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Prenatal origins of productivity and quality of beef

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ABSTRACT - The productive traits of beef cattle are orchestrated by their genetics, post-natal environmental conditions, and also by the intrauterine background. Both under- or overnutrition, as specific dietary components, are able to promote persistent effects on the offspring. This occurs because dietary factors act not only affecting the availability of substrates for fetal anabolism and oxidative metabolism, but also as signals that regulate several events toward fetal development. Therefore, this study aimed to summarize the gestational nutrition effects on the offspring performance and meat quality in a long term. Overall, studies have shown that many of these alterations are under the control of epigenetic mechanisms, as DNA methylation, histones modification, and non-coding RNA. The current knowledge has indicated that the fetal programming responses are dependent on the window of fetal development in which the dietary treatment is applied, the intensity of maternal nutritional stimuli, and the treatment application length. Collectively, studies demonstrated that muscle cell hyperplasia is impaired when maternal requirements were not achieved in the second third of gestation, which limits the formation of a greater number of muscle fibers and the offspring growth potential in a long term. Changes in muscle fibers metabolism and in collagen content were also reported as consequence of a dietary perturbation during pregnancy. In contrast, a maternal overnutrition during the late pregnancy has been associated with beneficial responses on meat quality. In summary, ensuring an adequate maternal environment during the fetal development is crucial to enhance the productive responses in beef cattle operations.

Keywords: adipogenesis, bovine, fibrogenesis, maternal nutrition, myogenesis, progenitor cells

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1. Introduction

Fetal programming is the response of an organism to an environmental challenge during a critical period of intrauterine development, which leads to persistent changes (Nathanielsz et al., 2007). Both maternal under- and overnutrition can trigger changes in the development, metabolism, and physiology of the offspring (Nissen et al., 2003; Greenwood and Cafe, 2007; Duarte et al., 2014; Gionbelli et al., 2018; Costa et al., 2021a). Such modifications are under the control of epigenetics, which act as a memory of the environment exposure (Wu et al., 2006; Sinclair et al., 2016; Paradis et al., 2017; Batistel et al., 2019).

Dietetic manipulations over pregnancy are an opportunity to improve the offspring performance and meat quality, but at the same time, is a way to compromise these characteristics irreversibly. The basic structure of skeletal muscle tissue is composed by muscle fibers, adipocytes, and connective tissue, all derived from the mesenchymal stem cells of mesoderm (Du et al., 2013) (Figure 1). In this sense, maternal nutrition acts to control the fate steam cell in the different lineages, regulating the balance between myogenesis, adipogenesis, and fibrogenesis (Du et al., 2013; Blair et al., 2021).

Overall, studies have shown that inadequate maternal diets in beef cattle have negative consequences such as a lower population of muscle fibers (Marquez et al., 2017; Costa et al., 2021a), due to changes in the mRNA abundance of myogenic regulatory factors (Jennings et al., 2016) involved with cell determination, proliferation, and differentiation. Those changes lead to a lower muscle growth potential (Costa et al., 2021b), which affects the whole-body energy expenditure in the post-natal life, once skeletal muscle is the major glucose utilization site (Mohammadabadi et al., 2021). Less muscle fiber hyperplasia can be replaced by intramuscular collagen deposits (Costa et al., 2021a), which may contribute to increase meat toughness (Fontes et al., 2021). Moreover, prenatal nutritional insults can also cause changes in muscle fiber metabolism regulated by transcription factors (Ramírez-Zamudio et al., 2022) known as skeletal muscle metabolic plasticity (Aragão et al., 2014), which can negatively affect marbling deposition (Marquez et al., 2017). Therefore, monitoring the gestational environment is crucial to enhance the efficiency of meat production.

This comprehensive review aimed to highlight the effects of maternal nutrition on the offspring performance and meat quality, once the identification of these responses plays a central role in the global beef satisfying demand. Here, we first discuss the maternal and placental metabolism changes in response to the availability of nutrients over gestation, as well as the underlying mechanisms

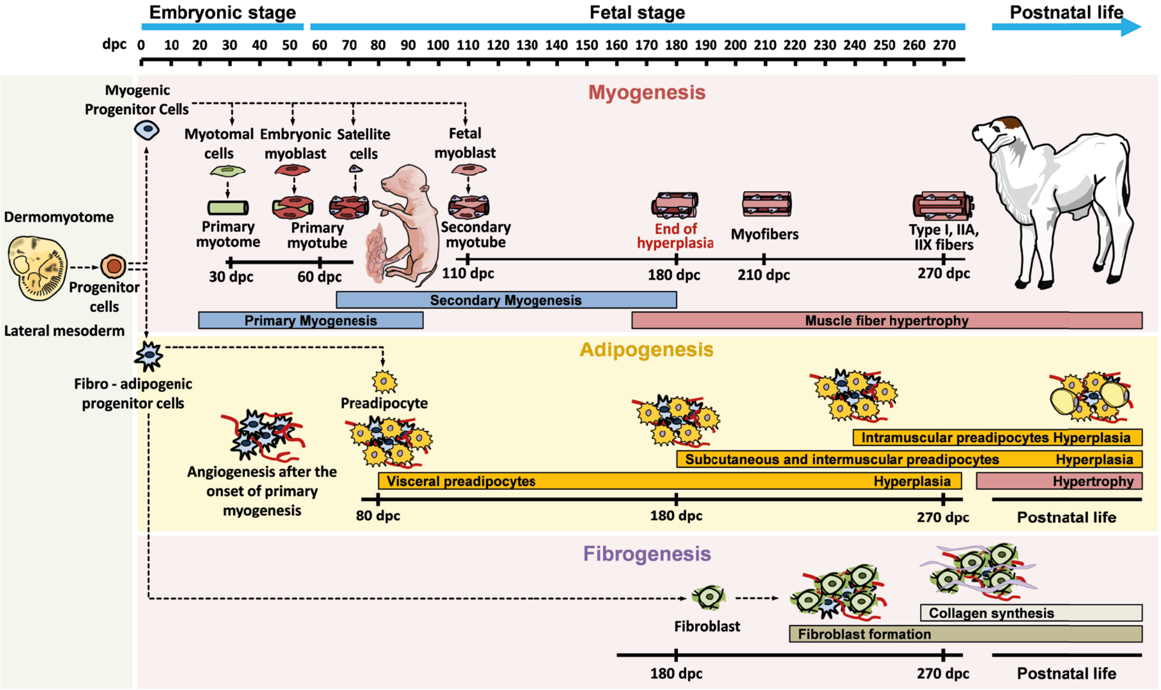


Diagram based on studies from Picard et al. (2002), Bonnet et al. (2010), Du et al. (2015), and Wang et al. (2016). Summary of the main processes involved in skeletal muscle cell differentiation during the embryonic and fetal stages and postnatal life according to the days post conception (dpc). Mesenchymal progenitor cells differentiate into myogenic and fibro-adipogenic cells during the embryonic stage in beef cattle. Primary myogenesis occurs in the embryonic stage, followed by secondary myogenesis that occurs in the fetal stage up to 180 dpc, approximately, with subsequent secondary myofibers maturing into types I, IIA, and IIX. Hypertrophy of muscle fibers begins around 170 dpc and extends to postnatal life. The determination of fibroadipogenic cells begins in the fetal phase, with the formation of preadipocytes in different fat deposits, including visceral, subcutaneous, intermuscular, and intramuscular. Fibrogenesis begins around 180 dpc, with the formation of fibroblasts followed by collagen synthesis that begins around 260 dpc and extends to postnatal life.

Figure 1 - Mesenchymal progenitor cells differentiate into myogenic and fibroadipogenic cells during fetal muscle development in beef cattle.

involved with phenotypic alterations observed in a long term. Then, we summarized the main effects of maternal nutrition on productive traits of beef cattle.

2. Changes in maternal and placental metabolism in response to nutritional challenges during gestation

During gestation, females from all species undergo homeorhesis, in which several physiological changes occur to ensure the continuous supply of essential metabolites to support fetal growth and development (Redmer et al., 2004). Thus, when fetal development is critical, due to nutrient deficiency, the mother tends to favor the fetal system, with coordinated changes in her own tissue metabolism that regulate the nutrient partitioning needed to supply the fetus (Bauman and Currie, 1980).

In addition to the utilization of propionate for glucose production during periods of low availability or high demand for glucose, energy reserves may also be mobilized and used as a gluconeogenic precursor (Funston et al., 2010a). Under conditions of nutrient deficiency, the amino acids provided by the mobilization of maternal skeletal muscle are used to improve fetal access to amino acids (Bell et al., 2005) or may also be used in maternal gluconeogenesis. The utilization of long-chain fatty acids, non-esterified fatty acids (NEFA), or ketoacids by the fetuses is limited due to the low placental ability to transport these substrates (Bell et al., 2005). However, although NEFA seem to be not utilized by the fetus as a carbon source for energy production, this substrate supplies the pregnant dam with substrates for their own maintenance, and thus it indirectly contributes to spare glucose and amino acids to supply fetal requirements (Bell and Ehrhardt, 2000).

Maternal tissue mobilization or deposition occurs as a function of dietary substrate supplies (McNeill et al., 1997). Thus, nutritional adjustments for pregnant cows undergoing nutritional restrictions have been the subject of studies (Lopes et al., 2020), which, in general, aimed to establish nutritional management that minimizes lean tissue catabolism and the negative effects on the fetus. For instance, Lopes et al. (2020) showed the importance of supplementation for undernourished beef cows and reported a tendency toward greater mRNA expression of skeletal muscle synthesis markers in cows that received protein supplementation during late gestation. Such results likely demonstrate that a consequence of protein supplementation during gestation is a reduction in the intensity of lean tissue mobilization.

Under conditions of low nutrient availability causing intrauterine growth restriction, an additional compensatory mechanism involving the placenta may occur (Redmer et al., 2004). Borowicz et al. (2007) reported that when metabolizable protein is reduced to 60% of requirements in sheep, uterine blood flow increased, indicating an adaptation of placental vasculature. Therefore, it is possible that nutrient deprivation due to inadequate placenta size and function affects fetuses from well-nourished dams. Additionally, fetuses from undernourished dams may not have difficulty meeting their nutrient requirements due to compensatory mechanisms in the placental system (Redmer et al., 2004). For instance, Vonnahme et al. (2007) showed that nutrient restriction from 30 to 125 days of gestation in bovine increased placental mRNA concentrations of placental growth factor, improving fetal weight due to a greater transfer of nutrients through the placenta. Under a moderate nutritional restriction, the placenta may contribute to an increase in the abundance of Glucose transporter 3 (GLUT-3) as an attempt to increase its ability to glucose transfer (Bell and Ehrhardt, 2000). However, under severe and prolonged nutrient restriction, the placenta may reduce glucose uptake and use glucose for its own demands (Bell and Ehrhardt, 2000). McCrabb et al. (1992) showed that pregnant sheep subjected to nutrient restriction in mid-gestation presented a decrease in placenta size without changing the number of individual placentomes or the fetal weight and dimensions. In contrast, Zhang et al. (2016) observed that undernourished animals presented lower concentrations of serum total polyamines in the uterine artery, fetal umbilical vein, and amniotic and allantoic fluids, which are crucial mediators of placental growth and angiogenesis, of fetal cellular function and synthesis of DNA and protein (Zhang et al., 2016).

Therefore, the compensatory mechanisms related to placental functioning may occur under conditions of nutritional restriction by the pregnant dam during gestation in attempt to mitigate the effects on fetal development, which may buffer the negative effects on the development of fetuses.

3. Maternal nutrition effects on epigenetic mechanisms underlying the skeletal muscle development

It is well established that among omics extracts (transcripts, proteins, and metabolites), a set of regulations and interactions generates a specific response according to the environment. These modulations may be explored through epigenetic analysis and systems biology approaches. Epigenetics explains how gene expression might be altered without affecting the nucleotide sequence (Feil, 2006). Moreover, this set of mechanisms is transferred between cell generations, constituting epigenetic memory. Of the epigenetic modifications, DNA methylation, chromatin remodeling, and noncoding RNA are relevant mechanisms for maternal nutrition and fetal programming.

DNA methylation is related to gene silencing, since the inclusion of a methyl group at the 5' position of the cytosine residues located in the CpG islands in the promoter region of a gene inhibits the interaction between the transcriptional machinery complex and the target gene (Osorio et al., 2017). This process is widely influenced by dietary precursors, which are responsible for donating chemical groups to positively or negatively regulate DNA methylation (Osorio et al., 2017). The methyl donor S-adenosylmethionine (SAM), synthesized in the methionine cycle, is transferred to DNA through DNA methyltransferases (DNMT) (Triantaphyllopoulos et al., 2016). Demethylation and, consequently, the reversion of gene silencing are catalyzed by the α-ketoglutarate (α-KG)-dependent ten-eleven translocation (TET) family of proteins (Ito et al., 2010). At the transcriptional level, energy restriction during late gestation has been found to alter the skeletal muscle and blood transcriptome of calves; specifically, genes related to energy metabolism and muscle development are downregulated in muscle cells, accompanied by a decrease in the expression of genes associated with the immune response (Sanglard et al., 2018). While evaluating the DNA methylation level of some important gene inducers of cell differentiation, Paradis et al. (2017) observed hypermethylation in the promoter region of *IGF2* in fetal skeletal muscle of offspring born from cows that were nutrient-restricted during mid- to late gestation, emphasizing the interaction between the nutritional plan and changes in gene expression.

Chromatin remodeling is mediated by histone post-translational modification (PTM), which involves the inclusion of a set of chemical or protein groups (e.g., methyl, acetyl, phosphate, and ubiquitin) to the histone tails (Triantaphyllopoulos et al., 2016). The combination of different PTM in a specific histone is called the histone code (Jenuwein and Allis, 2001). Depending on the histone code, chromatin may assume the structure of heterochromatin (compacted) or euchromatin (relaxed), which are associated with the repression or activation of gene expression, respectively (Jenuwein and Allis, 2001). As an example, a decrease in the histone code H3K27me3 (histone 3 lysine 27 trimethylation) marker of gene silencing promoted an increase in overall adipogenesis in fetal mice from obese mothers (Yang et al., 2013). In contrast, the increase in the histone codes H3K9Ac (histone 3 lysine 9 acetylation) and H3K4me3 (histone 3 lysine 4 trimethylation) markers of gene activation, in the promoter region of myostatin, resulted in the reduction in muscle mass of piglets born from sows fed low-protein diets during pregnancy and lactation (Jia et al., 2016).

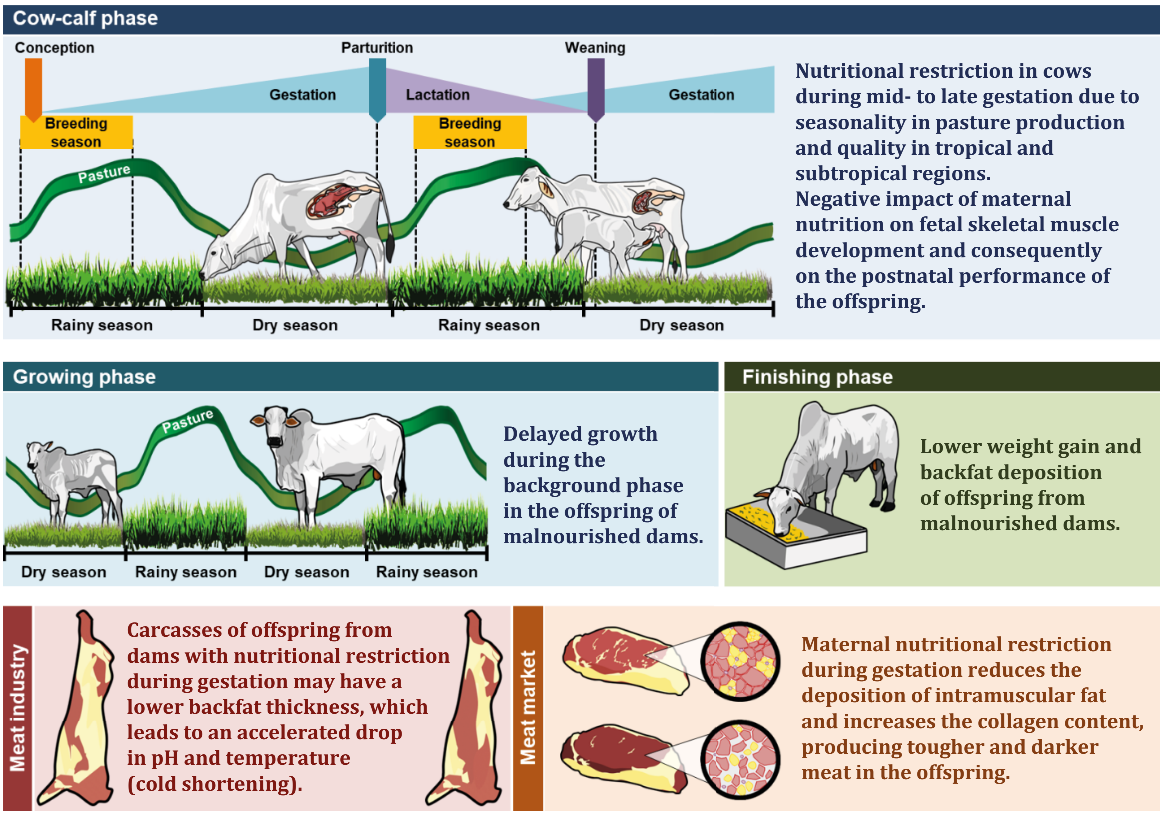
When the effects of maternal feed restriction during different stages of gestation on the newborn goat skeletal muscle transcriptome (Costa et al., 2021c) and proteome (Costa et al., 2022) were evaluated, it was observed that proteins exclusively expressed in each treatment (feed restriction in the first vs. last half of gestation) were present in both treatments at the transcriptional level. This suggested possible posttranscriptional regulation that repressed a set of genes in one of the treatments. The mechanism of post-transcriptional regulation may be mediated by noncoding RNA, called microRNA (miRNA). The inhibitory role of miRNA involves base-pairing with the target mRNA, which promotes repression (Wang et al., 2013). Imperfect base-pairing with the target mRNA inhibits translations and, consequently, protein synthesis, while perfect complementation causes the degradation of the target mRNA (Wang et al., 2013).

Therefore, maternal nutrition directly affects fetal metabolism through the pool of available nutrients, which mediate epigenetic mechanisms. The integration of omics data using a systems biology approach, combined with epigenetic analysis, may contribute valuable information on the effects of maternal nutrition on offspring skeletal muscle development and metabolism at the cellular level, which is reflected in the skeletal muscle growth and development and may cause changes in the quality traits of meat.

4. The impact of maternal nutrition on the performance, carcass, and meat quality traits of the offspring

In tropical and subtropical regions, forages are the main components of the diet in most cow-calf herds (Bell and Greenwood, 2013). Such a scenario promotes variation in pasture availability and quality throughout the year, which is insufficient to meet the nutritional requirements of pregnant cows, mainly during mid- to late gestation (Lemos et al., 2012). Therefore, maternal restriction during critical periods of fetal skeletal muscle and adipose tissue development may compromise the performance and meat quality of the offspring (Figure 2).

During the dry season, pastures are deficient in proteins; thus, the restriction of energy and other nutrients in pregnant cows is also observed. In fact, the reduction of protein intake affects ruminal microorganism growth, which is responsible for the degradation of dietary fibers, causing a limitation of energy and dry matter intake (DMI) by cows (Sampaio et al., 2010). Therefore, the use of nutritional strategies that increase the protein intake of pregnant cows improves the digestibility of low-quality fibers and, consequently, enhances maternal-fetal nutrient flow (Marquez et al., 2017). However, studies examining the effects of maternal nutritional strategies on offspring performance and carcass characteristics have had variable results (Tables 1a and 1b).



Nutritional restriction in cows during mid- to late gestation due to seasonality in pasture production and quality in tropical and subtropical regions.
Negative impact of maternal nutrition on fetal skeletal muscle development and consequently on the postnatal performance of the offspring.

Delayed growth during the background phase in the offspring of malnourished dams.

Lower weight gain and backfat deposition of offspring from malnourished dams.

Carcasses of offspring from dams with nutritional restriction during gestation may have a lower backfat thickness, which leads to an accelerated drop in pH and temperature (cold shortening).

Maternal nutritional restriction during gestation reduces the deposition of intramuscular fat and increases the collagen content, producing tougher and darker meat in the offspring.

Figure 2 - The impact of maternal nutrition on the performance and carcass characteristics of the offspring.

Table 1a - Effects of nutritional management of pregnant cows on performance and carcass characteristics of the offspring

Item	Underwood et al. (2010)[A,1]		Stalker et al. (2007)[B,2]		Stalker et al. (2006)[C,3]		Larson et al. (2009)[D,3]	
	REST	NR	REST	NR	REST	NR	REST	NR
Birth weight (kg)	38.7±2.0	36.6±1.9	38.4±0.4a	39.8±0.4b	36.1±0.5	36.6±0.5	36.9±1.1a	38.4±1.1b
Weaning weight (kg)	242.1±3.7a	256.2±3.5b	199.8±2.3a	210.1±2.3b	211.0±2a	217.5±2b	235±8	241±8
Feedlot performance								
Slaughter weight (kg)	520.6±7.7a	543.9±7.1b	557.5±8a	586.5±8b	-	-	602.5±13	615.5±13
Dry matter intake (kg/d)	-	-	11.2±0.2a	12.1±0.2b	8.48±0.17	8.53±0.17	8.94±0.21a	9.19±0.24b
Average daily gain (kg/d)	1.49±0.07a	1.66±0.06b	1.60±0.04a	1.68±0.04b	1.56±0.02	1.56±0.02	1.66±0.05a	1.70±0.05b
Feed efficiency (kg:kg)	-	-	0.144±0.004	0.139±0.004	0.185±0.002	0.183±0.002	0.186±0.07	0.186±0.07
Carcass characteristics								
Carcass weight (kg)	329.5±4.8a	348.2±4.5b	346.5±5a	365.0±5b	363±4	369±4	364±8	372±8
Yield (%)	-	-	-	-	64.6±2	64.9±2	-	-
Rib eye area (cm²)	-	-	87.2±1.8	87.7±1.8	86.9±1.0	88.1±1.0	89.1±1.9	89.4±1.9
Backfat thickness (cm)	1.11±0.15a	1.51±0.14b	1.24±0.06	1.21±0.06	1.31±0.06	1.34±0.06	1.17±0.08	1.24±0.08
Marbling score	420±16	455±15	548±20	561±20	467±9	479±9	443±20a	492±20b

REST - nutritional restriction during gestation; NR - no nutritional restriction during gestation.

[A] REST = native pasture with ~6% CP; NR = improved pasture with ~11% CP; treatment for 30 days during the second half of gestation. Twenty-six crossbred dams carrying male offspring from Angus sires (REST, n = 12; NR, n = 14). Offspring slaughtered at 430±2 days of age.

[B] REST = native pasture with ~7.5 CP; NR = native pasture with ~7.5% CP + 0.45 kg supplement/day/3 times a week (42% CP) during the last third of gestation. One hundred thirty-six dams (¼ Angus, ¼ Gelbvieh, ¼ Hereford, and ¼ Simmental) from 3 to 5 years of age pregnant with male offspring. Offspring slaughtered at ~314 days of age.

[C] REST = native pasture with ~7.5 CP; NR = native pasture with ~7.5% CP + 0.45 kg supplement/day/3 times a week (42% CP) during the last third of gestation. One hundred thirty-six dams (¼ Angus, ¼ Gelbvieh, ¼ Hereford, and ¼ Simmental) from 3 to 5 years of age pregnant with male offspring. Offspring slaughtered at ~372 days of age.

[D] REST = native pasture with ~6.8% CP or corn residues with ~5.2% CP; NR = native pasture with ~6.8% CP or corn residues with ~5.2% CP + 0.45 kg supplement (28% CP) during the last third of gestation. One hundred and nine Red Angus × Simmental cows between 3 and 5 years of age pregnant with male offspring. The offspring was slaughtered when they reached 1.3 cm of backfat thickness.

[1] Marbling score: trace = 200; slight = 300; small = 400.

[2] Marbling score: slight = 400; small = 500.

[3] Marbling score: small = 400; modest = 500.

a,b - Significant differences between the groups ($P<0.05$).

Table 1b - Effects of nutritional management of pregnant cows on performance and carcass characteristics of the offspring

Item	Mulliniks et al. (2012)[E,2]		McLean et al. (2018)[F,4]		Maresca et al. (2019)[G,5]	
	REST	NR	REST	NR	REST	NR
Birth weight (kg)	-	-	37.6±0.5	37.7±0.5	-	-
Weaning weight (kg)	253±5	253±5	176.2±4.2	180.8±4.2	-	-
Feedlot performance						
Slaughter weight (kg)	511±8	512±8	647.9±7.7a	631.2±7.7b	493.6±12.5	480.5±16.0
Dry matter intake (kg/d)	-	-	-	-	11.6±0.66	10.4±0.68
Average daily gain (kg/d)	1.38±0.04	1.46±0.04	1.86±0.03a	1.78±0.03b	1.45±0.10	1.29±0.23
Feed efficiency (kg:kg)	-	-	-	-	-	-
Carcass characteristics						
Carcass weight (kg)	322±6	323±6	386.6±5.5	377.8±5.5	284.3±7.7	289.5±9.9
Yield (%)	63.1±0.19	62.9±0.19	63.6±0.4	63.8±0.4	57.6±0.6a	60.2±0.8b
Rib eye area (cm^2)	80.5±1.16	82.3±1.16	87.0±1.4	87.8±1.4	63.7±1.65a	69.4±2.22b
Backfat thickness (cm)	1.36±0.07	1.42±0.07	1.55±0.09	1.45±0.09	0.67±0.07	0.57±0.08
Marbling score	487±13	487±13	364±16	366±16	455±15	435±20

REST - nutritional restriction during gestation; NR - no nutritional restriction during gestation.

[E] REST = forage *Bouteloua gracilis*, *Aristida* spp., *Lycurus phleoides* + supplement (36% CP) in high stress phases; NR = forage *Bouteloua gracilis*, *Aristida* spp., *Lycurus phleoides* + 202 g/cow/day supplement with 50% NDCP (blood and feather meal) during the last third of gestation. Three hundred thirty-three Angus dams or crossbreds with Angus from 3 to 9 years of age pregnant with male. The offspring was slaughtered at ~340 days of age.

[F] REST = native pasture (≤ 6% CP) + 0.2 kg/day/4 days a week supplement (8% CP); NR = native pasture (≤ 6% CP) + 1.82 kg/day/4 days a week supplement (38% CP). Supplementation of the treatments REST and NR during the breeding season and the initial third of gestation. One hundred eighty-nine multiparous Angus cows with male pregnancy. Slaughter of offspring at ~699 days of age.

[G] REST = feedlot diet with 6% CP; NR = feedlot diet with 12% CP. Both diets were isoenergetic and were provided from 134±14 days of gestation to term. Sixty-eight multiparous Angus cows pregnant with an Angus sire. Twenty-four male offspring was selected and subsequently slaughtered at 687±13 days of age.

[2] Marbling score: slight = 400; small = 500.

[4] Marbling score: slight = 200-299; small = 300-399.

[5] Marbling score: trace = 200; slight = 300; small = 400; modest = 500.

a,b - Significant differences between the groups (P<0.05).

Underwood et al. (2010) showed that cows fed improved pasture for 30 days at mid-gestation exhibited an increase of 10% in the offspring weaning and feedlot weight compared with the offspring resulting from cows fed native range pasture (~6% crude protein). In addition, an increase of approximately 19 kg carcass and 13.6% subcutaneous fat was observed in the resulting offspring (Underwood et al., 2010). These results may suggest that outcomes of fetal programming through maternal nutrition may have an indirect effect on meat quality traits. The increased subcutaneous fat thickness in the carcass of offspring born from dams in better nutritional conditions likely help to prevent the rapid decline in temperature during the transformation process of muscle to meat, avoiding cold-shortening, which contributes to meat toughness (Ockerman and Basu, 2014). Moreover, the heaviest carcasses in progeny born from dams that received adequate nutrition during gestation may result from greater muscle fiber development during the fetal stage. Costa et al. (2021a) showed that maternal protein restriction during mid-gestation reduces the number of muscle fibers in offspring.

In general, progeny from dams that receive an adequate nutritional plan shows better performance during the initial stages of life (Stalker et al., 2006; Stalker et al., 2007; Funston et al., 2010a; Funston et al., 2010b; Rodrigues et al., 2020), while few studies have reported significant gains throughout the production cycle (Stalker et al., 2007; Underwood et al., 2010). In contrast, other studies have failed to find an effect of adequate nutrition during mid- to late gestation on offspring performance throughout the production cycle or on carcass characteristics (Larson et al., 2009; Mulliniks et al., 2012; Mulliniks et al., 2013). Such variations in the phenotypic responses of progeny affected by maternal nutrition depend on multiple factors, such as herd management during the production phases, genetic composition, maternal nutritional history, and adaptability to the environment (Broadhead et al., 2019).

Maternal nutritional status during gestation may impact the qualitative properties of the meat from offspring (Alvarenga et al., 2016; Maresca et al., 2019; Webb et al., 2019). For instance, the meat of steers born from dams raised under improved pastures for 30 days at mid-gestation was more tender than that of steers born from dams fed native pasture (~6% crude protein) (Underwood et al., 2010). In addition to tenderness, the pH, color, water-holding capacity, and marbling of the meat may be affected by maternal nutrition due to alterations in the metabolic characteristics of muscle fibers (Fahey et al., 2005; Picard and Gagaoua, 2020), as well as the proportion of muscle, adipose, and connective tissue formed during the prenatal phase (Duarte et al., 2014; Du et al., 2015). For example, a 50% nutrient restriction in sheep during the first 30 days of gestation enhanced the proportion of muscle fibers with the characteristics of slow contraction and oxidative metabolism in offspring (Fahey et al., 2005). Muscles with a greater proportion of slow-twitch fibers and oxidative metabolism show a low rate of *postmortem* pH decline due to low glycogen storage, resulting in an elevated final pH of the meat (Kim et al., 2016). When the pH is higher than 5.6, there is a change in the negative charge and structures of the muscular matrix, which results in greater intracellular water retention, negatively affecting meat color (Ramanathan et al., 2020). Moreover, changes in the final pH interfere with the activity of proteolytic enzymes, which are responsible for tenderness (Matarneh et al., 2017).

However, some changes may occur at the molecular level (Table 2) without resulting in phenotypic changes. Jennings et al. (2016), evaluated the effects of energy levels [72, 87, or 146% of net energy for maintenance (NEm) requirements] during early to mid-gestation and did not find effects of maternal nutrition on muscle histology characteristics (fiber area, diameter, and number), despite the effects on mRNA expression in skeletal muscle. In this study, *myogenin* was upregulated in the skeletal muscle of fetuses from cows fed at 72% NEm compared with those from cows fed at 87% NEm, indicating a potential reduction in myoblast differentiation, followed by an earlier fusion of these cells in fetuses exposed to undernutrition.

Rodrigues et al. (2020) investigated the effects of protein supplementation during mid- to late gestation in grazing beef cows with moderate nutritional restriction on performance and molecular markers in offspring (Table 2). Protein supplementation of the dams did not affect the expression of myogenic genes. However, a downregulation of *C/EBPA* and *FABP4* was observed in 11-day-old calves

Table 2 - Effects of prenatal nutrition on gene expression and characteristics of skeletal muscle in cattle

Reference	Period of gestation	Genes with altered expressions	Genes with unaltered expression	Phenotypic trail
Jennings et al. (2016)[A]	85 to 180 d	Upregulated in OVER: *PREF-1***; *µ-Calpain***; *IGF-II**; upregulated in RES: *CEBPB***; *FAS**; *MyoG***; *IGF-II**	*PPARG*; *C/EBPA*; *SCD*; *MyoD*; *MyF5*; *MRF4*; *Myostatin*; *m-Calpain*; *Calpastatin*; *IGF-I*	No effects on fetal weight, fiber area (µm^2), fiber diameter (µm), or fiber number in *longissimus dorsi* and *semitendinosus*.
Paradis et al. (2017)[B]	147 to 247 d	Upregulated in RES *longissimus dorsi*: *MyoD***; *MyoG***; *PPARG***; *IGFI***; *IGF1R***; *IGF2R***; *INSR***	*IGF2*; *MEF2A*; *SRF*	No effects on fetal weight or crown-rump length.
Marquez et al. (2017)[C]	MID = 30 to 180 d LATE = 181 to 281 d	*PPARA*** = greater for MID and lower for LATE; *FGF2*** = greater for MID, lower for CON and LATE	*TGFβ1*; *COL1A1*; *FGF2R1*; *COL3A3*; *PPARG*; *MCDA*; *UCP3*; *PPKAA2*; *HADH*; *MYH7*; *PDK4*; *PGC1α*; *CPT1*; *ZFP423*; *C/EBPA*	No effects on fiber area (µm^2) or BW at birth and weaning. Greater number of muscle fibers for MID and lower for CON**. Greater ribeye area (cm^2) for MID and LATE**.
Gionbelli et al. (2018)[D]	60 to 139, 199, 241 or 268 d	*CTNNB***; *ZFP423*** and *PPARG*** = greater expression at 139 d for OVER; *FN1*** = greater for OVER	*MyoD*; *MyoG*; *C/EBPA*; *COL1A1*; *COL3A1*; *TGFβ1*	Crude protein content in skeletal muscle (g/kg) greater for OVER**. No effects on fat content of skeletal muscle, intramuscular collagen deposition (percentage), or the number of myocytes.
Rodrigues et al. (2020)[E]	124 to 270 d	Birth: *PPARG***, *WNT10B***, *CD36***, *TGFβ1*** = greater for SUP; 11 days of age: *C/EBPA***; *FABP4*** = lower for SUP; weaning: *PPARG**, *ZFP423***; *TGFβ1*** = greater for SUP	*β-catenin*; *COL3A1*; *FN1*; *MyoD*; *MyoG*; *IGFR1*; *mTOR*; *MyHC1*; *MyHC2a*; *MyHC2x*	Greater BW at birth for SUP**. No effects on BW at 120 and weaning.
Costa et al. (2021a)[F]	100 to 200 d	30 d: *PAX7** and *MHC2X*** = greater for CON. 450 d: no effects. Maternal nutrition × offspring sex interactions: 30 d: *ZFP423**; *FN**; *PDGFRα**; *MHC1**; *MHC2X**; *LOX*. 450 d: *FN**; *TGFβ**; *MMP2**; *MHC1**; *COL1***; *COL3***; *MHC2X***	30 d: *C/EBPA*; *PPARG*; *TGFβ*; *COL1A1*; *COL3*; *P4Ha1*; *TIMP1*; *TIMP2*; *MHC1*; *MHC2A*; 450 d: *ZFP423*; *C/EBPA*; *PPARG*; *LOX*; *P4Ha1*; *TIMP1*; *TIMP2*; *PAX7*; *PDGFFRα*; *MHC1*; *MHC2A*; *MHC2X*	Lower number of muscle fibers for CON**. Increase skeletal muscle collagen content for CON**.

18S = 18 S ribosomal; *CD36* = cluster of differentiation 36; *C/EBPA* = enhancer-binding protein α; *C/EBPB* = enhancer-binding protein β; *COL1A1* = collagen type I, α 1; *COL3A3* = collagen type III, α 3; *CPT1* = carnitine palmitoyltransferase 1; *CTNNB1* = cadherin-associated protein, beta-1; *FABP4* = adipocyte-type fatty acid-binding protein; *FAS* = fatty acid synthase; FGF2 = fibroblast growth factor 2; *FGF2R1* = fibroblast growth factor 2, receptor 1; *FN1* = fibronectin 1; *HADH* = hydroxyacyl-CoA dehydrogenase; *IGF1* = insulin-like growth factor 1; *IGF1R* = insulin-like growth factor 1 receptor; *IGF2* = insulin-like growth factor 2; *IGF2R* = insulin-like growth factor 2 receptor; *INSR* = insulin receptor; *LOX* = lysyl oxidase; *MCAD* = medium-chain acyl-CoA dehydrogenase; *MEF2A* = myocyte enhancer factor 2A; *MMP2* = matrix metalloproteinase-2; *MRF4* = myogenic regulatory factor-4; *mTOR* = mammalian target of rapamycin; *MyoD* = myogenic differentiation 1; *MyoG* = myogenin; *MYH7* = myosin heavy chain 7; *MyHC1* = myosin heavy chain type I; *MyHC2a* = myosin heavy chain type IIa; *MyHC2x* = myosin heavy chain type IIx; *P4Ha1* = prolyl 4-hydroxylase subunit alpha 1; *PDK4* = pyruvate dehydrogenase kinase 4; *Pax7* = paired box 7; *PDGFRa* = platelet-derived growth factor receptor A; *PGC1α* = peroxisome proliferator-activated receptor γ coactivator 1 α; *PPARα* = peroxysome proliferator-activated receptor α; *PPARG* = peroxysome proliferator-activated receptor γ; *PRKAA2* = protein kinase AMP - activated catalytic subunit α 2; *PREF-1* = preadipocyte factor-1; *SCD* = stearoyl-CoA desaturase; SRF = serum response factor; *TGFβ1* = transforming growth factor-β1; *UCP3* = uncoupling protein 3; *TIMP1/2* = TIMP metallopeptidase inhibitor 1 or 2; *ZFP423* = zinc finger protein 423; *WNT10B* = wingless-type MMTV integration site family member 10B; NEm - net energy for maintenance; CP - crude protein.

[A] LOW = fed 72% of NEm of NRC requirements; CON = fed 87% of NEm of NRC requirements; HIGH = fed 146% of NEm of NRC requirements.

[B] LOW = fed 85% of ME requirements; HIGH = fed 140% of ME requirements.

[C] CON = unsupplemented; MID = fed 30% CP supplement from 30 to 180 days of pregnancy; LATE = fed 30% CP supplement from from 181 to 281 days of pregnancy.

[D] CON = fed 100% of NRC requirements; ON = fed 190% of NRC requirements.

[E] CON = unsupplemented; SUP = fed on pasture plus a mineral-protein supplement (36% CP) from 124 days of pregnancy to parturition.

[F] CON = unsupplemented; SUP = fed on pasture plus a protein supplement (40% CP) from 100 to 200 days of pregnancy.

* P<0.10; ** P<0.05.

from supplemented dams. These findings indicate that offspring from non-supplemented cows showed early adipogenic differentiation, which may impair the proliferation of intramuscular adipocytes. In summary, maternal restriction during critical periods of fetal skeletal muscle and adipose tissue development may compromise the performance and meat quality of the offspring; however, the use of maternal nutritional strategies shows better performance and carcass characteristics on offspring.

5. Summary and future perspectives

Maternal nutrition affects the skeletal muscle development of the fetus, exerting long-term effects on offspring performance and growth. Maternal undernutrition during fetal development reduces the number of muscle fibers, alters muscle fiber composition, and impacts fetal adipogenesis. However, adequate supplementation with nutrients improves skeletal muscle development and adipogenesis, increasing marbling in offspring. Thus, understanding the effects of maternal supplementation during different gestational periods on the performance and final carcass composition of the progeny may help improve meat production and carcass and meat quality traits.

Conflict of interest

The authors declare no conflict of interest.

Author contributions

Conceptualization: M.M. Santos, T.C. Costa, G.D. Ramírez-Zamudio, K.B. Nascimento, M.P. Gionbelli and M.S. Duarte. Funding acquisition: M.P. Gionbelli and M.S. Duarte. Investigation: M.M. Santos, M.P. Gionbelli and M.S. Duarte. Methodology: M.M. Santos. Project administration: M.P. Gionbelli and M.S. Duarte. Resources: M.P. Gionbelli and M.S. Duarte. Supervision: M.P. Gionbelli and M.S. Duarte. Writing – original draft: M.M. Santos, T.C. Costa, G.D. Ramírez-Zamudio, K.B. Nascimento, M.P. Gionbelli and M.S. Duarte. Writing – review & editing: M.M. Santos, T.C. Costa, G.D. Ramírez-Zamudio, K.B. Nascimento, M.P. Gionbelli and M.S. Duarte.

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