Effect of maternal nutrition on fetal development and offspring growth in beef cattle

Molly Rainforth[1]

[1]Department of Agricultural, Food, and Nutritional Sciences, University of Alberta, Edmonton, Alberta, Canada, T6G 2P5

Key points:

1. Nutritional status of cows during gestation influences their offsprings' average daily gain, weaning weight, and health status.
2. Maternal malnutrition in mid-to-late gestation (e.g., winter in Western Canada) has the most negative long-term effects on calf performance.
3. Carcass quality is not affected by maternal nutrition during gestation, but by external factors closer to time of slaughter.

Abstract

Health, growth efficiency and carcass quality are major considerations in beef production. The foundation for this is thought to be linked to fetal development. Maternal nutrition during pregnancy is one factor that can influence fetal development and offspring growth. However, its specific effects on postnatal growth of castrated calves (steers) raised for meat are not well understood. This review considers nutritional requirements of pregnant cows and summarizes the effect of maternal nutritional restriction throughout gestation on calf growth. It also evaluates the different developmental stage at which nutritional restriction will have the greatest impact. It is found that even though early gestation is a critical period for the formation of the placenta and the initial organ development, the fetus has the ability to compensate for developmental restrictions resulting from maternal malnutrition during this period. Meanwhile, during mid-to-late gestation maternal nutritional restriction has the greatest impact on offspring performance. Maternal malnutrition during this key period can reduce birth weight, which is strongly correlated to the lifetime performance of steers in terms of health and growth efficiency. Proper nutritional management of cows is essential throughout gestation, but additional attention should be given to the mid-to-late gestational period to ensure calves are born at an optimal birth weight. Further, it is suggested that maternal nutrition does not appear to have a consistent effect on carcass quality, instead, external factors near the time of slaughter may be the major determinants.

Key words:
maternal nutrition, beef cattle, feed restriction, compensatory growth

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Corresponding author:
Molly Rainforth (rainfort@ualberta.ca)

albertaacademicreview.com

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1. Introduction

Maternal nutrition is one of the main factors influencing fetal growth and development (Funston et al. 2010), and thus a better understanding of the relationships between cow nutrition and calf performance could have a dramatic impact on the efficiency and quality of beef production. Producers should be able to better manage the nutrition of pregnant cows by accounting for the effects of the gestation stage and seasonal nutritional requirements. This consideration would aid in the production of healthy steers that grow efficiently and yield quality carcasses, all of which would improve return for the producer and a higher-grade product for the consumer. While genetics control an animal's potential for growth, and environmental factors such as handling, disease exposure and climate, dictate the extent of growth, nutrition supplies the resources for and determines the rate of growth. Although other factors may also influence the rate of growth, the above listed are the underlying drivers of any animal's growth. Changes in maternal nutrition during early gestation have been found to influence placental development (Funston et al. 2010; Van Eetvelde et al. 2016), which sets the foundation for further development of the fetus. However, any related impairment of fetal development, including development of the gastrointestinal tract and respiratory system, does not appear to have long-term effects on steer growth and health. This is likely because the fetus has sufficient time to compensate for the damage incurred by parental malnutrition during early gestation. The gestation processes that will ultimately determine the quality of the carcass, namely, myogenesis, adipogenesis, and fibrogenesis, are suggested to occur later, during mid-to-late gestation (Du et al. 2010). Therefore, maternal nutrition during this mid-to-late gestation period could potentially have long term effects on the carcass. Recent research, on the other hand, suggests that deleterious effects associated with these processes could be lessened through compensatory growth during the remainder of the prenatal stage (Long et al. 2010; Duarte et al. 2013a; Van Eetvelde et al. 2016). This discord in the literature highlights that the relationship between maternal nutrition and carcass quality is still not well understood.Overall, it was found that nutritional restriction of the cow at any point during gestation had no consistent effects on fetal development or carcass quality of the offspring. However, a restriction towards the later stages of gestation decreased birth weight (Micke et al. 2010). Thus, this restriction appears to be the most significant in terms of having an impact on steer performance, because birth weight is linked to rate of growth and weight throughout life. A calf born with a higher than average body weight (BW) is at lower risk for disease contraction and has a better postnatal growth projection when compared to a calf born with below-average BW (Funston et al. 2010). Hence, a better understanding of ideal management of cow nutrition during this time will reduce the impact on the performance of postnatal calves. This literature review will evaluate nutritional requirements of the beef cow, the effects of maternal nutrition on both prenatal and postnatal development, and the growth of offspring. It also comments on the influence that these factors have on the value of a beef carcass.

2. Financial

2.1 Feed costs for a cow-calf operation in Canada

A survey conducted across Canada found that on average, feed costs were the greatest component of expenses sustained by livestock operations (Lachapelle 2014). Beef operations had lower feed costs in comparison to other livestock industries, as cattle are primarily grazing animals and do not require a pre-formulated diet such as that which swine or poultry receive (Lachapelle 2014). However, feeding expenses in beef production still comprise a large proportion of operational costs.

A large factor influencing feed costs is seasonal changes throughout the year. Feed expenses for a cow-calf operation are typically lowest over the summer, as during this period cows are put on pasture grazing and generally do not need supplementation of any kind (Sheppard et al. 2015). Supplementation in terms of added forage or grain is almost always required over

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winter; therefore, the grazing period is usually extended as long as possible to reduce costs of not only feed, but that of labour as well (Sheppard et al. 2015). Corrals or drylots are often used by producers over the winter, especially during calving season (Sheppard et al. 2015). This may be required if pasture is not available, but can also be done so that producers can better observe cattle in the final days of gestation and during calving. Hence, feeding expenses become increasingly critical over the winter months to account for these changes. In order to manage these expenses, producers should optimize the nutritional requirements of their cattle, while making the most efficient use of available feed.

2.2. Maximizing profitability for the producer

The primary source of income for a cow-calf operation is generated through the sale of calves at weaning. This income is dependent on individual calf size; consequently, it is economically beneficial for all calves to have reached their maximum potential weight at an early age (Khakbazan et al. 2015; Sheppard et al. 2015). Calves who have experienced slower growth prior to weaning will either bring a lower price at weaning or will require the producer to further invest in their feeding and care to allow them to reach a higher BW over a longer period. Both alternatives come at a cost to the producer. In this regard, it would be highly beneficial for producers to understand the effect of maternal nutrition on both prenatal and early postnatal calf growth. Knowledge of this relationship can help producers determine the proper feeding strategies for cows that will ensure maximum pre-weaning growth rate and BW at weaning. This knowledge will also allow producers to maximize profitability through proper management of cow nutrition during pregnancy. For instance, this can reduce the resources, such as extra feed and management, that may otherwise be needed at a post-weaning stage to grow out calves for sale.

Another important consideration is that improved early management of cows not only impacts the income of cow-calf producers, but it also has implications for feedlot operations and the consumer market. Prenatal development has been shown to influence postnatal calf performance, and carcass quality and characteristics (Du et al. 2010; Long et al. 2010; Underwood et al. 2010). Feedlot profitability is based on animal weight and carcass grading. Further, the sale of meat is dependent on consumer preference and acceptability of the product. Thus, the prenatal environment influences the entire chain of beef production, and the proper management of the expectant cow is critical in ensuring a good product.

3. Dam nutrition

3.1. Nutritional requirements throughout gestation

Although variation exists, most beef cows in Canada are bred between June and August, and have a 9-month gestation period. Early-gestation then corresponds to late-summer and fall, mid-gestation to winter, and late-gestation to late-winter and early-spring. This will vary depending on whether a given operation prefers early or late calving, which is influenced by the seasons. A survey taken across Western Canada in 2014 revealed that cow-calf producers begin calving in January, but the majority of calving occurs in March and April (Western Canadian Cow-Calf Survey 2015). Therefore, gestation energy intake is generally lower than required, because producers focus on aligning the post-natal lactation period with the nutrient-rich spring grass (Rooke et al. 2015). However, similar to the lactation period, cows have increased nutritional requirements during mid-to-late gestation as the fetus takes in appropriate nutrients (Sheppard et al. 2015). As the later stages of gestation typically fall in the season of winter, the addition of extra hay, silage, or grain is typically required to ensure that the cows do not enter a state of negative energy balance prior to calving. Consideration must also be given to the order of parity. Heifers (i.e., young cows expecting a calf for the first time) require more nutrients throughout gestation than do higher parity cows, because they are still experiencing a large increase in their own growth (Van Eetvelde et al. 2016). A heifer will partition relatively fewer nutrients to the fetus than a cow will, as a heifer needs more for her own growth and this is prioritized over development of the fetus. Therefore, heifers will often require extra energy via feed supplementation during gestation when cows may not.

3.2. Common feeds

Many cow-calf producers in Alberta and Western Canada rely on pasture throughout the summer. This can be native pasture or improved pasture. Improved pasture is often seeded with a legume, primarily alfalfa, to increase energy and protein availability (Funston et al. 2010; Sheppard et al. 2015). Native pastures are often low in crude protein, and thus a protein supplement may be required. However, this depends on the forage present as some native pastures can provide sufficient energy and protein (Mohrhauser et al. 2015). Grains such as barley can be fed during the winter, but more commonly, cows are provided with hay, silage, or straw (Sheppard et al. 2015). The nutrient composition of different feeds varies greatly, and the specific feedstuff provided can greatly influence maternal nutritional status.

3.3. Annual changes in feeding strategies

Cow-calf operations depend largely on pasture to achieve the nutritional requirements of cows. Because cattle are grazing animals, their nutritional intake is largely dependent on the quality of grazing forage, which in turn is greatly influenced by weather conditions. In Western Canada, cows are typically on summer pasture from June to October (Sheppard et al. 2015). Summer pasture generally provides sufficient nutrients for cattle without any grain or hay supplementation being required. However, winter conditions can cause an involuntary feed restriction by limiting the producer's overall feed availability or decreasing the nutrient content of feed, or a combination of both. Pasture is a near-unfeasible option throughout the winter in Western Canada due to snow cover and cold temperatures restricting forage growth. The remaining forage that exists is of poor quality with minimal nutrients. Producers rely on the proper storage of silage, grain, and hay to provide cattle with proper feed sources throughout the winter. Operations must be managed with seasonal changes in mind in order to maintain appropriate dam body condition score (BCS) and BW throughout reproduction to ensure maximum calf performance is achieved.

4. Prenatal development

4.1. Placental development and attachment

The effects of maternal nutrition on fetal growth during the first trimester of pregnancy have been studied less than those later in gestation. It is commonly thought, because the developing embryo is so small during early gestation, that it requires fewer nutrients from the cow than the large fetus would at later stages (Funston et al. 2010). However, development is more energy-demanding than growth. During this early-stage the placenta develops, the blood flow between the mother and the embryo is established, and the organs start developing, calling for the critical importance of nutrition during this period (Funston et al. 2010).

The attachment sites of the placenta to the uterus are called placentomes and are composed of caruncles on the uterine wall and cotyledons on the placental membrane (Funston et al. 2010). Little research has been done in cattle to determine the factors that affect this attachment, but maternal nutrition has been shown to be important (Funston et al. 2010). The placenta does have the potential to respond to negative environmental conditions by altering cotyledon features, specifically through a decrease in cotyledon size but an increase in number (Van Eetvelde et al. 2016). This alteration was seen to occur with a nutritional restriction early in pregnancy and is thought to allow for the potential expansion of cotyledons later in the pregnancy if more resources become available to the fetus. However, this compensation may not eliminate the adverse effects of the nutritional restriction (Van Eetvelde et al. 2016).

Nutritional restriction during the second trimester seems to have the largest impact on the cotyledon number relative to restriction during the first trimester (Van Eetvelde et al. 2016), suggesting that the number can be increased throughout the second trimester if there are remaining caruncles to which the

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cotyledons can attach (Sullivan et al. 2009). The cotyledon number is thought to be inversely related to the surface area and weight of cotyledons (Sullivan et al. 2009). This is supported by a study conducted by Van Eetvelde et al. (2016) that compared placenta development in heifers and cows. Heifers partition more energy to their own growth, which can result in a state of nutritional restriction in the fetus as it must compete with the growth of the heifer. Placentas from heifers showed a higher number of cotyledons but a smaller cotyledon weight and surface area relative to cows (Van Eetvelde et al. 2016). During early gestation, the placenta compensates for a nutritional restriction by increasing the number of cotyledons, while towards the end of gestation the size of cotyledons is increased (Van Eetvelde et al. 2016). In heifers, while the number of cotyledons did increase, the size of cotyledons did not become larger relative to cows in late gestation (Van Eetvelde et al. 2016). This is likely because heifers remained on a negative energy balance throughout gestation, due to competition for energy with their offspring.

Maternal nutrition during early gestation is thus critical for the development of the fetus, as it determines the characteristics of the placenta and influences attachment to the uterine wall. Therefore, careful attention to the nutritional requirements of a cow, and more so of a heifer, is of crucial importance for proper placental development, attachment, and further development of the fetus. However, if the nutrition of the cow is improved later in gestation, the placenta has the capacity to recover from the damage incurred during the early gestation due to maternal malnutrition.

4.2. Tissue development

Myogenesis, adipogenesis, and fibrogenesis are three processes that contribute to carcass quality and composition of beef cattle. Myogenesis produces muscle, for which beef cattle are raised; adipogenesis gives rise to fat depots, one of which is crucial for marbling (distribution of fat between muscle fibre that is visible within a cut of meat); and fibrogenesis forms other connective tissue, such as collagen, that are, in part, responsible for meat toughness (Du et al. 2010;Duarte et al. 2013b). All three processes begin with mesenchymal stem cells, and thus are related to one another (Du et al. 2010). An understanding of the factors that influence the production of one tissue over another will allow producers to make informed and profitable management practice decisions to increase calf growth efficiency and final carcass quality.

4.2.1. Myogenesis: protein content

Skeletal muscle is selected for in beef cattle, with a higher proportion of lean tissue rather than fat being desirable in the carcass (Du et al. 2010; Long et al. 2012). Consequently, myogenesis should be selected for over adipogenesis. Myogenesis occurs in two stages. The primary wave of myofibers develop during early-gestation, while the second wave occurs mid-gestation; the number of muscle cells is established by the time of parturition (Du et al. 2010). After this point, muscles can only grow in width and length.

The development of other organs takes precedence over myogenesis, resulting in this process having an increased sensitivity to environmental factors (Du et al. 2010). Nutritional restriction in early-gestation has been found to impact myofiber size. Long et al. (2010) found that low maternal nutrition during early-gestation increased the amount of deoxyribonucleic acid (DNA) in the muscle of offspring and increased the area of muscle fibers. This suggests that the number of primary myofibers was decreased through nutritional restriction, which in turn decreased the number of secondary myofibers. However, when cows were returned to an unrestricted diet, more nutrients could be partitioned to the fetus and the muscle growth could again increase. This re-growth of muscle was through an increase in hypertrophy of muscle cells that compensated for the shortage of cells present. Because muscle cells are multinucleated, they can sustain a large increase in size by acquiring more nuclei, which would then cause an increase in the DNA found in the cells.

A nutritional restriction during mid-gestation may also impact muscle development in cattle. A trend towards a larger longissimus muscle area was seen in steers from a negative energy balance mid-gestation compared to a positive energy balance (Mohrhauser et al. 2015). By mid-gestation, the number of primary myofibers has been established (Du et al. 2010) but the number of secondary myofibers could still be affected. Similar to the research done by Long et al. (2010), the trend seen by Mohrhauser et al. (2015) would suggest that the number of myofibers was decreased with restriction, leading to a compensatory growth in muscle cell size once the cow was returned to a positive energy balance. This is supported by a study comparing Angus cattle and Wagyu cattle, where the latter have a higher marbling level (Duarte et al. 2013b). Although Wagyu cattle have higher marbling (higher fat deposits and lower muscle fibers), they were found to have larger muscle fibers than Angus (Duarte et al. 2013b). This suggests that fewer muscle cells develop in Wagyu cattle compared to Angus cattle, but because there are fewer cells, they have the potential to grow larger than if they were more numerous. These results demonstrate that maternal nutrition in both early- and mid-gestation has an impact on myogenesis. However, the consequences of changes in muscle fiber size on calf growth and later carcass quality are still unclear. Long-term consequences of this effect were also not seen in other studies (Long et al. 2012; Underwood et al. 2010), indicating that changes in myogenesis during prenatal development may not necessarily have significant effects on postnatal calf performance.

4.2.2. Adipogenesis: degree of marbling

Intramuscular fat (IMF), also known as marbling, is crucial in cattle, as it contributes to eating qualities of meat such as flavour and juiciness. Adipocyte (fat cells) size and number contribute to the extent of marbling (Du et al. 2010). There are four main fat depo in an animal: visceral, intermuscular, subcutaneous, and intramuscular. The goal for ideal meat production is to increase the marbling of a carcass by increasing IMF, while avoiding an increase in the other three depots (Duarte et al. 2013b). Adipogenesis begins mid-gestation and continues after parturition (Du et al. 2010). Maternal nutrition early in gestation can have an impact on adipocyte formation, and thus the number adipocytes (Du et al. 2010), while the later stage of gestation are responsible for the size of adipocytes, as they accumulate fat once everything else is complete. Adipocytes and fibroblasts arise from the same precursor cells, so an increase in adipocytes is generally linked to an increase in connective tissue (Du et al. 2010).

Long et al. (2012) found that a decrease in the energy content of the diet for dams throughout early- to mid-gestation resulted in a larger size of adipocytes when measured in offspring at slaughter compared to steers from unrestricted dams. When the stage at which adipogenesis begins in the fetus is considered, restriction early in gestation would not be expected to affect adipogenesis. However, the research of Long et al. (2012) shows that there was a tendency for this nutritional restriction, in terms of a lower energy diet, to cause a decrease in the weight of the semitendinosus muscle. Rather than directly influencing adipogenesis, the nutritional restriction may have reduced myogenesis in the fetus, which would have led to a greater availability of stem cells for adipogenesis once it began. This possibility is supported by the comparison of Wagyu and Angus cattle, as Wagyu cattle had a higher level of intramuscular adipocytes than Angus but a smaller number of muscle cells (Duarte et al. 2013b). Angus cattle, in comparison, tend to give a leaner carcass with less IMF. The extent of adipocyte hyperplasia may be influenced more by maternal nutrition during mid-gestation, as the adipocyte number tended to be greater in steers from unrestricted cows when compared to steers from restricted treatments (Underwood et al. 2010). A definite conclusion cannot be made as the difference was not significant. However, the tendency of the adipocyte number to be greater with no nutritional restriction is expected when considering the timing of adipocyte formation during mid-gestation. Nutritional restriction of the cow may reduce adipocyte number, but this can be compensated for later in the calf's life through an increase in size of adipocytes.

4.2.3. Fibrogenesis: beef tenderness

Limited studies have been done to determine the effects of maternal nutrition on fibrogenesis, possibly because post-mortem conditions are thought to be the major factor influencing meat

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toughness (Mohrhauser et al. 2015). Fibrogenesis begins mid-gestation, correlating with adipogenesis and the second wave of myogenesis (Du et al. 2010). Fibroblasts and adipocytes originate from the same precursor cell, so there is no competition between the two processes until the precursor cells stop replicating. Once this occurs, the number of precursor cells becomes finite and competition between fibrogenesis and adipogenesis begins (Duarte et al. 2013b). This concept is supported in a study done by Mohrhauser et al. (2015), where steers born to cows who experienced a negative energy balance mid-gestation had a lower carcass shear force and trended towards increased IMF compared to those who experienced a positive energy balance throughout gestation. This indicates a trade-off between fibrogenesis and adipogenesis, as shear force provides an estimate of the collagen content of meat. However, the same decrease in shear force was not seen in carcasses when dams were protein-restricted during mid-gestation; rather, restriction in this case was associated with an increase in shear force (Underwood et al. 2010). This difference could be related to the treatments in the two studies, as Mohrhauser et al. (2015) used an energy restriction, while Underwood et al. (2010) researched a protein restriction.

Though maternal nutrition is likely to affect fibrogenesis, more studies are required to determine the true relationship between nutritional restriction and fibrogenesis. The small number of recent studies that have been done on this topic may suggest that maternal nutrition during gestation has little effect on fibrogenesis, and that factors later in the offspring's life have a greater influence.

4.3. Organ/System development

4.3.1. Gastrointestinal tract

Proper development of the gastrointestinal tract is important for digestion and feed efficiency later in life (Duarte et al. 2013a). The survival of a newborn calf largely depends on its ability to absorb immunoglobins from colostrum immediately after birth; the absorption of these large molecules across the gut wall can occur without the molecules being digested (Duarte et al. 2013a). Determining whether maternal nutrition is a factor that may affect this process can increase knowledge regarding the prevention of gastrointestinal problems during postnatal growth.

Decreasing the energy content of feed during early-gestation had no effect on fetal body weight at any stage of gestation, but it was associated with a larger small intestine as a proportion of weight, a longer small intestine, and longer villi within the small intestine compared to the unrestricted group (Duarte et al. 2013a). This demonstrates the ability of the small intestine to adapt to altered conditions during development. The function of the small intestine did not appear to be impaired, yet the structure was altered to increase its efficiency through enlarging the surface area available for absorption of nutrients. Although characteristics such as villi length were not measured, Long et al. (2010) found no difference in weight between the fetal gastrointestinal tracts of restricted and unrestricted cows during mid-gestation. This restriction was more severe than that in the former study, as cows were both energy and protein restricted (Long et al. 2010). A more severe restriction would be expected to have a greater influence on the small intestine; however, the absence of an effect on gastrointestinal weight may suggest that the initial formation of this system is complete by mid-gestation, and thus nutritional restriction will no longer alter its structure as it did during early gestation.

4.3.2. Respiratory system

The integrity of the respiratory system seems to be closely linked with the size of calves at birth, as smaller calves at birth have a higher risk of contracting respiratory diseases than larger calves (Shoup et al. 2015). It is unclear why the respiratory system seems to be the compromised system when fetal growth is less than the potential, but it may have a lesser ability to resist or recover from impaired development compared to other organs.

A protein and energy restriction of cows from early- to mid-gestation had no effect on the weight of any organs except for the lungs and the trachea, which had a smaller weight in calves from the restricted group than from the unrestricted group (Long et al. 2010). Although the lungs are not used in utero, and lungs are not used in utero, and consequently are one of the last organs to finishing developing before birth, initiation of development begins early in gestation (Funston et al. 2010). Thus, a nutritional restriction during early-gestation may impact the early stages of lung development. Such a restriction could also have indirect effects on the respiratory system by influencing early processes such as myogenesis and fibrogenesis that could eventually result in the compromised development of the lungs and trachea.

In the prior study, cows were energy and protein restricted from day 32 to day 115 of gestation, receiving 55% and 50% of required energy and protein levels, respectively (Long et al. 2010). A second study was done in which cows were restricted to 70% of their overall requirements, with a second group restricted to 70% of their energy requirements but given a protein supplement (Long et al. 2012). This restriction occurred from day 45 to day 185 of gestation, and neither treatment affected lung weight (Long et al. 2012). Because the latter study continued longer into gestation than the former study, and the restriction was more severe, an impact on lung weight would have been expected. The absence of any impact on lung weight by a later, more severe nutritional restriction is puzzling, when considering that an earlier, less severe nutritional restriction can decrease lung weight. This could be linked to the development of the fetus requiring more energy than growth. In such case, early development would be more susceptible to a smaller restriction in energy intake, while growth is more tolerant and can compensate for the energy requirements at a later stage in gestation. No recent studies were found that have explored the relationship between lung development and maternal nutrition during late-gestation, but such a study could provide more information regarding the true effect of a nutritional restriction.

5. Postnatal growth

5.1. Birth weight

Maternal BW and nutrition during gestation are the greatest factors influencing calf birth weight; however, the effects of these factors alone seem to decline during postnatal growth of the calf (Robinson et al. 2013). Although external influences contribute to postnatal growth, birth weight is important as it is linked to the health and performance of steers over their lifetime (Funston et al. 2010).

Long et al. (2010) found that energy and protein restriction of the cow, at 55% of energy requirements and 50% of protein requirements during the first trimester only, did not affect calf birth weight or the growth of calves between birth and weaning. Likewise, no negative effects on birth weight were seen when cows were restricted during early-gestation to approximately 70% of their protein requirement (Micke et al. 2010), and 70% of their energy requirement (Long et al. 2012). In all studies, realimentation to 100% of requirements during the second and third trimesters allowed for compensatory growth in the fetus.

In one study found, calves born to cows who were protein-restricted during mid-gestation had a lighter BW compared to calves from cows that were not nutritionally restricted (Micke et al. 2010). This result conflicts with Underwood et al. (2010), who found no difference in the birth weight of calves who were born to cows grazing on native pasture and calves born to cows grazing on improved pasture. This difference between the two studies could be attributed to the differences in the severity of restriction. For instance, one could assume that a diet restricted to 70% of the protein requirement as in Micke et al. (2010) is the more severe treatment, and thus conclude that this level of severity is needed before a negative effect on birth weight is seen. However, as the protein content of the native pasture used by Underwood et al. (2010) is unknown, no definite conclusion can be made. Regardless, these studies demonstrate that increasing nutritional value during mid-gestation does not allow the fetus to compensate for the slower growth, as the length of time for compensatory growth may not be sufficient.

5.2. Weaning weight

Parallel to birth weight, weaning weight was not influenced by maternal nutritional restriction in early-gestation (Long et al. 2010; Long et al. 2012). Moreover, while weaning weight has been

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shown to be highly correlated with birth weight, maternal nutrition during lactation seems to be the largest factor determining weaning weight (Robinson et al. 2013). This implies that nutritional restriction during gestation can be compensated for during the pre-weaning period, provided that the cow is given a high-quality diet to increase the nutritional value of milk during lactation.

Similarly, protein-restriction during mid-gestation did not result in calves born with a low birth weight, or a subsequent low weaning weight (Underwood et al. 2010). In the experiment done by Micke et al. (2010) as described above, calves were not monitored until weaning, so no information can be drawn from the pre-weaning performance of calves who demonstrated different birth weights. All the results given demonstrate that there is a strong relationship between birth weight and weaning weight, provided that dams are provided with a sufficient diet during the pre-weaning period. A nutritional restriction during this time may alter the relationship between these weights as it would inhibit calf growth.

5.3. Feedlot performance and slaughter weight

Relatively few studies investigate the relationship between maternal nutrition during gestation and feedlot performance of steers, likely because many other external factors influence feedlot performance. These factors include stress involved with introduction to a new environment and other animals, and operational practices like handling, diet composition, vaccinations, and treatments. Individual measures of performance were not assessed during the finishing period, but the final slaughter weight of steers was the same, regardless of whether dams' nutrition had been restricted during early gestation or not (Long et al. 2010; Long et al. 2012). However, it is reasonable to expect that growth throughout the finishing period should have been the same, because there was no difference in birth or weaning weights between restricted and unrestricted groups.

Underwood et al. (2010) found that a maternal protein restriction during mid-gestation had no effect on birth weight or weaning weight of calves. However, they found that mid-gestation protein restriction reduced the average daily gain (ADG) and live weight at slaughter in steers from the restricted group. Meanwhile, a nutritional restriction throughout late-gestation had no impact on ADG, dry matter intake (DMI), gain-to-feed ratio, or slaughter weight (Shoup et al. 2015). These results suggest that more developmental processes are affected by a dietary restriction mid-gestation, resulting in long term effects on growth.

5.4. Carcass quality

Shoup et al. (2015) suggested that the time of weaning, either early or late, has a greater influence than maternal nutrition on carcass quality. They imply that postnatal management of calves is more critical to carcass yield and quality than the prenatal environment. This helps explain why more studies focus on the immediate consequences of maternal nutritional restriction postpartum, such as birth weight. However, the effects of this nutritional restriction, unless it is severe, seem to diminish with time.

Long et al. (2010) found that energy and protein restriction during the first trimester had no influence on the overall carcass composition of steers, including yield grade, hot carcass weight (HCW), and marbling, even though there were physiological differences in the composition of muscle and adipose. For instance, more DNA in muscle was found in calves whose dams experienced a nutritional restriction early in gestation (Long et al. 2010). This suggests that early restriction influences myogenesis, particularly by increasing the number of primary myofibers (and thus increasing DNA in the muscles). Meanwhile, a more severe energy and protein restriction negatively affected yield grade but had no impact on other carcass characteristics such as marbling, 12th rib fat thickness, and HCW (Long et al. 2012). The differences between these two studies suggest that a severe parental malnutrition in the early stages of gestation can impact developmental processes that will affect growth until slaughter. However, a mild nutritional restriction does not appear to influence carcass composition or yield.

Furthermore, a study in which cows were restricted during mid-gestation showed that this had a negative effect on the 12th rib fat thickness of carcasses as well as HCW and meat tenderness, yet it did not affect yield grade or marbling (Underwood et al. 2010). In contrast, Mohrhauser et al. (2015) found that a mid-gestation restriction had no impact on carcass composition or meat tenderness when the proportions of protein, fat, bone, and water were determined. In the latter study, cows were restricted to 80% of their maintenance energy requirements, while in the former study cows were placed on improved pasture that had been seeded with other forages, or on native pasture (with no specifications on the level of nutrient restriction). The different dietary restriction would render a direct comparison of these two studies unreliable. The inconsistency of these results demonstrates that more research is needed to clarify the effects of malnutrition during mid-gestation period on HCW and meat tenderness. In terms of meat tenderness, the conflicting results suggest that post-mortem conditions may have a greater influence than prenatal or postnatal factors, as the conditions between these two studies were likely not the same. Only a single study was found that determined the effect of a maternal nutritional restriction during late gestation on carcass characteristics, which was found to be negligible on HCW, yield grade, and marbling (Shoup et al. 2015). Although more research should be done to explore the relationship between maternal nutrition and offspring carcass characteristics, and the influence of other factors such as post-mortem conditions on meat quality, these studies suggest that mid-gestation nutrition has the greatest effect on carcass quality.

6. Conclusions

A restriction in maternal nutrition during gestation will have an impact on the growth of the offspring, but in some cases compensatory growth can occur which allows the offspring to recover from any developmental delays caused by this restriction. Early-gestation is a critical period for placental development, organs and tissue formation. Maternal nutritional restriction during this period can have numerous detrimental effects on the fetus, but they can be lessened or reversed through compensatory growth at a later stage in gestation if maternal nutritional restrictions are lifted. However, there are still open questions as to whether the effects of maternal malnutrition on the fetus at a cellular level have a long-term impact on growth and performance, as the lack of research in this field did not allow for a thorough review on the topic.

A strong relationship was found between birth weight and postnatal growth. Maternal nutrition during mid-gestation in particular is a large determinant of birth weight, and a higher birth weight correlates with increased performance of the steer. Due to the typical beef breeding cycle in Canada, mid-gestation for a beef cow occurs during the winter months. This implies that pregnant cows, especially heifers, should be provided with supplemental feed to meet the dietary requirements of both the cow and the fetus. Nutritional restriction in this period can have long-term consequences on offspring performance.

Conflicting results exist in regard to the relationship between the time during which maternal restriction occurs and carcass characteristics of the offspring. Previous studies suggest that over time the effects of maternal nutrition become less pronounced due to compensatory growth if nutritional requirements are met. Feedlot performance of cattle is indirectly influenced by maternal nutrition through its impact on calf birth weight; however, other external factors such as stress, handling and diet composition may also influence feedlot performance. Finally, it is recommended that long-term studies focusing on the entire process of development, from the prenatal period to mature slaughter age, could further clarify the effects of maternal nutrition on carcass and meat quality.

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