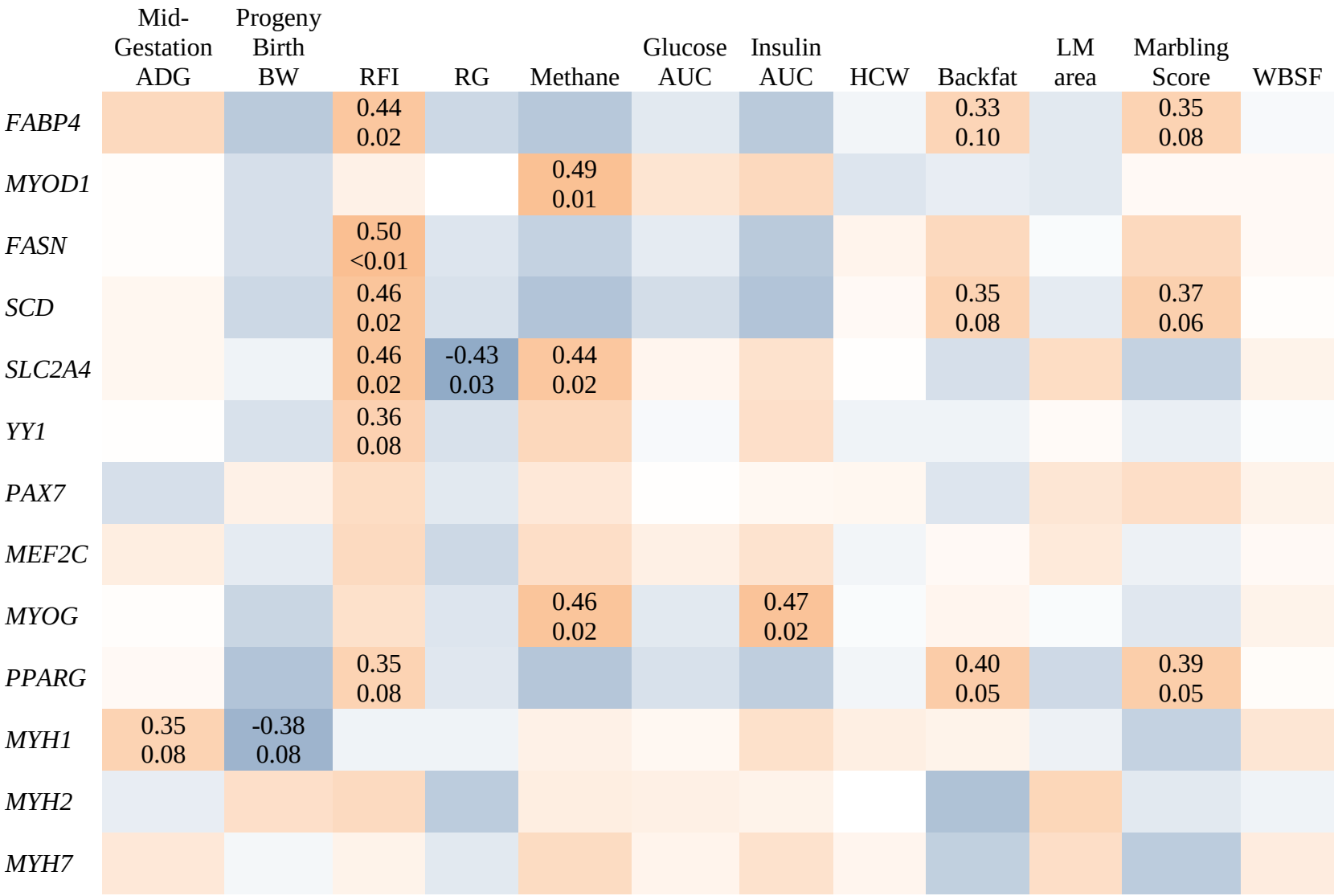

Figure 5.12 (cont.). Correlation between gene expression in progeny LM at 99 ± 14 d of age and cow and progeny response variables. Transformed values for gene expression were correlated to cow ADG during mid-gestation and progeny birth BW, RFI, RG, methane production, glucose and insulin area under the curve (**AUC**), HCW, carcass 12th rib fat thickness (**backfat**), carcass LM area, carcass marbling score, and Warner-Bratzler Shear Force (**WBSF**). Within cell, top values are Pearson correlation coefficients and bottom values are correlation *P*-values. Only Pearson correlation coefficients with $P \leq 0.10$ are shown.

Figure 5.13 (cont.). Correlation between gene expression in progeny LM at 197 ± 14 d of age and cow and progeny response variables. Transformed values for gene expression were correlated to cow ADG during mid-gestation and progeny birth BW, RFI, RG, methane production, glucose and insulin area under the curve (**AUC**), HCW, carcass 12th rib fat thickness (**backfat**), carcass LM area, carcass marbling score, and Warner-Bratzler Shear Force (**WBSF**). Within cell, top values are Pearson correlation coefficients and bottom values are correlation *P*-values. Only Pearson correlation coefficients with $P \leq 0.10$ are shown.

Figure 5.14 (cont.). Correlation between gene expression in progeny LM at 392 ± 14 d of age and cow and progeny response variables. Transformed values for gene expression were correlated to cow ADG during mid-gestation and progeny birth BW, RFI, RG, methane production, glucose and insulin area under the curve (**AUC**), HCW, carcass 12th rib fat thickness (**backfat**), carcass LM area, carcass marbling score, and Warner-Bratzler Shear Force (**WBSF**). Within cell, top values are Pearson correlation coefficients and bottom values are correlation *P*-values. Only Pearson correlation coefficients with $P \leq 0.10$ are shown.

CHAPTER 6

CONCLUSIONS

Objectives

The objective of this dissertation was to evaluate potential fetal programming effects of beef cow nutrition in beef production systems. Chapters 2, 3, and 4 were designed as applied experiments to evaluate influences of cow nutrition during late gestation on subsequent feedlot progeny in beef production systems found in the upper Midwest. Chapter 5 of this dissertation was designed to evaluate the effects of maternal nutrient restriction or overfeeding on not only cow and calf performance, but also progeny feed efficiency, insulin sensitivity, and gene expression in LM.

Prepartum DDGS Supplementation

Fall-calving cows grazing endophyte-infected tall fescue are subject to a decline in forage quality and increased symptoms of fescue toxicosis during late gestation. These factors may negatively impact fetal growth and development. Prepartum supplementation of DDGS did improve cow BW, but did not affect milk production or subsequent reproduction. Prepartum supplementation also did not improve progeny performance from birth to slaughter or carcass characteristics. Despite a decrease in forage quality during late summer, quality of cool-season grasses may be great enough to avoid nutrient deficiency in dams, and thus avoid detrimental programming effects on subsequent progeny. The cows used in our experiment may have also been in adequate enough body condition to compensate for a short-term decrease in nutrient supply.

Drylot Feeding of Corn Coproducts

A high percentage of cows in the upper Midwest are wintered in drylots because of unavailability of forage. Drylot feeding systems require cow/calf producers to provide a balanced, least-cost ration. Over the last decade, incorporation of corn coproducts into drylot rations has increased substantially. Because of the elevated energy and CP concentrations of corn coproducts, error in ration formulation can result in easily exceeding cow nutrient requirements. Feeding cows 125% of TDN requirement during late gestation improved cow BW through breeding and increased progeny birth BW. Greater dietary energy did not improve subsequent reproduction or progeny growth and carcass characteristics.

Drylot rations that provide excessive dietary protein intake result when using corn coproducts, such as DDGS, as an energy source in rations utilizing low-quality forages. Feeding cows 129% of CP requirement during late gestation did not affect cow performance or progeny pre-weaning performance. Feeding dams 129% of CP requirement did negatively affect progeny post-weaning growth or carcass adiposity.

Maternal Plane of Nutrition during Mid-Gestation

Previous research that sparked interest in fetal programming within the animal science field has investigated either extreme maternal nutrient restriction or overfeeding to 50% or 150% of energy and protein requirements, respectively. Much of this work also focused on early to mid-gestation because mid-gestation is a critical time for development of skeletal muscle and adipose tissue. Our experiment was designed to investigate maternal nutrient restriction and overfeeding during mid-gestation within a range that more closely represent beef production systems, 70% to 130% of energy and protein requirements. The results of this experiment indicated that maternal nutrient restriction and overfeeding did affect cow BW and BCS, had

effects on progeny ADG during the transition period and HCW; yet, did not dramatically impact methane emissions, insulin sensitivity, or gene expression in LM. These data indicate that to impart greater programming effects on subsequent progeny, maternal nutrient restriction or overfeeding may need to span a longer period of time or be to a greater extent.

Conclusions and Recommendations

The group of experiments that compose this dissertation have found instances of fetal programming effects imparted by maternal nutrition. Many of these responses have not been of the magnitude hypothesized. In beef production systems in the upper Midwest, many cows are maintained in above adequate body condition throughout the year. Our findings indicate that when cows are in adequate body condition, short-term manipulation of maternal nutrition may not be adequate to impart developmental programming effects on subsequent progeny. Our data do indicate that feeding up 129% CP requirement during late gestation should be avoided to avoid detrimental effects on subsequent progeny post-weaning growth and carcass characteristics. However, these findings need to be confirmed by future research.