



### Maternal Nutrition and Meat Quality of Progeny

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Abstract: The concept of fetal programming is based on the idea that nutritional status and environmental conditions encountered by the dam during pregnancy can have lifetime impacts on her offspring. These changes in the gestational environment have been shown to influence fetal development and subsequent growth performance, carcass composition, and meat quality characteristics. Beef fetuses can be particularly prone to experiencing variations in the maternal environment during development owing to a relatively long duration of pregnancy potentially exposing the dam to environmental temperature stress and/or seasonal conditions that can compromise feed quality or quantity. If feed is limited or forage conditions are poor, a maternal deficiency in protein and/or energy can occur as well as fluctuations in body condition of the dam. As a result, the fetus may receive inadequate levels of nutrients, potentially altering fetal development. There are critical windows of development during each stage of gestation in which various tissues, organs, and metabolic systems may be impacted. Skeletal muscle and adipose tissue are particularly vulnerable to alterations in the gestational environmental event or stressor as well as the ability of the dam to buffer negative effects to the fetus will dictate the developmental response. Much of the current research is focused on the influence of specific nutrients and timing of nutritional treatments on offspring carcass composition and meat quality, with the goal of informing strategies that will ultimately allow for the use of maternal nutritional management as a tool to optimize performance and meat quality of offspring.

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# Introduction

The phenotype of any individual is a combination of its inherited genetic code and the impact of the environment on the expression and function of genes influencing a particular trait. Just as the genome is made up of genes controlling the phenotype, the environment provides a myriad of biological and physical factors, which—independently or in combination can affect the genome through epigenetic mechanisms (Baye et al., 2011; for a review of epigenetic mechanisms, see Funston and Summers, 2013; Scholtz et al., 2014; Blair et al., 2016; Elolimy et al., 2019). However, the role of the gestational environment is often overlooked when evaluating management practices to maximize the genetic potential of livestock species. Through advances in human and animal research, we have begun to understand the role of the gestational environment in "programming" an offspring's potential for a host of production outcomes, such as body composition, health, reproductive performance, and meat quality (Wu et al., 2006; Caton and Hess, 2010; Funston et al., 2010; Reynolds and Caton, 2012; Greenwood et al., 2017). This concept is referred to as fetal or developmental programming and is based on the idea that stressors encountered during critical windows of development can alter the trajectory of development and have shortand long-term consequences in offspring (Godfrey and Barker, 2001; Caton et al., 2019). Additional complexity is introduced when the influence of these stressors is transmitted to subsequent generations through epigenetic mechanisms (Baye et al., 2011). Therefore, the ability of an offspring to fully express its genetic potential can be linked to environmental factors experienced by the dam such as weather, stress, and nutrient availability.

The concept of developmental programming originated from human epidemiological data with the "fetal origins" hypothesis. This theory linked poor maternal nutrition and low birth weights with increased incidences of cardiovascular, metabolic, and endocrine disease in adults (Barker et al., 1993; Barker, 1995; Godfrey and Barker, 2001). Subsequent studies using animals have focused on understanding how developmental programming might be harnessed to regulate a variety of outcomes related to livestock production, profitability, and end-product quality (reviewed by: Bell, 2006; Wu et al., 2006; Funston et al., 2012; Bell and Greenwood, 2016; Blair et al., 2016; Du et al., 2017; Broadhead et al., 2019; Greenwood and Bell, 2019).

### **Fetal Development Timeline**

The majority of developmental processes occur during the embryonic, fetal, and neonatal periods of life. This early time period is also when cellular, tissue, organ, metabolic, and hormonal systems are established (Greenwood et al., 2017). Considering that the majority of livestock raised for food production are subjected to the gestational environment for a considerable amount of time relative to their life span, opportunities to influence performance, composition, and meat quality traits prior to parturition should not be overlooked. For example, a steer raised for beef and slaughtered at 16 mo of age would spend approximately 37% of its entire life span (conception to slaughter) in utero. While the developing fetus is entirely subjected to the gestational environment until parturition, tissues will vary in their susceptibility to the maternal environment depending on the timing and severity of the environmental event or stressor (Nathanielsz, 2006) as well as the ability of the dam to buffer negative effects to the fetus (Robinson et al., 2013).

#### Early gestation

The first trimester of gestation is often overlooked because fetal requirements are minimal, and producers

are typically more focused on the offspring at the dam's side rather than the gestating fetus. However, a number of important developmental events begin early in gestation. Shortly after fertilization, the placenta attaches to the uterine wall and begins to develop (Reynolds and Redmer, 1995). Early gestation is also when development of economically important tissues such as skeletal muscle and adipose tissue is initiated. Myogenic, adipogenic, and fibrogenic cells develop from common progenitor cells known as pluripotent mesenchymal cells (Du et al., 2010). These cells become further differentiated based on which cell lineage they become committed to. Myogenic progenitor cells further differentiate into myofibers and form muscle, adipogenic progenitor cells differentiate into adipocytes and contribute to adipose tissue, and fibrogenic progenitor cells differentiate into fibroblasts to form connective tissue proper (Du et al., 2017). Alterations in the nutrient supply available to the fetus can impact signaling pathways that dictate differentiation of cells, potentially altering composition of these tissues postnatally (Zhu et al., 2004; Du et al., 2010). Given that adipocytes and fibroblasts are derived from the same progenitor cells, adipogenesis and fibrogenesis could be considered competitive processes. Strategies that reduce fibrogenic differentiation could enhance adipogenic differentiation, resulting in increased marbling and improved tenderness (Du et al., 2017). Furthermore, it has been demonstrated that influences from the maternal environment early in development can shift myogenic cell differentiation to adipogenic cell differentiation, indicating the potential to manipulate composition early in development (Du et al., 2010).

In beef cattle, it is estimated that primary myogenesis begins just before the first month of gestation and continues until just before the fourth month of gestation (Russell and Oteruelo, 1981; Du et al., 2010), whereas secondary myogenesis begins just before the third month of gestation and continues until month 7 or 8 (Russell and Oteruelo, 1981; Du et al., 2010). From this point of gestation on, primary and secondary muscle fibers continue to grow via hypertrophy. Thus, the majority of skeletal muscle fibers are formed between 2 and 8 months of gestation, and there is no net increase of myofibers after birth (Du et al., 2013; Greenwood and Bell, 2019). This is significant because any challenges or restrictions that compromise muscle development in utero could result in reduced muscle mass throughout the lifetime of the animal. In addition to muscle and adipose development, fetal limbs and critical organs such as the brain, heart, liver, lungs, and reproductive organs also begin to develop within the first months of gestation (Summers and Funston, 2013).

#### Mid to late gestation

As noted, primary muscle fibers begin to form during early gestation and function as scaffolding to support secondary muscle fiber development during mid-gestation. It is these secondary fibers that form the majority of muscle mass of an animal (Du et al., 2010, 2017). Early adipogenic commitment is estimated to overlap with secondary myogenesis, whereas the major formation of adipocytes occurs during late gestation and continues postnatally given adequate energy in the diet (Du et al., 2013, 2017). Adipocytes will eventually form distinct adipose depots detectable first in visceral fat depots, followed by subcutaneous and intermuscular fat (Du et al., 2013, 2017). Early adipogenesis occurring during mid-gestation is primarily associated with the development of visceral adipocytes (Robelin, 1981). It is estimated that development of subcutaneous adipocytes occurs between the mid to late fetal stage to approximately 8 months of age (Hood and Allen, 1973). Development of intramuscular adipocytes is estimated to occur from the late fetal stage to approximately 250 d of age (Du et al., 2017). Unlike myofibers, adipocytes can continue to develop postnatally; however, the number of adipocytes is primarily determined early in the postnatal period, and therefore insults to early development may alter the establishment of cell numbers and influence the distribution of those cells within different depots (Du et al., 2017). Because adipocyte formation occurs sequentially, there may be an opportunity to enhance marbling while not increasing overall fatness through strategic supplementation, although the mechanisms for this have not been defined (Du et al., 2013). Management practices that could alter adipocyte numbers and distribution among depots during development have the potential to influence carcass composition, yield grade, quality grade, and palatability of meat products.

#### Competition for nutrients

Research has shown that maternal nutrition in beef cattle can alter placental growth and function, impact uterine blood flow and nutrient transfer to the fetus, and affect organ development and differentiation of various tissues such as fat and muscle (Funston and Summers, 2013). During gestation, the partitioning of nutrients to different body tissues depends on their metabolic rate, with tissues having a lower metabolic rate given less priority than tissues with higher

metabolic rates (Redmer et al., 2004). Nutrients are carried in the blood stream, and therefore partitioning of nutrients is also dependent on the rate of blood flow. In the maternal body, the brain and central nervous system are of highest priority, followed by the placenta and fetus, and finally, bone, muscle, and fat are given the lowest priority (Redmer et al., 2004). In the fetus, skeletal muscle and adipose tissue have a lower priority in nutrient partitioning when compared with other organs. Insufficient maternal nutrition in early gestation reduced the number and size of myofibers in skeletal muscle (Zhu et al., 2004, 2006; Du et al., 2010, 2017). This reduction in the formation of fibers may result in irreversible long-term effects on growth, performance, and carcass characteristics (Du et al., 2010).

The partitioning of nutrients has also been reported to differ between mature and adolescent dams, with a higher priority for nutrients given to the growth of maternal tissues and fat deposition in heifers and young cows (Redmer et al., 2004). Multiparous cows that experienced a global nutrient restriction during mid and late gestation had calves with lighter birth weights compared with multiparous cows that did not experience a nutrient restriction (Greenwood and Cafe, 2007). Heifers experiencing the same level of restriction experienced more extreme reductions in calf birth weights compared with the mature cows (Greenwood and Cafe, 2007). Therefore, it appears that mature females are more able to buffer the effects of a nutritional insult than younger females. The completion of maternal growth likely contributes to this difference, because mature dams do not have to partition nutrients to both their own growth as well as their offspring growth, suggesting that maternal nutrition has a greater impact on fetal growth and development when dams are not mature. Therefore, it is important to consider the effect of maternal age on nutrient partitioning to support fetal growth and development.

### Influence of Maternal Nutrition on Offspring Performance and Carcass Traits

Cyclical body weight change of cows is often accepted by beef producers given changes in feedstuff availability, feed costs, forage quantity, and forage quality throughout the production year. However, awareness of the concept of developmental programming challenges this paradigm (Summers and Scholljegerdes, 2019). In recent years, there has been growing interest among beef producers and researchers regarding how to manage gestating cows to minimize the consequences of adverse environmental effects or enhance specific production or product traits of their offspring (Greenwood et al., 2017). Given that feed costs account for approximately two-thirds of the total operating costs of a cow–calf operation (USDA ERS, 2010) and nutritional deficiency during gestation is a common occurrence in many production situations (Caton and Hess, 2010), much of this interest has been directed toward controlled nutrition studies investigating the impacts of maternal nutrient restrictions or strategic supplementation on developmental and physiological impacts in offspring.

From a meat production perspective, management decisions made in response to drought, availability of feedstuffs, or cost of feedstuffs could alter the gestational environment, potentially leading to changes in fetal development and subsequent offspring composition. Additionally, the growing demand for highquality beef requires the consideration of all options to produce more consistently flavorful, juicy, and tender products. As developmental programming research expands, the influence of specific nutrients (energy and protein) and timing of nutritional treatments on offspring carcass composition and meat quality are of specific interest.

#### **Energy-based studies**

Energy supplements are typically utilized to meet nutrient deficiencies in cow herds during times of low forage quality and/or quantity, and offspring response to maternal energy deficiencies and varying energy source have been documented. In an early study, Corah et al. (1975) reported that restricted energy intake for 100 d prepartum in heifers (65% of National Research Council [1970] energy levels) and in cows (50% of National Research Council [1970] energy levels) caused a reduction in birth and weaning weights of calves. Additionally, calving death loss was 7% greater in heifers on the restricted diet than in control heifers. The percentage of calves from restricted cows that were alive at weaning was 71%-compared with 100% in control cows-indicating the potential for maternal energy restriction to impact operational profitability. In a study conducted at South Dakota State University, cows were exposed to diets that would either cause them to maintain a body condition score of 5 during mid-gestation or lose approximately 1 body condition score during mid-gestation (primarily through an energy restriction). At the end of mid-gestation, all

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cows were placed on the same adequate energy diet. These treatments resulted in cows that were in either a positive or negative energy status during midgestation. Following the mid-gestation treatment period, all cows were managed as a common group. At weaning, calves were transported to a feedlot and were fed common diets throughout a 28-d receiving period (days 1 through 28 of the feeding period), a 100-d backgrounding period (days 29 through 128 of the feeding period), and an 80-d finishing period (days 129 through 208 of the feeding period). Offspring were marketed when they were estimated to average 1.0 cm of 12th rib backfat thickness (208 d on feed). As with many studies evaluating mid-gestation nutrient restriction, no differences were detected in birth weight. However, offspring from the restricted cows were lighter at the receiving period at the feedlot, and this difference persisted until 57 d post-weaning (Taylor et al., 2016). After day 57, no differences were detected in body weight between treatments. Additionally, no differences were detected for hot carcass weight, ribeye area, meat color, or tenderness (Mohrhauser et al., 2015). There was an increase in the ratio of marbling to backfat in offspring from dams in a negative energy status, indicating that maternal restriction shifted the distribution of fat within the body as well as a tendency for decreased backfat and improved yield grade (Mohrhauser et al., 2015). Offspring in this study were also exposed to an immune challenge during the feeding phase to evaluate their ability to mount an immune response. Results show that calves from dams in a negative energy status during mid-gestation had a reduced immune response when challenged with a novel antigen (Taylor et al., 2016). While there may have been some benefits to carcass outcomes when cows were allowed to lose a body condition score during mid-gestation, the effects on receiving weight and potential health in the feedlot should be considered.

In a similar study, Gardner et al. (2021) investigated the change in dam plane of nutrition on offspring performance and meat quality traits. Offspring from cows managed to maintain a body condition score of 5.0–5.5 or lose one body condition score during midgestation did not differ in birth weight, feedlot performance, hot carcass weight, ribeye area, 12th rib fat thickness, or yield grade. However, a tendency for an improved marbling to backfat ratio was detected in offspring from restricted dams, which is similar to the findings of Mohrhauser et al. (2015) indicating a more favorable distribution of fat within the carcass when dams are restricted. Steaks from offspring of restricted dams were also rated as more tender by

Radunz et al. (2012) investigated the effects of 3 dietary energy sources (grass hay, corn, or dried corn distiller's grains) fed to mature beef cattle at day 160 of gestation through parturition. Calf birth weight was greater for progeny from cows fed corn or distillers grains than those fed hay, and weaning weight tended to be less in calves from cows fed hay versus corn. As stated by Radunz et al. (2012), high-concentrate diets may allow more energy to be partitioned to the fetus, which could help explain increased fetal growth in calves from dams that were fed corn or distillers grains. Cows in this study were fed to meet or exceed nutrient requirements, and therefore no nutrient restriction was imposed; however, cows in the hay and corn treatments gained less body weight during the treatment period compared with the cows fed dried distiller's grains (Radunz et al., 2010). Progeny ultrasound backfat and ribeye area measurements recorded at 24 and 72 h after birth and 84 d into the finishing period did not differ between treatments, and when fed to a common backfat, treatments did not influence average daily gain, dry matter intake, feed efficiency, receiving body weight, final body weight, hot carcass weight, ribeye area, USDA Yield Grade, or Warner-Bratzler shear force. However, dressing percentage was higher in progeny from dams fed a high-fiber diet, and calves from corn-fed dams had the lowest marbling scores and more carcasses grading USDA Select compared with offspring from hay-fed cows.

Gubbels et al. (2021) investigated the influence of maternal prepartum dietary carbohydrate source (concentrate-based diet or forage-based) in mid and late gestation on growth performance, carcass characteristics, and meat quality of offspring. Maternal carbohydrate source did not influence offspring body weight, ultrasound measurements assessed during the backgrounding and early feeding period, hot carcass weight, ribeye area, marbling score,  $L^*$  values, percentage moisture, crude fat, Warner-Bratzler shear force, or consumer sensory responses. However, offspring from the forage treatment tended to have decreased 12th rib fat thickness and tended to have lower USDA Yield Grades compared with offspring from the concentrate treatment. Offspring from the concentrate treatment had increased  $a^*$  and  $b^*$  values compared with the forage treatment. In addition, the concentration (milligrams per gram of wet raw tissue) of arachidonic (C20:4n6), nervonic (C20:1n9), and docosapentaenoic

(C22:5n3) acids were also increased in samples from the concentrate treatment. Although there is limited information on the effects of maternal diet on the fatty acid profile of meat from offspring, this result suggests that fatty acid composition is susceptible to maternal influence and warrants further investigation.

Overall, the results of these energy-based developmental programming studies have begun to highlight the susceptibility of adipose tissue to maternal nutrition, specifically the influence of maternal dietary energy levels and sources. Additionally, it appears that fat depots respond differently to maternal dietary influences, which may be related to the varied metabolic and physiological functions of each depot. Future work that continues to refine the understanding of how maternal energy levels and sources can influence adipose deposition in offspring will increase the capacity to improve growth, carcass composition, and meat quality.

#### Protein-based studies

Protein is often the first limiting nutrient for gestating beef cows consuming forage-based diets, and a protein restriction in ruminants can also impact energy status (Cochran et al., 1998). As described earlier, myofibers, adipocytes, and fibroblasts are all derived from a common pool of mesenchymal stem cells, and evidence suggests that a nutrient-restricted gestational environment can shift cell differentiation away from myogenesis, resulting in depressed muscle fiber development and enhanced adipocyte formation (Du et al., 2010). This phenomenon, proposed by Hales and Barker (1992) and termed the "thrifty phenotype" hypothesis, suggests that maternal undernutrition during pregnancy may cause a developmental adaptation (increased adiposity and reduced muscle mass) that is more prepared to deal with sparse nutrient availability after parturition (Barker, 2007; Ford et al., 2007). Research has demonstrated that mature mass and body composition can be altered by starvation or protein deficiency early in fetal life (Owens et al., 1993), potentially leading to performance and production differences regardless of whether early measures such as calf birth weight are affected (Funston et al., 2012). Given the value of muscle tissue to carcass weight and value, as well as the differential value of fat distribution within a carcass, studies specifically evaluating the influence of maternal protein levels on offspring carcass characteristics and meat quality have been completed.

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Micke et al. (2011a) fed heifers 240% or 70% of crude protein recommendations during the first and second trimesters of gestation (high or low protein during the first or second trimester). Skeletal muscle fibers and regulators of adipogenesis (insulin-like growth factor 1 [IGF-1], insulin-like growth factor 2 [IGF-2], and their receptors) in skeletal muscle were measured in offspring at 680 d of age. Cross-sectional areas of longissimus dorsi and semitendinosus muscles measured via ultrasound were greater for male offspring born to dams fed low-protein diets in the first trimester compared with dams fed high-protein diets; however, there were no differences in muscle size of female offspring during either trimester due to maternal treatment. Additionally, messenger RNA (mRNA) expression of IGF-1, IGF-2, and the IGF-2 receptor was increased in the semitendinosus muscle of male offspring born to heifers that were on a protein-restricted diet during the first trimester. Micke et al. (2011a) suggested that there may be an interaction between fetal sex steroid and maternal nutrient intake that resulted in sex-specific effects on fetal muscle development (Micke et al., 2011a). Micke et al. (2011b) also evaluated the relative expression of leptin in addition to IGF-1, IGF-2, and their receptors in various adipose depots (subcutaneous, perirenal, and omental) in offspring. High-protein diets in the first trimester increased leptin mRNA in perirenal fat depots of male progeny and IGF-1 mRNA in perirenal fat depots of female progeny. High-protein diets in the second trimester increased IGF-1 receptor mRNA in perirenal and omental fat depots of both steers and heifers, with increased leptin mRNA detected in perirenal depots of male progeny only. Carcass evaluation of offspring from this study was reported by Micke et al. (2010) and revealed no differences in hot carcass weight of steers. However, heifer progeny from dams receiving high protein during early gestation had heavier hot carcass weights. No differences were detected in fat thickness, but ribeye area was larger for offspring exposed to low maternal protein levels during mid-gestation; additionally, offspring of dams provided low protein during mid-gestation tended to have increased marbling scores compared with those provided high protein (Micke et al., 2010).

Data from Underwood et al. (2010) also indicated that mid-gestation responses to maternal nutrition may influence adipose tissue development as well as tenderness. In this study, cows were placed on improved pasture (6% to 11% crude protein) or native range (5% to 6.5% crude protein) during mid-gestation. Treatment had no impact on calf birth weight; however, increased weaning weight was observed in steer progeny from Blair et al.

cows on improved pastures, which could have been partially due to increased forage quality. Steers from dams grazing improved pasture had increased average daily gains and tended to finish at a heavier final body weight. The progeny from dams grazing improved pastures also had heavier hot carcass weights, increased fat thickness, and increased adjusted fat thickness. Progeny from dams grazing improved pastures produced steaks with reduced moisture content, tended to have a greater percentage of crude fat as evaluated by ether extract of the *longissimus* muscle, and reduced Warner-Bratzler shear force values, indicating a more tender product.

Kincheloe (2016) investigated impacts of a metabolizable protein restriction during mid and/or late gestation on progeny carcass characteristics from primiparous heifers provided either a control (101% of metabolizable protein requirements) or restricted (80% of metabolizable protein requirements) diet during mid or late gestation in a cross-over design. Hot carcass weight, 12th rib fat thickness, yield grade, marbling score, and proportion of carcasses in each USDA Quality Grade were not influenced by maternal diet. Progeny of dams on the restricted treatment in late gestation had greater ribeye area compared with progeny from control dams, similar to results reported by Micke et al. (2010), but this difference was not significant when adjusted on a hot carcass weight basis. Webb et al. (2019) utilized carcasses from this study and evaluated carcass composition and meat quality characteristics of offspring. Maternal metabolizable protein restriction during mid-gestation followed by no restriction during late gestation influenced meat tenderness as steaks from progeny that experienced restriction were less tender than progeny from dams that were not restricted during mid-gestation. In addition, proteinrestricted dams in mid-gestation had progeny that produced steaks with increased fatty acid content, whereas progeny from dams that were protein restricted in late gestation had decreased fatty acid content, suggesting that the timing of maternal metabolizable protein restriction can influence meat quality of progeny.

Larson et al. (2009) conducted a 3-y trial measuring steer growth performance from dams grazing either winter range or corn stalk residue and receiving no supplement or a protein supplement during late gestation and reported no impact due to winter grazing system or protein supplement on external fat thickness or yield grade. However, steers from protein-supplemented dams had increased marbling scores and a greater proportion that graded Choice or higher. The authors suggested that the increased marbling scores in calves from protein-supplemented dams are potentially due to changes in the site of nutrient deposition and intramuscular fat deposition from late gestation supplementation (Larson et al., 2009). These results are in partial agreement with Summers et al. (2011), who reported no differences in 12th rib fat thickness, ribeye area, or yield grade in steers born to dams receiving high (0.95 kg/d) and low (0.37 kg/d) levels of protein supplement during late gestation; however, marbling scores were increased in steers from dams receiving high levels of protein. Shoup et al. (2015) also evaluated the influence of maternal protein supplementation during late gestation and reported that high levels of protein supplementation did not influence 12th rib backfat thickness but increased the percentage of steer offspring grading average Choice or better compared with offspring from non-supplemented cows.

Overall, the general responses to the manipulation of maternal dietary protein might appear inconsistent. However, it is important to note that the differences in timing of the treatments (mid vs. late gestation) as well as the specific treatment applied (protein restriction vs. supplementation) can differentially influence fetal tissues and systems. Similar to the results reported earlier regarding fetal responses to maternal dietary energy, it appears that adipose tissue is also responsive to maternal dietary protein levels. Additionally, although there are a limited number of studies investigating the influence of maternal protein restriction on measures of meat quality, both Webb et al. (2019) and Underwood et al. (2010) reported a decrease in tenderness of steaks from offspring of protein-restricted dams. Future work investigating the mechanisms by which maternal protein levels can impact carcass composition and meat palatability traits is warranted.

### Conclusions

Fetal programming is still an emerging area of research in animal and meat science, and we often have more questions than answers as new data are collected. Although there are inconsistencies across research reports, trends are emerging that indicate that adipose depots may have differential responses to maternal nutrient status. Adipose tissue may be particularly sensitive to alterations in the maternal diet owing to its low priority for nutrients compared with vital organs during gestation and its adaptable nature throughout animal growth and development. It is clear that the timing and severity of maternal nutrient restriction can affect carcass and meat quality of offspring. In addition, diet composition, protein supplementation levels, and energy sources can influence nutrient availability and uptake by the fetus and subsequent postnatal outcomes. Continued research aimed at understanding the mechanisms involved in the response of offspring to maternal nutrient status is critically important for developing management strategies that will ultimately allow for the use of maternal dietary management as a tool to promote positive, directed changes to optimize performance and meat quality of offspring.

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