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Long-term effects of early maternal undernutrition on the growth, physiological profiles, carcass and meat quality of male beef offspring

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ABSTRACT

The effects of maternal undernutrition in early gestation on growth, metabolic and endocrine profiles, carcass and meat quality of male offspring in cattle were assessed. Twenty-one Parda de Montaña and 14 Pirenaica cows received a CONTROL (100% nutrition requirements) or a SUBNUT (65%) diet from day 0 to 82 of gestation and thereafter were fed to requirements until calf weaning at 4 months of age. The performance and physiological profiles of male offspring during an 8-month fattening period were analyzed. Bulls were slaughtered at 12 months of age, and their carcasses and meat color, tenderness and intramuscular fatty acid profile were evaluated. Maternal undernutrition increased plasma NEFAs and impaired the growth of Pirenaica bulls, resulting in lower weights at slaughter and fatter carcasses with impaired meat tenderness. Irrespective of the breed, maternal undernutrition affected meat color and increased the meat content of some healthy fatty acids. In summary, early maternal undernutrition affected the fetal programming of beef male offspring with persistent consequences at slaughter.

KEYWORDS: prenatal undernutrition, fetal programming, testosterone, NEFA, tenderness, fatty acid profile.

1. Introduction

Poor nutrition is a common scenario in beef cattle production systems. Dams are usually managed under extensive conditions in which feed availability depends exclusively on pastures and limited forage resources. Undernutrition during cow

pregnancy will have important consequences not only for the cow but also for the progeny (Fleming, Velazquez, Eckert, Lucas, & Watkins, 2012). Although the nutrient requirements for the conceptus are negligible in the earliest stages of gestation, maternal dietary intake could influence critical processes for embryo/fetus development (Velazquez, 2015). To deal with sparse nutrient availability, the embryo will have to adapt its physiology to a poor intrauterine environment by acquiring a "thrifty phenotype" (Hales & Barker, 2001). Through epigenetic mechanisms, some endocrine and metabolic functions may be modified to ensure survival (Chavatte-Palmer, Velazquez, Jammes, & Duranthon, 2018). Therefore, the maternal undernourished status will affect fetal programming, leading to irreversible changes with potential metabolic diseases in postnatal life (Ford & Long, 2011).

In a sparse-nutrient environment, the fetus attempts to create a more efficient body composition, potentially resulting in reduced muscle mass and greater fat deposition to increase energy storage (Mohrhauser et al., 2015). During fetal development, primary myogenesis occurs during the 2nd to 3rd month of gestation, and adipogenesis takes place from the 5th month (Du et al., 2010). Muscle fiber number is determined during the prenatal stage, with no increase after birth. This means that fetal tissue development will have irreversible consequences on postnatal growth, body tissue composition and meat quality traits (Du et al., 2013). There is increasing evidence that inadequate dam nutrition during mid- to late gestation will impact offspring meat yield (Greenwood, Cafe, Hearnshaw, & Hennessy, 2005), with long-term consequences on carcass weight (Greenwood & Cafe, 2007), carcass composition (Maresca et al., 2019), muscle fiber size and number of intramuscular adipocytes (Du et al., 2010) and meat quality (Webb et al., 2019). However, few studies have focused on dam nutritional status during the first third of pregnancy.

In a previous phase of this study, we evaluated the effects of maternal nutrient restriction in early gestation on the performance of lactating calves (Noya, Casasús, Ferrer, & Sanz, 2019b) and replacement heifers (Noya, Casasús, Ferrer, & Sanz, 2019a). These effects were compared in two beef breeds, Parda de Montaña (PA), a dual-purpose breed, and Pirenaica (PI), a fast-growth breed (Álvarez-Rodríguez, Blanco, Ripoll, Sanz, & Casasús, 2009). Here, we hypothesize that bull growth and carcass and meat characteristics could be detrimentally influenced by a negative energy status of

the dam in early pregnancy. Furthermore, these long-term effects could vary depending on the genetic background. The aim of this study was to analyze the effects of maternal undernutrition during the first third of gestation on growth, body size, metabolic (glucose, nonesterified fatty acid (NEFA), urea, creatinine) and endocrine (insulin-like growth factor 1 (IGF-1) and testosterone) profiles during the fattening period and on carcass and meat quality traits in yearling male offspring of the PA and PI breeds.

2. Materials and Methods

All procedures were approved by the Animal Ethics Committee of the Centro de Investigación y Tecnología Agroalimentaria de Aragón (CITA), Spain. The care and use of animals were performed in accordance with the guidelines of the European Union (Directive 2010/63/EU) regarding the protection of animals used for experimental and other scientific purposes.

2.1. Animal management

2.1.1. Cow management during maternal nutritional treatment

Cow gestation and the lactation phase of the suckling bulls were conducted at CITA-La Garcipollera Research Station (central Pyrenees, Huesca, Spain), as described in Noya, Casasús, Rodríguez-Sánchez, Ferrer, and Sanz (2020). For this study, 21 PA and 14 PI multiparous cows were fixed time artificially inseminated using a synchronization GnRH-based protocol plus a progesterone-releasing intravaginal device. Cows were randomly inseminated with semen of one of three registered sires per breed, which were equally distributed across the subsequent maternal nutritional treatments. After artificial insemination (AI), cows were blocked into two groups according to the nutritional treatment they would receive during the first third of pregnancy (day 0 to 82 of gestation). Both groups were fed with a total mixed ration composed of alfalfa hay (25.0%), cereal straw (25.0%), crushed barley (25.0%), dehydrated alfalfa (10.0%), rapeseed meal (6.5%), citrus pulp (4.5%), soybean meal (2.5%), and vitamin-mineral complex (1.5%, Table 1). The control group (CONTROL, n = 13) was fed an amount that supplied 100% of the estimated energy requirements for cow maintenance, lactation and gestation, and the nutrient-restricted group (SUBNUT, n = 22) only received 65% of

these requirements. At AI, cow groups were balanced for live weight (LW) and body condition score (BCS). After the first third of gestation, CONTROL cows maintained their LW and BCS (563 ± 13.3 kg and 2.9 ± 0.07 BCS (on a 5-point scale) at IA *vs.* 567 ± 13.0 kg and 2.9 ± 0.07 BCS at the end of nutritional treatment, P > 0.5), whereas SUBNUT cows reduced their LW and BCS (579 ± 10.9 kg and 2.9 ± 0.05 BCS at IA *vs.* 549 ± 10.7 kg and 2.7 ± 0.06 BCS at the end of nutritional treatment, P <0.001), as reported in Noya et al. (2020). All dams were fed 100% of their requirements during the remainder of gestation and the following lactation period, using the total mixed ration described above. After parturition, calves were fed exclusively on maternal milk in a restricted twice-daily nursing system. During the study, the feed was provided at 08:00, and cows were tied up for a maximum of 2 h until they finished the amount assigned to each one. Calves were weaned at 4 months of age.

2.1.2. Management of the male offspring during the fattening period

After weaning, calves (hereafter, bulls) were transported and loosely housed at the fattening facilities of CITA-Montañana Research Station (Zaragoza, Spain). They were allocated in different pens according to their prenatal nutrition (CONTROL *vs.* SUBNUT). They had a 7-day transition period during which they were fed increasing amounts of barley straw and a commercial concentrate for growing cattle composed of corn (47%), corn gluten feed (15%), barley (15%), soya flour (6%), sunflower pulp (6%), carob flour (4%), palm oil (4%) and vitamin-mineral complex (3.2%, Table 1). Once this transition period was finished (day 0), all animals were fed *ad libitum* the same commercial concentrate plus barley straw during the whole fattening period, which lasted 231 days until the day prior to slaughter (at 12 months of age). Concentrate intake was recorded daily (offer minus refusals) per group (CONTROL *vs.* SUBNUT), and values were expressed as the mean values to calculate the feed conversion ratio.

2.2. Performance of the male offspring during the fattening period

2.2.1. Bull growth and development

Bulls were weighed fortnightly to calculate their average daily gain (ADG) by linear regression. Their body development was studied by recording their size measurements at the beginning and at the end of the fattening period (4 and 12 months of age,

respectively). The variables assessed were height at withers (distance from the floor to the highest point of the withers), height at rump (distance from the floor to the highest point of the internal tuberosity of ilion), rump width (maximum distance between iliac tuberosities), rump length (distance from the ischial tuberosity to the external iliac tuberosity), body length (distance from the cranial side of the shoulder blades to the caudal side of the ischial tuberosity) and chest girth (circumference immediately behind the shoulder blades in a plane perpendicular to the body axis). Testicle growth was determined by measuring scrotal circumference at 9 and 12 months of age using a measuring tape.

2.2.2. Metabolic and endocrine profiles

To assess the metabolic and endocrine status of bulls, blood samples were collected every two months by coccygeal venipuncture into EDTA tubes (BD Vacutainer Becton-Dickenson and Company, Plymouth, UK) to determine the concentrations of glucose and NEFA and into heparinized tubes to determine the concentrations of urea, creatinine, IGF-1 and testosterone. Furthermore, in the case of IGF-1, blood samples were previously taken every month from bull mothers during the first third of gestation (when maternal nutritional treatment was applied, as described in Noya et al. (2020)). Samples were centrifuged at 1500 × g for 20 min at 4 °C immediately after collection, and the plasma was harvested and frozen at −20 °C until analysis.

2.3. Slaughter and carcass characteristics

Bulls were slaughtered at 12 months of age in a commercial European Union licensed slaughterhouse (Fribin, Huesca, Spain). The animals were transported on the day of slaughter without a fasting period. They were stunned by a captive bolt pistol and slaughtered by exsanguination through the jugular vein. Carcass weight was recorded after slaughter to calculate the dressing percentage (cold carcass weight divided by the LW at slaughter and expressed as a percentage). Carcasses were classified using the European Union grading system (E.U., 2006). The registered values of carcass conformation were transformed to an 18-point scale (1 = poor and 18 = excellent), and the fatness degree values were transformed to a 15-point scale (1 = very low and 15 =

very high). Carcasses were chilled for 24 h at 4 °C. The *M. longissimus thoracis* (LT) from the 5th to the 12th thoracic vertebrae of the left half of the carcass was collected.

2.4. Meat quality traits

2.4.1. Size measurements, pH and color of *M. longissimus thoracis*

Digital images of LT at the level of the 5th thoracic vertebra were acquired 24 h *postmortem* with an Olympus Pen E-PL1 camera (Olympus Imaging Corp., Shinjuku-ku, Tokyo). *M. longissimus thoracis* and subcutaneous fat measurements were conducted using ImageJ v1.48 (National Institutes of Health, EEUU). At the same time, LT pH was measured with a Crison pH meter (Crison Instruments, S.A., Spain), and meat color was determined using a Minolta CM-2006 d spectrophotometer (Konica Minolta Holdings Inc., Tokyo, Japan) in the CIELAB color space. The measuring area had a diameter of 8 mm that was covered with a CM-A149 dust cover with a specular component at 0% UV, standard illuminant D65 and an observer angle of 10°. White and zero calibrations were made before the readings. The lightness (L*), redness (a*) and yellowness (b*) indexes were recorded, and the hue angle ($h_{ab} = \tan^{-1}\left(\frac{b*}{a*}\right) \cdot \frac{180^{\circ}}{\pi}$) and chroma ($C^*_{ab} = \sqrt{(a*)^2 + (b*)^2}$) were calculated.

2.4.2. Chemical composition of *M. longissimus thoracis*

Samples of the LT from between the 5th and 6th vertebrae were sliced into steaks, vacuum-packed and frozen at −20 °C until freeze-drying (VirTis Wizard 2.0 lyophilizer, SP Scientific, Gardiner, NY, USA). The steaks were weighed before and after freeze-drying to calculate the moisture content. After that, the steaks were ground into particles with a diameter ≤ 0.5 mm. The crude protein was measured using a protein analyzer (Model NA2100, CE Instruments, Thermoquest SA, Madrid, Spain). The fatty acid methyl esters (FAMEs) were prepared following the method described by Lee, Tweed, Kim, and Scollan (2012), and their determination was carried out by performing gas chromatography (Bruker 436 Scion gas, Massachusetts, USA) equipped with a cyanopropyl capillary column (BR-2560, 100 m x 0.25 mm ID x 0.20 µm thickness, Bruker, Massachusetts, USA), a flame ionization detector and Compass CDS software. Fatty acid identification was performed using the GLC-532, GLC-401, GLC-

643, GLC-642, GLC-463, C18:1 t11, C19:0, and C23:0 standard references (Nu-Chek-Prep Inc., Elysian, Minnesota, USA) and the relative retention times observed in the bibliography (Alves & Bessa, 2009; Bravo-Lamas, Barron, Kramer, Etaio, & Aldai, 2016; Lee et al., 2012; Yoshinaga et al., 2013). Fatty acid quantification was performed as described in the UNE-EN 12966-4 Official Method (2015) and expressed according to its concentration in fresh meat and/or as a percentage of the total amount of the total identified fatty acids. The total contents of saturated fatty acids (SFAs), monounsaturated fatty acids (MUFAs), polyunsaturated fatty acids (PUFAs), conjugated linoleic acids (CLAs), and n-3 and n-6 fatty acids were calculated.

2.4.3. Texture of *M. longissimus thoracis*

The remaining LT from between the 7th and 12th thoracic vertebrae was sliced into 3.5-cm-thick steaks, vacuum-packed and aged in a cooler at 4 °C for 7, 14 and 21 days. After the aging period, steaks were stored at -20 °C until analysis. The day before texture analysis, the steaks were thawed and heated in a water bath (75 °C) to an internal temperature of 70 °C and cooled overnight at room temperature. A minimum of ten probes per steak were cut perpendicularly to the long axis of the core into 10 x 10 × 30 mm cross-sections. The dimensions of the samples were measured with a Mitutoyo digital caliper (Mitutoyo Co., Japan) with a resolution of 0.01 mm. The samples were sheared perpendicular to the long axis of the core using an Instron machine (Model 5543, Instron Ltd., Barcelona, Spain) that implemented a Warner-Bratzler device and had a cross-head speed of 150 mm/min. The maximum stress values (maximum load per unit of cross section, measured in N/cm^2) were recorded.

2.5. Assays

An automatic analyzer (GernonStar, RAL/TRANSASIA, Dabhel, India) was used to measure blood concentrations of glucose (glucose oxidase/peroxidase method, sensitivity: 0.056 mmol/L), urea (kinetic UV test, sensitivity: 0.170 mmol/L) and creatinine (enzymatic method, sensitivity: 0.088 mmol/L). The mean intra-assay and interassay coefficients of variation for these molecules were <5.4% and <5.8%, respectively. Concentrations of NEFAs (enzymatic method, sensitivity: 0.06 mmol/L) were analyzed using a commercial kit (Randox Laboratories Ltd., Crumlin Co., Antrim,

UK). The mean intra-assay and interassay coefficients of variation were 5.1% and 7.4%, respectively. Plasma concentrations of testosterone (enzyme immunoassay method, sensitivity: 15 ng/dL) and IGF-1 (enzyme immunoassay method, sensitivity: 20 ng/mL) were analyzed using a solid-phase competitive chemiluminescent enzyme immunoassay (Immulite®, Siemens Healthcare, Llanberis, Gwynedd, UK). The mean intra-assay and inter-assay coefficients of variation for these molecules were <4.85% and <12.0%, respectively.

2.6. Statistical analyses

All statistics were calculated using SAS statistical package v.9.4 (SAS Institute Inc., Cary, NC, USA). The normal distribution of data was assessed with the Shapiro-Wilk test ($P > 0.05$). Bull ADG, carcass traits, LT measurements, meat color and intramuscular fat chemical composition were analyzed with generalized linear models (GLM procedure) with maternal nutritional treatment (CONTROL *vs.* SUBNUT), breed (PA *vs.* PI) and their interaction as fixed effects. Live weight of bulls, body size measures, scrotal circumference, metabolite and hormone concentrations and meat texture were analyzed using mixed linear models (MIXED procedure) for repeated measures based on Kenward-Roger's adjusted degrees of freedom solution. The fixed effects were maternal nutritional treatment, breed and their interactions as the between-subject effects, the day as the within subject effect, and animal as the random effect (experimental unit). The least squares means were estimated per fixed effect, and pairwise comparisons of the means were obtained by the probability of difference (PDIFF). The relationships among the variables were determined using Pearson's correlation coefficients. A tendency was defined as $P < 0.10$ and a significant difference was defined as $P < 0.05$. The results are presented as least square means ± standard error in the text and as least square means with the residual standard deviation (RSD) in the tables. Since feed intake was registered on a group basis, feed intake and feed conversion ratio were not statistically tested; therefore, only group means are presented.

3. Results

3.1. Performance of the male offspring during the fattening period

3.1.1. Bull growth and development

Bull growth results are presented in Table 2. The interaction between maternal nutrition and breed affected bull LW, both at weaning (P = 0.016) and at slaughter (P = 0.026). SUBNUT-PI bulls weighed 26 kg less than CONTROL-PI bulls at the beginning (4 months of age, P < 0.05) and 59 kg less at the end (12 months of age, P < 0.05) of the fattening period, whereas no differences were found between PA bulls (P > 0.05). Regarding the testicular growth, an interaction between maternal nutrition and breed was observed (P = 0.001). Parda de Montaña bulls had a higher scrotal circumference than PI bulls both at 9 and at 12 months of age (P < 0.05). The ADG of the bulls during the fattening period was positively correlated with their scrotal circumference at 9 months (r = 0.50, P = 0.002) and at 12 months (r = 0.40, P = 0.018) of age.

Body size measures during the fattening period are presented in Table 3. Height at withers (P = 0.034), rump width (P = 0.013) and chest girth (P = 0.007) at slaughter were affected by the interaction between maternal nutrition and breed. According to the weight results, SUBNUT-PI bulls had lower values of height at withers (P < 0.05) and chest girth (P < 0.05) at slaughter than CONTROL-PI bulls.

According to their prenatal nutrition group, the mean concentrate intake throughout the fattening period were 6.86 *vs.* 6.25 kg dry matter (DM)/bull/d, and the mean feed conversion ratio were 4.36 *vs.* 4.52 for CONTROL and SUBNUT bulls, respectively.

3.1.2. Metabolic and endocrine profiles

The concentrations of metabolites and hormones during the fattening period are presented in Figure 1 according to the interaction between maternal nutrition, breed and age. Glucose concentrations were similar among groups, except at 8 months of age, when values of SUBNUT-PA bulls were higher than those of CONTROL-PA bulls (P < 0.05). In general, the NEFA concentrations increased throughout the fattening period in all groups. SUBNUT-PI bulls had higher values than their CONTROL counterparts at 4, 6 and 10 months of age (P < 0.05), whereas no differences were found between NEFA concentrations in PA bulls (P > 0.05). The mean NEFA values of the bulls during the fattening period were negatively correlated with their LW at slaughter (r = −0.42, P = 0.011), ADG during the fattening period (r = −0.34, P = 0.043) and scrotal circumference at 9 months of age (r = −0.43, P = 0.009). Regarding the urea

concentration, SUBNUT-PI bulls had, in general, the lowest values throughout the fattening period, whereas CONTROL-PA bulls had the highest concentration at 12 months of age ($P < 0.05$). CONTROL-PI bulls had higher creatinine values than SUBNUT-PA bulls at 10 months of age ($P < 0.05$), with no differences among groups during the rest of the fattening period ($P > 0.05$). Creatinine concentrations were positively correlated with urea concentrations at 4 months ($r = 0.36$, $P = 0.035$), 6 months ($r = 0.61$, $P = 0.001$) and 12 months ($r = 0.37$, $P = 0.027$) of age. The plasma concentration of IGF-1 increased throughout the fattening period in all groups. SUBNUT-PI bulls had lower IGF-1 concentrations during the first half of the fattening period, with significant differences from CONTROL-PI and SUBNUT-PA bulls at 6 months of age ($P < 0.05$). The IGF-1 concentrations were negatively correlated with NEFA concentrations at 6 months ($r = -0.37$, $P = 0.027$) and 12 months ($r = -0.40$, $P = 0.019$) of age. The IGF-1 concentrations of bulls during the fattening period were not correlated with the IGF-1 concentrations of their mothers during the first third of pregnancy (when maternal nutritional treatment was applied, $P > 0.05$). In general, testosterone concentrations increased over time in all groups. However, PI bulls had a temporary decrease at 10 months of age, which resulted in PA testosterone concentrations being higher than those of PI bulls at that time ($P < 0.05$). Testosterone concentrations were positively correlated with IGF-1 concentrations at 6 months of age ($r = 0.41$, $P = 0.015$). Furthermore, the mean testosterone values of the bulls during the fattening period were positively correlated with their LW at slaughter ($r = 0.49$, $P = 0.003$), ADG during the fattening period ($r = 0.36$, $P = 0.034$) and scrotal circumference at 12 months of age ($r = 0.69$, $P = 0.001$).

3.2. Carcass characteristics

Carcass characteristics are presented in Table 4 according to the interaction between maternal nutrition and breed. Regarding the carcass weight, although the interaction of the fixed effects was not significant ($P = 0.113$), carcasses of SUBNUT-PI bulls weighed 38 kg less than those from CONTROL-PI bulls whereas the difference between CONTROL-PA and SUBNUT-PA carcasses was 1 kg. The dressing percentage and the carcass conformation were similar in all groups ($P > 0.05$). The interaction of maternal

nutrition and breed affected the carcass fatness degree (P = 0.048). Carcass fat cover was higher in SUBNUT-PI bulls than in CONTROL-PI bulls (P < 0.05).

3.3. Meat quality traits

3.3.1. Size measurements, pH and color of *M. longissimus thoracis*

The size measurements and pH of LT are presented in Table 5 according to maternal nutrition and breed effects. No differences were found in LT diameters and area at the level of the 5th thoracic vertebra between CONTROL and SUBNUT bulls or between breeds (P > 0.05). PA bulls had higher subcutaneous fat thickness and pH than PI bulls (P = 0.001 and P = 0.026, respectively).

The meat color results are shown in Table 6. The interaction of maternal nutrition and breed affected the L* (P = 0.009), b* (P = 0.020), h* (P = 0.072) and C* (P = 0.067) values. Specifically, CONTROL-PA bulls had lower L* values than SUBNUT-PA bulls (P < 0.05), whereas no differences were found between PI bulls (P > 0.05). All groups had similar values of a* (P > 0.05), and SUBNUT-PI bulls had the highest b* (P < 0.05), h_{ab} (P < 0.1) and C^*_{ab} (P < 0.1) values.

3.3.2. Chemical composition of *M. longissimus thoracis*

The meat chemical composition is presented in Table 7 according to maternal nutrition and breed effects. The protein content was similar in all groups regardless of maternal nutrition or breed (P > 0.05). Maternal nutrition had no effects on the total contents of FAMEs or on the contents of CLAs, n-3 and n-6 fatty acids, SFAs, MUFAs and PUFAs (P > 0.05). Regarding the breed, meat from PA bulls had a higher content of total FAMEs (P = 0.040), CLAs (P = 0.045), n-6 fatty acids (P = 0.046), SFAs (P = 0.062), MUFAs (P = 0.030) and PUFAs (P = 0.040) than meat from PI bulls. However, there were no differences between breeds for the ratios of n-6:n-3 and PUFAs:SFAs (P > 0.05).

The FAME profiles are presented in Table 8 according to maternal nutrition and breed effects. Based on their percentage, the dominant fatty acids of the intramuscular fat were oleic (C18:1 cis-9), palmitic (C16:0), stearic (C18:0) and linoleic (C18:2 n-6), which represented approximately 28%, 25%, 18% and 9% of the total FAME content, respectively. Both maternal nutrition and breed influenced meat fatty acid profiles. In summary, the percentage of myristoleic acid (C14:1 cis-9) tended to be lower in meat

from CONTROL bulls (P = 0.051), and the percentages of palmitoleic acid (C16:1 cis-9) and cis-9, trans-11 CLA isomer (C18:2 cis-9, trans-11, the most abundant CLA isomer) were higher in meat from SUBNUT bulls (P = 0.009 and P = 0.046, respectively). This meant that meat from SUBNUT bulls tended to have a higher percentage of CLAs than that from CONTROL bulls (P = 0.055). Regarding the breed, meat from PA bulls had a higher percentage of oleic (P = 0.045), stearic (P = 0.042) and MUFAs (P = 0.041), among others, than PI meat.

3.3.3. Texture of *M. longissimus thoracis*

Texture values of LT throughout a 21-day aging period are presented in Figure 2 according to the interaction between maternal nutrition and breed. Meat toughness from CONTROL groups slightly decreased throughout aging, whereas the values from SUBNUT groups remained more stable; however, no significant differences were found when comparing samples within each group at 7, 14 or 21 days of aging (P > 0.05). The values of meat texture were similar among groups at day 7 (P > 0.05). CONTROL-PI bulls had lower values than SUBNUT-PA and CONTROL-PA bulls at day 14 (P < 0.05), and at day 21, CONTROL-PI bulls had the lowest values (P < 0.05).

4. Discussion

4.1. Performance of the male offspring during the fattening period

4.1.1. Bull growth and development

Maternal nutrition affected PI bull growth and size measures. SUBNUT-PI bulls were 16.0% and 11.4% lighter than their CONTROL counterparts at weaning and at slaughter, respectively. Some studies that described a growth delay of the calf due to poor maternal nutrition reported compensatory growth in the following stages of development if high-quality diets and feed availability were ensured after birth (Freetly, Ferrell, & Jenkins, 2000; Greenwood & Cafe, 2007; Noya et al., 2019a). Indeed, Long, Prado-Cooper, Krehbiel, DeSilva, and Wettemann (2010a) showed that steers exposed to low prenatal nutrition tended to be heavier at slaughter than steers exposed to moderate nutrition during early gestation. In contrast, Greenwood and Cafe (2007) reported that the capacity of maternally undernourished cattle to exhibit compensatory growth during their postnatal life was limited, which would agree with

our observations. Conflicting results may be explained because the effects of maternal nutrition could vary as a function of the intensity and the time when the maternal nutritional treatment was applied or the breed. In our experiment, although all bulls were fed *ad libitum*, SUBNUT-PI bulls were not able to compensate for the weight differences at slaughter, which has a significant economic impact. The lower body development of SUBNUT-PI bulls was according to their lower mean scrotal circumference, although the differences from CONTROL-PI bulls were not statistically significant. Some studies associated prenatal nutrition with alterations in the volume (Sullivan, Micke, Greer, & Perry, 2010), weight (Bielli et al., 2002) or seminiferous tubule diameter (Kotsampasi, Balaskas, Papadomichelakis, & Chadio, 2009) of the testicles during the postnatal life of the bull. Our results indicated that the breed had great relevance in determining scrotal circumference. Parda de Montaña bulls had a greater scrotal circumference than PI bulls, suggesting that PA bulls reached puberty earlier, in line with other studies describing that PA females were more precocious than PI females (Revilla, Olleta, Sanjuan, & Blasco, 1992; Rodríguez-Sánchez et al., 2018). A fast testicular growth rate is associated with early sexual maturity (Menegassi et al., 2019). Lunstra and Echternkamp (1982) reported that bulls from different European beef breeds reached puberty at scrotal circumference values of 27.9 cm, regardless of the LW or age. According to this criterion, in our study, PA bulls would have reached puberty before 9 months of age, whereas PI bulls would have done so between 9 and 12 months of age.

4.1.2. Metabolic and endocrine profiles

Neither maternal nutrition nor breed showed relevant effects on glucose profiles, which would indicate that glucose metabolism development during the fetal life of the bulls was not affected. This agrees with another study that reported no effect of maternal nutrient restriction in early pregnancy on the basal glucose concentration of calves (Long, Prado-Cooper, Krehbiel, & Wettemann, 2010b).

The higher NEFA profiles of SUBNUT-PI bulls throughout the fattening period indicated increased fatty acid mobilization from lipid stores, which allows glucose concentrations to remain stable (McMullen, Osgerby, Milne, Wallace, & Wathes, 2005). The higher NEFA concentrations, which were correlated with a lower LW at slaughter, ADG and

scrotal circumference, indicate that the energy metabolism status of SUBNUT-PI bulls could be compromised.

Urea concentration is related to dietary protein intake and is a good indicator of anabolic metabolism (Walsh, O'Kiely, Moloney, & Boland, 2008). In our experiment, the lower mean values of the urea concentration of SUBNUT-PI bulls were associated with their lower LW.

In the current study, the overall creatinine profiles of bulls were similar throughout the fattening period. Plasma creatinine concentration is related to muscle mass and is therefore proportional to animal LW (Chizzotti, Valadares Filho, Valadares, Chizzotti, & Tedeschi, 2008). It is likely that the LW differences found between SUBNUT-PI bulls and the other groups were not relevant enough to be reflected in the creatinine profiles. In our study, urea and creatinine concentrations were correlated at different times throughout the fattening period, indicating that both metabolites are related to muscle mass and feed intake.

Insulin growth factor-1 has a key role in the control of animal growth and is related to both skeletal and muscle development (Yelich et al., 1995). A higher IGF-1 concentration is associated with a faster growth rate and a higher body weight (Kerr, Manns, Laarveld, & Fehr, 1991). In the current study, the correlation between lower IGF-1 and higher NEFA concentrations of SUBNUT-PI bulls agrees with the hypothesis that although bulls were fed *ad libitum*, their energy metabolic status and the energy metabolism pathways could have been compromised, which impaired their growth. However, in the second half of the fattening period, the IGF-1 profiles of SUBNUT-PI bulls were similar to those of the other groups, which could suggest that they started to compensate for their growth rates. In another phase of this study, maternal nutrient-restricted heifers with lower LW and IGF-1 concentrations during the lactation period compensated for their LW at 12 months of age (Noya et al., 2019a). In line with our results, Maresca et al. (2018) described that calves born from undernourished dams, with a lower IGF-1 concentration at birth, compensated for the difference during their postnatal growth.

Maternal nutrient restriction had no effect on testosterone production, suggesting that the development of fetal Leydig cells and the endocrine mechanisms required for testosterone synthesis were not affected (Shima et al., 2013). However, the breed

influenced testosterone profiles. Parda de Montaña bulls steadily increased their concentrations up to 8 months of age, whereas those from PI bulls had a transitory decline in the fattening period. The higher scrotal circumference and the stable testosterone concentrations of PA bulls suggest that they reached puberty earlier, as previously observed when comparing these breeds (Revilla, Olleta, Sanjuan, & Blasco, 1992; Rodríguez-Sánchez et al., 2018). The fluctuation of testosterone secretion observed in PI bulls is a common pattern observed in prepubertal bulls, described in several studies (Amann, 1983; Bagu, Cook, Gratton, & Rawlings, 2006; McCarthy, Convey, & Hafs, 1979; Rawlings, Fletcher, Henricks, & Hill, 1978; Thibier, 1975), until the testosterone concentration is settled at later stages (Thibier, 1975).

4.2. Carcass characteristics

All carcasses had similar conformations and dressing percentages, which meant that the percentages of LW attributable to visceral organs, skin, head and feet were similar among the groups. However, mean carcass weight value of SUBNUT-PI bulls, and therefore the retail beef yield value, was 11.8% lower than that from CONTROL-PI bulls, which implies significant economic losses. Few studies have evaluated the long-term impact of poor maternal nutrition on growth and meat performance in bulls, with inconclusive results. Greenwood et al. (2005) reported reduced carcass weights at 30 months of age in steers from undernourished cows during the last two thirds of gestation. Long et al. (2012a) described no effect of early prenatal nutrition on the hot carcass weight of steers slaughtered at 22 months of age. In the current study, SUBNUT-PI bulls had the highest level of body fat, which agreed with their higher NEFA profiles. This meant that, in line with a thrifty phenotype hypothesis, these bulls used part of their dietary energy to increase their adiposity to the detriment of total muscle mass (Mohrhauser et al., 2015). Future histological studies will be needed to assess whether maternal undernutrition increases the number (hyperplasia) or diameter (hypertrophy) of adipocytes in SUBNUT-PI bulls. Greenwood et al. (2006) reported that cows fed on low-quality pastures from day 80 of pregnancy to parturition gave birth to calves with increased peripheral fat measured at rump (P8) at the same carcass weight but showed no other effect on indexes of carcass fatness. In another study, maternal nutrient-restricted calves during the last trimester of pregnancy showed no effects on

the fatness and distribution of carcass tissues (Tudor & O'Rourke, 1980). However, in a sheep model, 50% nutrient-restricted ewes from early to mid-gestation resulted in lambs with increased backfat, omental fat or perirenal adipose tissue deposits (Ford et al., 2007). The intensive postnatal environment where sheep were reared, which is less common in cattle (Greenwood, Cafe, Hearnshaw, Hennessy, & Morris, 2009), could explain the high capacity of maternal nutrient-restricted lambs to increase fat deposits. In our study, the bulls were fed *ad libitum* a commercial concentrate, which allowed SUBNUT-PI bulls to increase the fatness degree.

4.3. Meat quality traits

4.3.1. Size measurements, pH and color of *M. longissimus thoracis*

Measures of LT were similar between CONTROL and SUBNUT bulls, which agreed with their similar carcass muscle conformation. Although SUBNUT-PI bulls had the highest carcass fat cover, no differences were found in the subcutaneous fat thickness of LT between CONTROL and SUBNUT bulls. This meant that SUBNUT-PI bulls had increased the external fat deposits of the whole carcass, but not specifically those from the loin area. Similar to our results, neither LT area nor fat thickness at the 12th rib was affected in calves from dams fed 55% of their nutritional requirements during the first third of gestation (Long et al., 2019a), in calves from dams on a low dietary protein diet during the last three months of gestation (Maresca et al., 2019), or in calves from protein-supplemented dams during late gestation (Larson, Martin, Adams, & Funston, 2009; Stalker, Adams, Klopfenstein, Feuz, & Funston, 2006). In contrast, Underwood et al. (2010) reported that steers from cows with improved nutrition during mid- to late gestation had a greater 12th rib fat thickness but a similar LT area. Regarding the breed, the higher subcutaneous fat thickness values observed in PA were in accordance with previous studies (Ripoll et al., 2014), which suggests that the fat distribution of growing bulls would differ across both breeds. This could be due to their different purposes; PA is a dual-purpose breed (Álvarez-Rodríguez, Blanco, Ripoll, Sanz, & Casasús, 2009), while PI is a fast-growing and particularly lean breed (Blanco et al., 2020).

In the current study, meat from SUBNUT-PA bulls was brighter (higher L*) than that of their CONTROL counterparts, whereas no differences were found in PI bulls. In a study carried out with pigs, Kim et al. (2013) found that animals with a higher proportion of

large muscular fibers had brighter meat than animals with small fibers. In our study, further histological studies will be needed to assess whether maternal undernutrition affects muscle fiber size and its relationship with meat brightness in both breeds. Meat color, determined by the concentration and physicochemical state of myoglobin (Gagaoua, Picard, & Monteils, 2018), is the main quality trait influencing consumer decisions (Savoia et al., 2019). Bright red meat is associated with a higher consumer preference (Hughes, Clarke, Purslow, & Warner, 2017), which means that meat from SUBNUT-PA bulls could be better accepted by consumers. In our study, the a* index was similar in all groups, but SUBNUT-PI bulls had the highest b* index, resulting in a trend towards higher C^*_{ab} and h_{ab} indexes. Higher C^*_{ab} values are associated with higher color stability (Ijaz et al., 2020). This implies that meat from SUBNUT-PI bulls could preserve its color proprieties for a longer time, delaying the discoloration process derived from myoglobin oxidation and therefore increasing the meat lifetime at the point of sale. Some authors described an increase in meat lightness due to maternal nutrient restriction in female lambs but not in male lambs (Ithurralde et al., 2019) or in goats (Zhou et al., 2019). However, other studies showed no effects on the L*, a* and b* indexes in steaks from maternally nutrient-restricted calves during mid-gestation (Mohrhauser et al., 2015) or in calves from cows fed a low-protein diet during periconception and the first trimester of gestation (Alvarenga et al., 2016).

4.3.2. Chemical composition of *M. longissimus thoracis*

Maternal nutrition did not influence the protein or the total FAME contents of fresh meat. Although SUBNUT-PI bulls had the highest carcass fatness degree, the total amount of intramuscular fat was similar for all groups. According to our results, Long et al. (2010a) found no effects of maternal subnutrition in early gestation on meat protein or intramuscular fat content. In contrast, Underwood et al. (2010) reported that intramuscular fat content tended to be higher in steers from dams fed in improved pastures during mid- to late pregnancy. Late gestation is a critical period for fetal muscle, adipose and connective tissue development (Zago, Canozzi, & Barcellos, 2020), which means that any insult in the dam diet in this phase could have direct consequences on fetal tissue composition. However, Ramírez et al. (2020) and Maresca et al. (2019) found no effects of maternal nutrient restriction during late pregnancy on

meat protein or intramuscular fat content of the offspring. In the current study, although all groups had similar total intramuscular FAME contents, maternal nutrient restriction influenced the FAME profile. Meat from SUBNUT bulls had a higher percentage of palmitoleic acid and cis-9, trans-11 CLA isomer, resulting in a trend towards higher CLA contents in SUBNUT than in CONTROL bulls. These n-7 fatty acids have been associated with several health benefits for consumers (Araujo Nunes & Rafacho, 2017; Vahmani et al., 2020). The meat fatty acid profile is influenced by the type of diet (Renna et al., 2019). In our experiment, all bulls were *ad libitum* fed the same commercial concentrate during the fattening period. However, during the previous lactation period, their diet consisted exclusively of maternal milk. As reported in Noya et al. (2019b), the fat concentration of milk from dams that were undernourished during early pregnancy was higher than that of nonrestricted dams, which could have influenced the FAME profiles of suckling bulls. Furthermore, in early gestation (when nutritional treatment was applied), undernourished dams had higher plasma NEFA concentrations than nonrestricted dams (Noya et al., 2020), which might increase the fatty acid supply to the developing fetus and therefore modify adipogenesis in fetal tissues (Mulliniks et al., 2016). To the best of our knowledge, this is the first study to assess the long-term effects of maternal undernutrition in early pregnancy on intramuscular FAME profiles in cattle. Other studies reported some alterations in the intramuscular FAME profiles in the offspring of protein-restricted dams in mid- and late gestation (Webb et al., 2019) or in bulls from dams that had been protein supplemented during late gestation and lactation (Gunn, Bridges, Lemenager, & Schoonmaker, 2017). Alvarenga et al. (2016) found negligible effects on fatty acid composition in subcutaneous fat depots of bulls born to protein-restricted dams during early pregnancy, and Zhou et al. (2019) reported no effect on intramuscular FAME profiles in maternally nutrient-restricted goats during mid-gestation. Regarding the breed, meat from PA bulls had a greater total intramuscular fat concentration than that from PI bulls, which included a higher concentration of CLAs, SFAs, MUFAs and PUFAs, among others. Some breed differences were found in intramuscular FAME profiles, in accordance with previous studies investigating these two breeds (Ripoll et al., 2014), which highlights the influence of genetic background on fatty acid profiles and fat corporal distribution.

4.3.3. Texture of *M. longissimus thoracis*

In our study, tenderization occurred faster in meat from CONTROL bulls, especially in the PI breed. CONTROL-PI meat was classified as having intermediate tenderness at 0 and 14 days and as tender at 21 days of aging. However, meat from the remaining groups was classified as tough throughout the entire aging period (Destefanis, Brugiapaglia, Barge, & Dal Molin, 2008). Tenderness, the most important factor of consumer satisfaction for beef palatability (Miller, Carr, Ramsey, Crockett, & Hoover, 2001), is influenced by collagen characteristics and proteolytic enzyme activity (Gonzalez-Bulnes et al., 2016). During aging, Warner-Bratzler shear force values decrease due to the activities of calpain-2 and calpastatin. In the current study, maternal nutrient restriction maintained the Warner Bratzler shear force values throughout aging in PI bulls. There is limited research to hypothesize about the mechanisms by which an adverse uterine environment can affect meat texture in progeny. Karunaratne, Ashton, and Stickland (2005) showed that lower piglet birth weight, which is influenced by *in utero* nutrition, is related to an increased proportion of intramuscular collagen I (the most abundant subtype of collagen and the most important for meat quality) and therefore increased toughness. By contrast, Du, Zhu, Means, Hess, and Ford (2004) reported a higher calpastatin content in bovine fetal muscles due to a low plane of maternal nutrition from early to mid-gestation. In line with our results, some studies described a lower tenderness in *M. longissimus* from maternal protein-restricted calves in mid-gestation (Underwood et al., 2010; Webb et al., 2019) or late gestation (Maresca et al., 2019). Alvarenga et al. (2016) reported a higher Warner-Bratzler shear force in *M. semitendinosus* but not in *M. longissimus* from maternally protein-restricted bulls from periconception to the end of the first trimester of pregnancy. In contrast, Mohrhauser et al. (2015) found no differences in shear force at any aging period when comparing *M. longissimus* steaks of offspring from negative or positive energy status dams during mid-gestation.

5. Conclusions

The adverse intrauterine environment induced by maternal nutrient restriction during early pregnancy modified fetal programming in the developing fetus, with long-term

effects on bull growth and carcass, and meat quality traits. The PI breed was more sensitive to a prenatal negative energy balance, as reflected in their 11% lighter weight at slaughter and their higher degree of carcass fatness. The development of fetal energy metabolic pathways could have been altered, mainly reflected in increased NEFA profiles of PI bulls during the fattening period. Fetal undernutrition affected meat quality traits, modifying some color measures, increasing the percentage of some healthy fatty acids and impairing meat tenderness in maternally restricted PI bulls. In summary, early maternal undernutrition had long-term consequences on the postnatal performance, physiological profiles, carcass and meat quality traits of male beef offspring.

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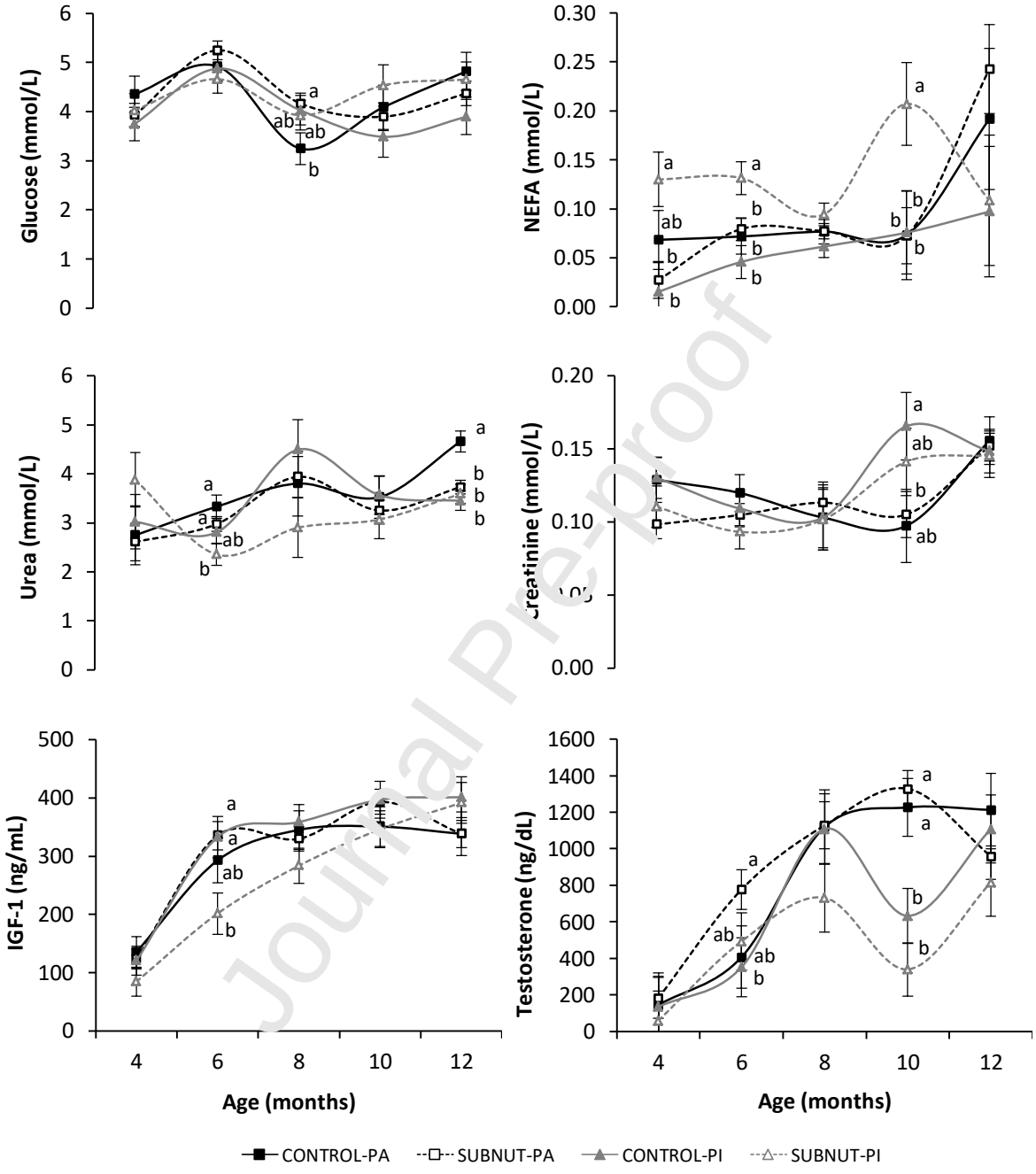
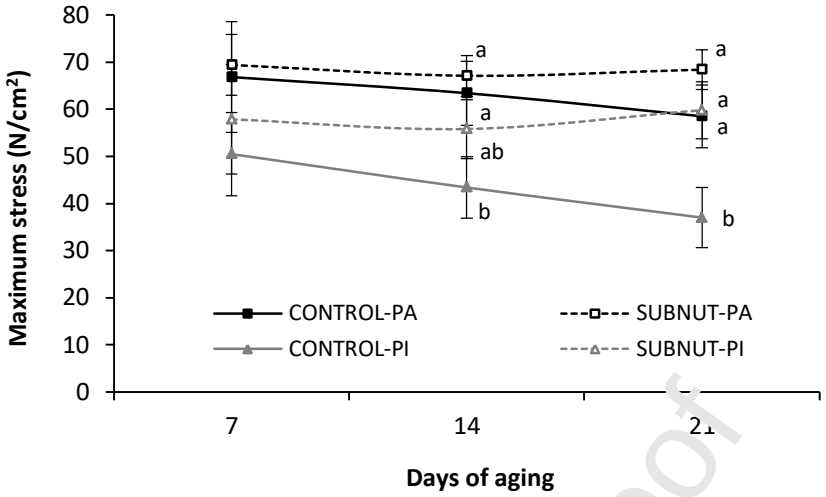
Figure 1. Bull metabolic and endocrine profiles during the fattening period according to the interaction between maternal nutrition and breed.



CONTROL, bulls from cows fed 100% of their requirements in early pregnancy; SUBNUT, bulls from cows fed 65% of their requirements in early pregnancy; PA, Parda de Montaña; PI, Pirenaica. [a,b] Means at a given age differ $P < 0.05$. Glucose P values: M. nutrition, P = 0.410; Breed, P = 0.609; Age, P = 0.001; M. nutrition x Breed x Age, P = 0.005. NEFA P values: M. nutrition, P = 0.031; Breed, P = 0.936; Age, P = 0.040; M. Nutrition x Breed, P = 0.049. Urea P values: M. nutrition, P = 0.143; Breed, P = 0.495; Age, P = 0.001; M. nutrition x Breed x Age, P = 0.090. Creatinine P values: M. nutrition, P = 0.339; Breed, P = 0.479; Age, P = 0.001; Breed x Age, P = 0.098. IGF-1 P values: M. nutrition, P = 0.244; Breed, P = 0.756;

Age, P = 0.001; M. nutrition x Breed x Age, P = 0.065. Testosterone P values: M. nutrition, P = 0.543; Breed, P = 0.024; Age, P = 0.001; M. nutrition x Age, P = 0.082; Breed x Age, P = 0.001.

Figure 2. Texture values of *M. longissimus thoracis* throughout a 21-day aging period at 4 °C according to the interaction between maternal nutrition and breed.



CONTROL, bulls from cows fed 100% of their requirements in early pregnancy; SUBNUT, bulls from cows fed 65% of their requirements in early pregnancy; PA, Parda de Montaña; PI, Pirenaica. [a,b] Means on a given day differ P < 0.05. Maximum stress P values: M. nutrition, P = 0.088; Breed, P = 0.016; Age, P = 0.568.

Table 1. Chemical composition of feedstuffs (on an as-fed basis).

Chemical composition	Total mixed ration†	Barley straw$^{\phi}$	Concentrate$^{\phi}$
DM (g/kg)	908	902	907
CP (g/kg DM)	124	40	152
NDF (g/kg DM)	466	796	262
ADF (g/kg DM)	253	456	62
ADL (g/kg DM)	40	58	8
Ash (g/kg DM)	113	65	60
ME (MJ/kg DM)	11.0	7.5	14.1

† Feed supplied to the bulls' dams during the gestation and lactation periods; ϕ Feed supplied *ad libitum* to the bulls during the fattening period; DM, dry matter; CP, crude protein; NDF, neutral-detergent fiber; ADF, acid-detergent fiber; ADL, acid-detergent lignin; ME, metabolizable energy.

Table 2. Bull growth performance during the fattening period according to the interaction of maternal nutrition and breed.

	Maternal nutrition x Breed					P-value		
	CONTROL PA	**SUBNUT PA**	**CONTROL PI**	**SUBNUT PI**	**RSD**	**Maternal nutrition**	**Breed**	**M. nutrition x Breed**
Fattening period (days)	231	231	230	231	0.5	0.684	0.879	0.267
Age at slaughter (days)	367	366	367	367	4.1	0.869	0.894	0.587
LW at weaning (Kg)	167[a]	168[a]	163[a]	137[b]	15.4	0.100	0.031	0.016
LW at slaughter (Kg)	514[a]	517[a]	516[a]	457[b]	41.0	0.081	0.073	0.026
ADG (kg/d)	1.59	1.56	1.56	1.43	0.144	0.114	0.130	0.364
Scrotal circumference at 9 months (cm)	30.0[a]	29.6[a]	27.3[b]	25.3[b]	2.20	0.151	0.001	0.001
Scrotal circumference at 12 months (cm)	34.3[a]	34.2[a]	31.1[b]	29.5[b]	2.23	0.308	0.001	0.001

CONTROL, bulls from cows fed 100% of their requirements in early pregnancy; SUBNUT, bulls from cows fed 65% of their requirements in early pregnancy; PA, Parda de Montaña; PI, Pirenaica; RSD, residual standard deviation; LW, live weight; ADG, average daily gain. [a,b] Means within a row differ $P < 0.05$.

Table 3. Body size measures of bulls during the fattening period according to the interaction of maternal nutrition and breed.

	Maternal nutrition x Breed					P-value		
	CONTROL PA	**SUBNUT PA**	**CONTROL PI**	**SUBNUT PI**	**RSD**	**Maternal nutrition**	**Breed**	**M. nutrition x Breed**
Height at withers (cm)								
At weaning	95^{c}	94^{c}	93^{cd}	90^{d}	3.5	0.150	0.056	0.089
At slaughter	124^{a}	124^{a}	124^{a}	118^{b}	4.3	0.062	0.055	0.034
Height at rump (cm)								
At weaning	101	101	99	98	4.5	0.524	0.138	0.431
At slaughter	131	130	130	125	4.8	0.112	0.121	0.143
Rump width (cm)								
At weaning	27	27	26	24	2.6	0.308	0.105	0.181
At slaughter	48^{a}	47^{a}	45^{b}	45^{b}	2.4	0.584	0.001	0.013
Rump length (cm)								
At weaning	36^{cd}	35^{cd}	37^{c}	33^{d}	3.2	0.038	0.826	0.089
At slaughter	50	51	51	50	3.2	0.996	0.769	0.824
Body length (cm)								
At weaning	98^{cd}	96^{cd}	101^{c}	93^{d}	4.4	0.015	0.649	0.056
At slaughter	147	144	148	143	7.5	0.168	0.993	0.557
Chest girth (cm)								
At weaning	118	118	120	113	6.3	0.135	0.558	0.207
At slaughter	186^{a}	188^{a}	185^{a}	177^{b}	6.4	0.272	0.015	0.007

CONTROL, bulls from cows fed 100% of their requirements in early pregnancy; SUBNUT, bulls from cows fed 65% of their requirements in early pregnancy; PA, Parda de Montaña; PI, Pirenaica; RSD, residual standard deviation. ^{a,b} Means within a row differ $P < 0.05$, ^{c,d} means within a row differ $P < 0.1$.

Table 4. Carcass characteristics according to the interaction between maternal nutrition and breed.

	Maternal nutrition x Breed					P-value		
	CONTROL PA	**SUBNUT PA**	**CONTROL PI**	**SUBNUT PI**	**RSD**	**Maternal nutrition**	**Breed**	**M. nutrition x Breed**
Carcass weight (kg)	313	312	322	284	31.8	0.106	0.418	0.113
Dressing percentage (%)	61.0	60.5	61.8	62.1	2.64	0.921	0.208	0.714
Conformation (1-18)	11	11	11	12	2.0	0.522	0.705	0.961
Fatness degree (1-15)	6.0^{ab}	5.8^{ab}	4.6^{b}	6.4^{a}	1.39	0.108	0.430	0.048

CONTROL, bulls from cows fed 100% of their requirements in early pregnancy; SUBNUT, bulls from cows fed 65% of their requirements in early pregnancy; PA, Parda de Montaña; PI, Pirenaica; RSD, residual standard deviation. ^{a,b} Means within a row differ $P < 0.05$.

Table 5. *M. longissimus thoracis* traits at the level of the 5th thoracic vertebra according to maternal nutrition and breed effects.

	Maternal nutrition		Breed			P-value		
	CONTROL	**SUBNUT**	**PARDA**	**PIRENAICA**	**RSD**	**Maternal nutrition**	**Breed**	**M. nutrition x Breed**
Horizontal diameter (cm)	10.1	10.2	10.1	10.2	0.99	0.824	0.978	0.500
Vertical diameter (cm)	5.5	5.6	5.6	5.6	0.59	0.537	0.974	0.742
Area (cm^2)	47.9	48.9	48.5	48.4	7.57	0.762	0.966	0.715
Subcutaneous fat thickness (mm)	3.9	3.9	5.1[a]	2.7[b]	1.68	0.984	0.001	0.549
pH	5.7	5.6	5.7[a]	5.6[b]	0.19	0.214	0.026	0.452

CONTROL, bulls from cows fed 100% of their requirements in early pregnancy; SUBNUT, bulls from cows fed 65% of their requirements in early pregnancy; RSD, residual standard deviation. [a,b] Means within a row differ $P < 0.05$.

Table 6. Meat color of *M. longissimus thoracis* according to the interaction of maternal nutrition and breed.

	Maternal nutrition x Breed					P-value		
	CONTROL PA	**SUBNUT PA**	**CONTROL PI**	**SUBNUT PI**	**RSD**	**Maternal nutrition**	**Breed**	**M. nutrition x Breed**
L*	34.6^{b}	37.2^{a}	37.2^{ab}	34.6^{b}	2.66	0.979	0.997	0.009
a*	14.1	14.1	14.1	14.1	2.27	0.993	0.929	0.992
b*	6.3^{b}	5.9^{b}	6.7^{b}	11.6^{a}	3.02	0.044	0.009	0.020
h_{ab}	22.5^{d}	22.6^{d}	25.4^{d}	38.4^{c}	9.63	0.069	0.011	0.072
C^*_{ab}	15.7^{d}	15.3^{d}	15.7^{d}	18.8^{c}	2.58	0.153	0.073	0.067

L*, lightness; a*, redness index; b*, yellowness index; h_{ab}, hue angle; C^*_{ab}, chroma; CONTROL, bulls from cows fed 100% of their requirements in early pregnancy; SUBNUT, bulls from cows fed 65% of their requirements in early pregnancy; PA, Parda de Montaña; PI, Pirenaica; RSD, residual standard deviation. ^{a,b} Means within a row differ P < 0.05, ^{c,d} means within a row differ P < 0.1.

Table 7. Chemical composition of *M. longissimus thoracis* according to maternal nutrition and breed effects.

	Maternal nutrition		Breed			P-value		
	CONTROL	**SUBNUT**	**PARDA**	**PIRENAICA**	**RSD**	**Maternal nutrition**	**Breed**	**M. nutrition x Breed**
Protein (%, FM)	21.9	21.8	21.9	21.8	0.54	0.677	0.602	0.836
FAMEs (g/g meat, FM)	0.017	0.018	0.020[a]	0.015[b]	0.0055	0.658	0.040	0.710
ΣCLAs (mg/g meat, FM)	0.02	0.03	0.03[a]	0.02[b]	0.011	0.199	0.045	0.510
n-3 fatty acids (mg/g meat, FM)	0.11	0.12	0.12	0.11	0.016	0.228	0.126	0.969
n-6 fatty acids (mg/g meat, FM)	2.0	2.0	2.1[a]	1.9[b]	0.20	0.670	0.046	0.873
n-6:n-3 ratio (%)	18.3	17.1	17.7	17.7	2.03	0.100	0.969	0.972
Saturated fatty acids (mg/g meat, FM)	8.9	9.3	10.1[c]	8.0[d]	3.01	0.677	0.062	0.688
Monounsaturated fatty acids (mg/g meat, FM)	5.8	6.3	7.0[a]	5.1[b]	2.40	0.614	0.030	0.722
Polyunsaturated fatty acids (mg/g meat, FM)	2.2	2.2	2.3[a]	2.1[b]	0.21	0.822	0.040	0.894
PUFAs:SFAs ratio (%)	26.5	25.3	24.3	27.4	6.83	0.628	0.211	0.563

FAMEs, fatty acid methyl esters; CLAs, conjugated linoleic acids; PUFAs, polyunsaturated fatty acids; SFAs, saturated fatty acids; FM, fresh matter; CONTROL, bulls from cows fed 100% of their requirements in early pregnancy; SUBNUT, bulls from cows fed 65% of their requirements in early pregnancy; RSD, residual standard deviation. [a,b] Means within a row differ $P < 0.05$, [c,d] means within a row differ $P < 0.1$.

Table 8. Fatty acid methyl ester profiles (expressed as a percentage of identified FAMEs) of the *M. longissimus thoracis* according to maternal nutrition and breed effects.

	Maternal nutrition		Breed			P-value		
FAMEs (%)	**CONTROL**	**SUBNUT**	**PARDA**	**PIRENAICA**	**RSD**	**Maternal nutrition**	**Breed**	**M. nutrition x Breed**
C10:0	0.04	0.03	0.03	0.04	0.008	0.857	0.379	0.749
C11:0	0.11	0.10	0.09[b]	0.12[a]	0.037	0.816	0.014	0.532
C12:0	0.06	0.08	0.05	0.09	0.069	0.372	0.189	0.411
C13:0	0.12	0.11	0.09[d]	0.14[c]	0.067	0.845	0.069	0.548
a-C13:0	0.27[a]	0.21[b]	0.22	0.26	0.065	0.031	0.113	0.528
C14:0	2.24	2.39	2.15[b]	2.47[a]	0.394	0.295	0.030	0.594
i-C14:0	0.20[a]	0.15[b]	0.17	0.18	0.057	0.043	0.741	0.229
C14:1 cis-9	0.24[d]	0.29[c]	0.23[b]	0.30[a]	0.055	0.051	0.003	0.120
C15:0	0.36	0.39	0.38	0.37	0.065	0.193	0.600	0.287
a-C15:0	0.28	0.27	0.27	0.29	0.056	0.642	0.433	0.424
i-C15:0	0.05	0.06	0.06	0.05	0.016	0.334	0.147	0.322
C15:1	0.06	0.06	0.05	0.06	0.023	0.819	0.426	0.731
C16:0	24.60	25.21	24.61	25.20	1.877	0.370	0.396	0.835
a-C16:0	0.25	0.23	0.24	0.24	0.080	0.408	0.990	0.773
i-C16:0	0.09	0.10	0.09	0.10	0.04	0.684	0.674	0.470
DMA-C16:0	2.84	2.60	2.50[d]	2.93[c]	[illegible]	0.348	0.097	0.722
C16:1 cis-7	0.11	0.11	0.11	0.11	0.012	0.107	0.590	0.203
C16:1 cis-9	2.23[b]	2.53[a]	2.24[b]	2.51[a]	[illegible]	0.009	0.020	0.541
C16:1 trans-9 + i-C17:0	0.20	0.21	0.22[a]	0.19[b]	0.021	0.429	0.002	0.680
C17:0	0.74	0.72	0.81[a]	0.64[b]	0.137	0.696	0.002	0.363
C17:1 cis-9	0.81	0.79	0.79	0.81	0.130	0.721	0.799	0.246
C18:0	18.17	17.74	18.41[a]	17.50[b]	1.180	0.316	0.042	0.267
i-C18:0	0.13	0.11	0.12	0.1[illegible]	0.037	0.172	0.841	0.938
DMA-C18:0	1.61	1.51	1.43	1.[illegible]9	0.450	0.540	0.114	0.950
C18:1 cis-9	27.76	28.37	29.15[a]	26.98[b]	2.881	0.560	0.045	0.747
C18:1 cis-11	0.11	0.12	0.1[illegible]	[illegible]11	0.030	0.542	0.570	0.684
C18:1 trans-11	1.92	1.80	2.[illegible]5[a]	1.57[b]	0.438	0.467	0.001	0.928
C18:1 cis-12	0.11	0.11	0.13	0.10[b]	0.029	0.901	0.006	0.971
C18:1 cis-13	0.04	0.03	0.04	0.03	0.014	0.145	0.270	0.993
C18:1 cis-15	0.03	0.03	0.03	0.03	0.010	0.832	0.917	0.616
C18:1 trans-15	0.15[a]	0.13[b]	0.14	0.13	0.025	0.032	0.250	0.717
C18:1 trans-16	0.03	0.04	0.04	0.04	0.014	0.756	0.933	0.269
C18:2 cis-9, trans-11	0.09[b]	0.11[illegible]	0.10	0.09	0.026	0.046	0.211	0.321
C18:2 trans-9, cis-11	0.01	0.01	0.01	0.01	0.006	0.458	0.653	0.941
C18:2 trans-10, cis-12	0.029	0.029	0.032[c]	0.027[d]	0.008	0.927	0.082	0.395
C18:2 n-6	9.64	9.06	8.93	9.77	2.362	0.494	0.328	0.599
C18:2 n-6 trans-9,12	0.03	0.04	0.04	0.03	0.014	0.454	0.196	0.475
C18:3 n-3	0.29	0.30	0.31[a]	0.28[b]	0.032	0.365	0.010	0.162
C18:3 n-6	0.03	0.03	0.02[b]	0.03[a]	0.010	0.637	0.003	0.703
C20:0	0.10	0.10	0.10[c]	0.09[d]	0.015	0.917	0.071	0.661
C20:1 n-9	0.01	0.01	0.01	0.01	0.008	0.737	0.704	0.871
C20:2 n-6	0.07	0.07	0.07	0.07	0.016	0.350	0.569	0.528
C20:3 n-6	0.51	0.51	0.43[b]	0.60[a]	0.185	0.972	0.015	0.308
C20:3 n-9	0.11	0.11	0.09[b]	0.13[a]	0.035	0.846	0.005	0.227
C20:4 n-6	2.27	2.17	1.92[b]	2.52[a]	0.641	0.652	0.014	0.841
C20:5 n-3	0.10	0.10	0.08[b]	0.12[a]	0.029	0.684	0.001	0.265
C22:0	0.10	0.09	0.09	0.11	0.032	0.416	0.292	0.284
C22:1	0.03	0.02	0.02	0.02	0.026	0.307	0.971	0.167
C22:3 n-3	0.004	0.003	0.003	0.004	0.002	0.789	0.281	0.719
C22:4 n-6	0.30	0.30	0.28	0.32	0.073	0.894	0.177	0.687
C22:5 n-3	0.28	0.28	0.25[b]	0.32[a]	0.077	0.949	0.016	0.712
C22:6 n-3	0.02	0.02	0.01[b]	0.03[a]	0.006	0.376	0.001	0.202
C24:0	0.004	0.003	0.002[b]	0.004[a]	0.001	0.206	0.001	0.464
C24:1 n-9	0.02	0.02	0.02	0.02	0.012	0.565	0.159	0.341
ΣCLA	0.12[d]	0.14[c]	0.14	0.13	0.030	0.055	0.146	0.506
Saturated fatty acids	52.36	52.23	51.95	52.64	2.067	0.865	0.358	0.576
Monounsaturated fatty acids	33.84	34.64	35.48[a]	33.00[b]	3.225	0.501	0.041	0.863
Polyunsaturated fatty acids	13.79	13.13	12.57	14.35	3.341	0.586	0.150	0.608

FAMEs, fatty acid methyl esters; CONTROL, bulls from cows fed 100% of their requirements in early pregnancy; SUBNUT, bulls from cows fed 65% of their requirements in early pregnancy; RSD, residual standard deviation. [a,b] Means within a row differ $P < 0.05$, [c,d] means within a row differ $P < 0.1$.

Long-term effects of early maternal undernutrition on the growth, physiological profiles, carcass and meat quality of male beef offspring

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Highlights

- Early maternal undernutrition reduced the live weight of Pirenaica bulls at slaughter
- Early maternal undernutrition increased carcass fat deposition in Pirenaica bulls
- Prenatal subnutrition raised the percentage of some healthy intramuscular fatty acids
- Maternal undernutrition was associated with lower meat tenderness in Pirenaica bulls