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Influence of maternal nutrition during gestation on feed efficiency, productive performance, and reproductive traits of finishing beef bulls

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ABSTRACT - This study evaluated the effects of maternal protein-energy supplementation during gestation on performance, reproductive traits, and carcass characteristics of Nellore bulls during the finishing phase. Twenty-eight bulls sired by the same bull and born to nulliparous dams were used. From pregnancy confirmation at 60 d of gestation until calving, dams received either mineral supplementation (non-programmed group, 0.3 g kg^{-1} body weight day^{-1}) or protein-energy supplementation (fetal programming group, 5.0 g kg^{-1} body weight day^{-1}). After birth, all calves were raised under similar management throughout the cow-calf, growing, and finishing phases. Body weight, dry matter intake, feed efficiency, and carcass traits were evaluated during a 97-day feedlot period, and reproductive traits (scrotal circumference, sperm motility, vigor, swirling, and defects) were assessed at 16 and 20 months of age. Maternal nutrition had no significant effect on growth performance or carcass characteristics (P≥0.18). However, bulls from the fetal programming group had fewer minor and total sperm defects (P≤0.04) and tended to have lower sperm motility (P = 0.06). Protein-energy supplementation during gestation influences sperm motility and morphological defects, suggesting that fetal programming can modulate specific andrology-related traits, even in the absence of changes in productive performance.

Keywords: carcass traits, fetal programming, grazing supplementation, Nellore cattle, prenatal modulation, semen quality

1. Introduction

Beef cattle production plays a key role in global food systems (USDA, 2023; FAO, 2025). Improving its efficiency and sustainability, however, requires the integration of genetic selection, nutritional management, and feedlot finishing strategies (Alves et al., 2024). Selecting animals with high feed efficiency and early sexual maturity accelerates genetic progress and improves meat quality (White et al., 2015; Fernandes Júnior et al., 2022; Baruselli et al., 2025). When combined with efficient reproductive and nutritional management, these strategies also improve performance, carcass yield, economic viability, while reducing resource use and emissions (White et al., 2015; Davis and White, 2020; Ojo et al., 2024). Feedlot finishing is particularly effective in shortening production cycles and supplying

premium beef (Morais et al., 2024). Moreover, producing bulls with high genetic merit is crucial for sustaining long-term genetic improvement (Berry et al., 2014; Carvalho et al., 2023). However, to fully realize this potential, nutritional management should also consider the gestational period (Polizel et al., 2025). This stage is often overlooked in tropical production systems, where cow herds rely on pastures with strong seasonal variations in availability and nutritional quality.

Most supplementation studies have focused on mid-to-late gestation to enhance muscle development and carcass traits (Summers et al., 2015; Marquez et al., 2017; Maresca et al., 2019; Ramírez-Zamudio et al., 2022; Nascimento et al., 2024). However, in tropical production systems, where pasture availability and quality vary seasonally (Silva and Nascimento Júnior, 2007; Rodrigues et al., 2021; Barcelos et al., 2022), supplementation restricted to mid-to-late gestation may be insufficient to support the nutritional requirements for optimal fetal development. Fewer studies have explored reproductive outcomes, and these primarily address female offspring (Martin et al., 2007; Funston et al., 2010; Mossa et al., 2013). Our research group has expanded this approach by evaluating the effects of fetal programming in male offspring, with a focus on reproductive traits relevant to their future breeding potential (Polizel et al., 2021, 2023).

Recent findings highlight early gestation as a critical period for placental development and organogenesis, with long-term impacts on growth, metabolism, and reproductive function (Caton et al., 2019; Reynolds et al., 2023; Baumgaertner et al., 2024a, 2024b). However, the subsequent development and maturation of fetal tissues and organ systems depend on adequate maternal nutrition throughout later gestation. Therefore, maternal nutrition across the entire gestational period is essential to support proper fetal programming and long-term offspring performance (Reynolds et al., 2023).

This study hypothesized that protein-energy supplementation throughout gestation would positively influence fetal programming, leading to improved growth performance, feed efficiency, carcass traits, and reproductive parameters in male progeny. Accordingly, the objective was to evaluate the long-term effects of maternal protein-energy supplementation on productive and reproductive performance of Nellore bulls during feedlot finishing.

2. Material and methods

Research on animals was conducted according to the ethics committee on animal use of the Faculdade de Zootecnia e Engenharia de Alimentos of the Universidade de São Paulo (FZEA/USP) (protocol number 1843241117).

2.1. Animals, management and experimental design

Twenty-eight Nellore bulls with an average body weight (BW) of 420 ± 45 kg and an average age of 18 months were used. All bulls were born to nulliparous dams artificially inseminated with sexed semen from a single Nellore sire. After pregnancy confirmation at 30 days of gestation, dams were allocated to two nutritional treatments based on body weight and body condition score. The treatments consisted of mineral supplementation (Non-Programmed group [NP]; 0.3 g/kg BW/day; n = 14) or protein-energy supplementation (Fetal Programming group [FP]; 5.0 g/kg BW/day; n = 14), which were provided daily until calving. During gestation, supplementation was provided in collective feeders, with daily allowance calculated based on the average body weight of the animals (g/kg BW), to standardize supplement supply among animals within each treatment. Management strategies, including adequate feeder space and uniform supplement distribution, were adopted to ensure access to the supplement by all animals and to minimize competition and variation in intake. Although individual supplement intake was not directly measured, this approach is widely used in grazing systems and is considered appropriate for evaluating maternal nutritional effects under practical production conditions. At the beginning of the supplementation period, dams averaged 460.7 ± 3.35 kg in the FP group and 456.0 ± 3.78 kg in the NP group, with average body condition scores of 5.40 ± 0.16 and 5.60 ± 0.16, respectively. Throughout

gestation, dams remained separated in *Urochloa brizantha* cv. Marandu paddocks to receive their respective treatments. Each treatment group was managed using two paddocks, with animals rotated between them according to forage availability. All paddocks were managed under similar conditions regarding forage availability, stocking rate, and management practices to minimize environmental variation between groups. After calving, all dams were relocated to a single *U. brizantha* cv. Marandu paddock and protein-energy supplementation was discontinued for the FP group, which then received 3 g/kg body weight of mineral supplement, identical to the NP group, until weaning. During the cow-calf, growing, and finishing phases, all calves were managed under the same environmental, nutritional, and sanitary conditions.

Calves were weaned at approximately eight months of age and subsequently raised for 10 months on *U. brizantha* cv. Marandu pasture, with supplementation adjusted to environmental conditions. During the dry season, each animal received 3 g/kg body weight per day of an energy supplement (Total digestible nutrients (TDN) = 67.6%; Crude protein (CP) = 24.8%; fat = 2.61%. During the rainy season, animals received a protein supplement at 1 g/kg body weight day (TDN = 53.2%; CP = 30.0%; fat = 1.65%). Further details regarding management and supplements during the growing phase can be found in (Polizel et al., 2023).

At 18 months of age, the bulls were finished in a feedlot and housed in individual pens measuring 7 × 2.5 m for 97 days, including 15 days of adaptation to the facilities and diet. After the adaptation period, they received a diet composed of 70% concentrate and 30% corn silage, offered *ad libitum*, with free access to water. After the finishing period, at an average BW of approximately 600 kg, all animals were slaughtered at the FZEA-USP teaching slaughterhouse, located 500 meters from the feedlot.

2.2. Pasture and ingredient sampling and nutritional composition analysis

Samples of the mineral and protein-energy supplements provided to the dams were collected from each new batch produced (Table 1). Pasture samples were collected monthly from each paddock throughout the experimental period. Subsequently, samples were composited by treatment to represent the average forage composition over time (Table 2). Samples were pre-dried in a forced-air oven at 55 °C for 72 h prior to grinding and subsequent chemical analysis. Pasture sampling was

Table 1 - Ingredient composition and nutritional profile of mineral and protein-energy supplements provided to the dams

Item	Mineral supplement	Protein-energy supplement
Ingredient (%)		
Ground corn	35.0	60.0
Soybean meal	-	30.0
Dicalcium phosphate	10.0	-
Urea	-	2.50
Sodium chloride	30.0	5.00
Mineral premix[1]	25.0	2.50
Nutritional composition (%)		
Dry matter (% as fed)	90.0	88.0
Crude protein	2.79	24.8
Non-protein nitrogen[2]	-	7.03
Ether extract	1.26	2.61
Neutral detergent fiber	4.29	11.24
Acid detergent fiber	1.25	4.76
Total digestible nutrients	26.8	67.6
Calcium (g/kg)	74.1	6.20
Phosphorus (g/kg)	59.4	7.24

[1] Minerthal 160 MD composition (Minerthal company, São Paulo, Brazil): Ca, 230 g/kg; P, 160 g/kg; S, 60 g/kg; Co, 160 mg/kg; Cu, 270 mg/kg; F, 1600 mg/kg; I, 135 mg/kg; Mn, 2700 mg/kg; Se, 80 mg/kg; Zn, 8100 mg/kg; sodium monensin, 4000 mg/kg.
[2] Non-protein nitrogen calculated based on the nitrogen content of urea.

conducted monthly in each paddock throughout the experimental period. At each sampling date, forage was collected using the hand-plucking technique at multiple random points within each paddock, simulating the grazing selection pattern of the animals. Subsamples from each paddock were pooled to generate a composite sample per paddock per month, which were subsequently used to represent the temporal variation in forage composition within each treatment. In grazing experiments where forage availability is not the primary treatment factor, maintaining comparable pasture conditions across treatments is essential. Stocking rate was adjusted and paddocks were rotated throughout the experimental period to minimize spatial and temporal variation among treatments. All paddocks were established with the same forage species (*Urochloa brizantha* cv. Marandu) and managed under similar environmental conditions. Pasture chemical composition was consistent across treatments throughout the experimental period (Table 2), supporting the uniformity of forage quality among groups. Although forage mass was not directly measured, stocking rate adjustments and rotational management were used to maintain comparable grazing pressure and reduce the risk of treatment-related differences in forage availability.

During the growing phase, the ingredients of the energy supplement (dry season) and the protein supplement (wet season) were sampled at each production batch. Composite samples were prepared by supplement type to represent each seasonal period (Table 3).

Table 2 - Nutritional composition of pasture provided to dams under different gestational treatments

Nutritional composition (%)	NP	FP
Dry matter (% as fed)	91.8	90.9
Crude protein	7.42	7.53
Ether extract	1.87	1.86
Neutral detergent fiber	61.0	62.4
Total digestible nutrients	60.2	60.5
Calcium	0.38	0.39
Phosphorus	0.19	0.20

NP - Bulls born to dams that received mineral supplementation during gestation (Non-Programmed); FP - Bulls born to dams that received protein-energy supplementation during gestation (Fetal Programming).

Table 3 - Ingredient composition and nutritional profile of the protein and energy supplements provided to calves during the growing phase

Item	Protein supplement	Energy supplement
Ingredient (%)		
Ground corn	36.5	61.5
Soybean meal	40.0	26.0
Urea	3.50	5.00
Sodium chloride	12.5	5.00
Mineral premix[1]	7.50	2.50
Nutritional composition (%)		
Dry matter (% as fed)	90.0	90.0
Crude protein	30.0	30.2
Non-protein nitrogen[2]	9.84	14.0
Ether extract	1.92	2.61
Neutral detergent fiber	9.65	10.9
Acid detergent fiber	4.80	4.47
Total digestible nutrients	56.8	65.8
Calcium (g/kg)	17.1	6.27
Phosphorus (g/kg)	15.2	7.05

[1] Minerthal 160 MD composition (Minerthal company, São Paulo, Brazil): Ca, 230 g/kg; P, 160 g/kg; S, 60 g/kg; Co, 160 mg/kg; Cu, 270 mg/kg; F, 1600 mg/kg; I, 135 mg/kg; Mn, 2700 mg/kg; Se, 80 mg/kg; Zn, 8100 mg/kg; sodium monensin, 4000 mg/kg.
[2] Non-protein nitrogen calculated based on the nitrogen content of urea.

In the finishing phase, concentrate ingredients were sampled at each production batch, while corn silage was sampled on a weekly basis. Composite samples were later prepared for each ingredient and the silage, covering the entire feedlot period (Table 4).

All samples (pasture, supplements, and silage) were stored at −20 °C until laboratory analysis. Prior to chemical analysis, samples were thawed and dried in a forced-air oven at 55 °C for 96 hours (AOAC, 2005) (method #934.01) and then ground in a knife mill (Marconi, Pirassununga, SP, Brazil) using a 1 mm mesh screen.

Dry matter (DM) was determined by oven-drying at 105 °C for 24 hours (AOAC, 2005) (method #934.01), and ash content was measured by incineration in a muffle furnace at 550 °C for 4 hours (AOAC, 1990) (method #942.05). Total nitrogen was determined using the Dumas method with a LECO FP-528 analyzer (Leco Corp., St. Joseph, MI, USA; AOAC (AOAC, 2005) (method #990.03), and crude protein (CP) was calculated as N × 6.25.

Neutral detergent fiber (NDF) and acid detergent fiber (ADF) were determined according to (Van Soest et al., 1991) using thermostable alpha-amylase and sodium sulfite. Ether extract (EE) was determined using a Soxhlet system with petroleum ether (AOAC, 1990) (method #920.39). Total digestible nutrients (TDN) were estimated for all feed components according to (Weiss et al., 1992).

Table 4 - Ingredient composition and nutritional profile of the finishing diet fed to bulls during the feedlot period

Indredient	(%)
Corn silage	30.0
Ground corn	61.8
Soybean meal	5.00
Urea	1.00
Limestone	1.00
Sodium chloride	0.50
Mineral premix[1]	0.75
Nutritional composition (%)	
Dry matter (% as fed)	89.7
Crude protein	13.4
Non-protein nitrogen[2]	2.81
Ether extract	3.56
Neutral detergent fiber	22.5
Acid detergent fiber	11.3
Total digestible nutrients	75.4
Calcium (g/kg)	6.62
Phosphorus (g/kg)	4.53

[1] Minerthal 160 MD composition (Minerthal company, São Paulo, Brazil): Ca, 230 g/kg; P, 160 g/kg; S, 60 g/kg; Co, 160 mg/kg; Cu, 270 mg/kg; F, 1600 mg/kg; I, 135 mg/kg; Mn, 2700 mg/kg; Se, 80 mg/kg; Zn, 8100 mg/kg; sodium monensin, 4000 mg/kg.
[2] Non-protein nitrogen calculated based on the nitrogen content of urea.

2.3. Performance and carcass traits during finishing phase

During the finishing phase, dry matter intake (DMI) was recorded daily for each bull as the difference between the amount of total mixed ration (TMR) offered and the feed refusals collected on the following day, both expressed on a dry matter basis. Body weight was measured every 14 days after a 14-hour withdrawal from solid feed and used to estimate average daily gain (ADG) by individual linear regression over the experimental period, allowing for a more accurate assessment of growth rate. Feed efficiency (FE) was calculated as the ratio of ADG to individual average DMI, while feed conversion ratio (FCR) was calculated as the ratio of DMI to ADG.

Residual feed intake (RFI) was calculated as the residual from a multiple linear regression model, in which DMI was adjusted for ADG and metabolic body weight, using individual records collected over 70 days during the feedlot period. Metabolic body weight was calculated as the average of initial and final body weights within the same interval. Negative RFI values indicate greater feed efficiency, i.e., animals that consumed less than expected for their performance and body size. The methodology used follows the approach described by (Koch et al., 1963), which defines RFI as the difference between observed and predicted feed intake based on productive performance and body size. Residual weight gain (RWG) was calculated as the residual from a model in which ADG was adjusted for DMI and metabolic weight, allowing for the identification of animals that gained more or less weight than expected for their intake and body size within the same 70-day period.

Carcass yield (CY) was calculated after slaughter by dividing the hot carcass weight by the body weight of the animal at slaughter (multiplied by 100). Carcass traits were evaluated by ultrasound every 28 days during the finishing period. Images were captured using an Exago ultrasound device (IMV Technologies, l'Aigle, Orne, France) equipped with a 180 mm, 3.5 MHz linear transducer. The following traits were measured: ribeye area (REA, cm^2), subcutaneous fat thickness (SFT, mm) between the 12th and 13th ribs, and rump fat thickness (RFT, mm), corresponding to the Gluteus medius muscle (Silva and Nascimento Júnior et al., 2007). All images were analyzed by a trained technician using Lince® V.15 software (M&S Consultoria Agropecuária Ltda, Pirassununga, Brazil) ensuring standardized and accurate measurements.

2.4. Reproductive data collection

Testicular measurements and evaluation of seminal characteristics were performed at 16 and 20 months of age, corresponding to the growing and finishing phases, respectively. Scrotal circumference was measured using a measuring tape positioned at the point of greatest diameter of the scrotum.

For semen analyses, semen was collected using an electroejaculator (Autojac V3, Neovet, Uberaba, MG, Brazil) operated by a trained veterinarian. Due to the variability associated with electroejaculation, which affects ejaculate volume and sperm concentration (Memon et al., 1986; Butler et al., 2021) and may not reflect physiological conditions, analyses were restricted to sperm motility and morphology.

The ejaculate was first examined to verify the presence or absence of spermatozoa using an optical microscope (Primostar 3, Carl Zeiss; Germany) at magnifications of 100× and 400×. Subsequently, another aliquot of the same sample was used to assess sperm motility and vigor, following the recommendations of the Brazilian College of Animal Reproduction (CBRA, 1998).

Sperm morphology was evaluated by counting 100 cells using the wet mount technique under differential interference contrast microscopy (Primostar 3, Carl Zeiss; Germany) at 1000× magnification by the recommendations of the Brazilian College of Animal Reproduction (CBRA, 1998). The proportion of abnormal sperm cells was classified as having major and minor defects, as described by Blom (1973). Major defects included abnormalities such as acrosome abnormalities, proximal cytoplasmic droplet, underdeveloped head, isolated pathological head, narrow head base, tail coiled around the head, pear-shaped head, abnormally small head, abnormal head contour, pouch formation, teratoid forms, midpiece pathologies, severely bent or coiled tail, and bent tail with distal cytoplasmic droplet. Minor defects included alterations such as thin head, giant head, short head, wide head, small head, isolated normal head, abaxial, retroaxial, oblique head, bent or coiled tail, distal cytoplasmic droplet.

2.5. Statistical analyses

Statistical analyses were performed using the GLM procedure of SAS software (version 9.3; SAS Institute Inc., Cary, NC, USA). Bulls were considered the experimental units, and maternal nutritional treatment (non-programmed, NP; or fetal programming, FP) was included as a fixed effect in the model. The statistical model applied was:

$$Y_{ij} = \mu + T_i + \varepsilon_{ij},$$

in which Y_{ij} represents the observed value of each response variable, μ is the overall mean, T_i is the fixed effect of maternal treatment, and ε_{ij} is the residual error. Residual normality and homogeneity of variances were verified using the Shapiro–Wilk and Levene tests, respectively. Performance, feed efficiency, and carcass traits were analyzed using the individual means obtained during the finishing phase. Reproductive traits measured at 16 and 20 months of age were analyzed separately using the same model structure.

Residual feed intake (RFI) and residual weight gain (RWG) were estimated through multiple linear regression models in which dry matter intake and average daily gain were adjusted for metabolic body weight, using the lm function in R software (version 4.1.2). Treatment means were compared using Tukey's test when applicable. Statistical significance was declared at $P<0.05$, and trends were considered when $0.05 \leq P < 0.10$.

3. Results

At calving, a significant difference in dam body weight (BW) was observed, with fetal programming (FP) dams averaging 593.3 ± 8.69 kg and non-programmed (NP) dams 504.8 ± 8.30 kg ($P<0.01$).

3.1. Feedlot performance and carcass traits assessed by ultrasound

Feedlot performance variables, including ADG, CY, FE, FCR, RFI, and RWG, were not influenced by the maternal nutrition received during gestation ($P \geq 0.21$; Table 5). Similarly, carcass traits assessed by ultrasound, represented by REA, SFT, and RFT, also showed no significant differences between the NP and FP groups ($P \geq 0.18$).

Table 5 - Performance and ultrasound carcass traits during the finishing phase of bulls born to dams supplemented with mineral or protein-energy diets during gestation

Item	Treatments[1]		P-value
	NP	FP	
Performance			
Initial body weight (kg)	226.8 ± 33.9	240.6 ± 40.4	0.07
Final body weight (kg)	564.6 ± 58.8	568.3 ± 54.7	0.87
Average daily gain (kg/d)	1.8 ± 0.32	1.72 ± 0.26	0.47
Dry matter intake (kg/d)	10.4 ± 1.0	10.4 ± 1.31	0.94
Feed efficiency (kg/kg)	0.173 ± 0.019	0.166± 0.011	0.26
Feed conversion rate (kg/kg)	5.86 ± 0.77	6.03 ± 0.38	0.45
Residual feed intake (kg/d)	−0.09 ± 0.45	0.08 ± 0.59	0.39
Residual weight gain (kg/d)	0.04 ± 0.18	−0.04 ± 0.12	0.21
Carcass yield (%)	60.4 ± 0.12	59.9 ± 0.14	0.34
Ultrasound carcass traits			
Ribeye area (cm^2)	114.6 ± 7.5	113.1 ± 8.2	0.59
Subcutaneous fat thickness (mm)	7.9 ± 3.3	9.5 ± 3.5	0.19
Rump fat thickness (mm)	10.4 ± 3.5	12.2 ± 3.2	0.18

[1] NP - Bulls born to dams that received mineral supplementation during gestation (Non-Programmed); FP - Bulls born to dams that received protein-energy supplementation during gestation (Fetal Programming).

3.2. Reproductive traits and semen quality

No significant differences were observed in scrotal circumference, at 16 or 20 months of age between bulls whose dams received either mineral or protein-energy supplementation during gestation ($P \geq 0.51$; Table 6). Regarding seminal characteristics and sperm morphology, bulls from the FP group had fewer

minor and total sperm defects than those from the NP group at 20 months of age (P≤0.04). In contrast, bulls from the FP group tended to have lower sperm motility than those from the NP group at the same time point (P = 0.06; Table 6). No differences were observed between FP and NP bulls in seminal characteristics or sperm morphology traits at 16 months of age (P≥0.19).

Table 6 - Reproductive traits and semen quality of bulls born to dams supplemented with mineral or protein-energy diets during gestation

Item	Treatments[1]		P-value
	NP	FP	
	16 months of age		
Scrotal circumference (cm)	29.8± 2.7	29.8 ± 3.5	0.98
Seminal characteristics			
Motility (%)	35.0 ± 27.1	40.0 ± 28.6	0.67
Swirling[2]	2.0 ± 1.0	2.2 ± 1.5	0.64
Vigor[3]	2.5 ± 0.8	3.0 ± 1.0	0.28
Sperm morphology			
Minor defects (%)	5.67 ± 4.09	3.64 ± 2.42	0.19
Major defects (%)	19.8 ± 5.62	14.5 ± 3.30	0.43
Total defects (%)	21.2 ± 6.38	18.1 ± 2.90	0.28
	20 months of age		
Scrotal circumference (cm)	33.6 ± 2.1	33.0 ± 2.8	0.51
Seminal characteristics			
Motility (%)	77.3 ± 14.5	64.6± 19.7	0.06
Swirling[2]	4.1 ± 1.32	3.8 ± 1.37	0.61
Vigor[3]	4.0 ± 0.9	3.9 ± 0.9	0.69
Sperm morphology			
Minor defects (%)	4.62 ± 2.26	2.93 ± 1.82	0.03
Major defects (%)	15.4 ± 4.79	12.6 ± 5.09	0.16
Total defects (%)	20.0 ± 5.15	15.5 ± 5.89	0.04

[1] NP - Bulls born to dams that received mineral supplementation during gestation (Non-Programmed); FP - Bulls born to dams that received protein-energy supplementation during gestation (Fetal Programming).
[2] Classification from 0 to 5, where 0 represents the absence of swirling, and 5 represents the maximum value assigned to an intense mass movement.
[3] Classification from 0 to 5, based on the velocity of progressive movement, where 0 represents the absence of progressive movement, 1 indicates slow movement, 2 corresponds to active movement, 3 to very active movement, 4 to highly active movement, and 5 represents movement with great energy.

4. Discussion

Feedlot performance and ultrasound-evaluated carcass traits in bulls were not influenced by maternal nutritional history during gestation. This lack of response may be explained by the limited magnitude of the prenatal nutritional contrast and potential compensatory growth during postnatal development, which may have attenuated early programming effects. Additionally, the variability inherent in tropical production systems may have further masked subtle prenatal influences, resulting in similar performance during the finishing stage. Together, these factors suggest considerable phenotypic plasticity and a context-dependent expression of fetal programming effects.

This lack of response contrasts with studies that have reported benefits of protein supplementation in pregnant cows, particularly under tropical pasture conditions where protein is often a limiting nutrient (Marquez et al., 2017; Rodrigues et al., 2021; Nascimento et al., 2024). Although protein-energy supplementation was used in the present study, the available literature on protein supplementation alone still serves as a valid basis for comparison, as both approaches aim to correct deficiencies in the basal diet during gestation. Furthermore, it is well established that protein supplementation in

ruminants fed low-quality forages not only corrects nitrogen deficiencies but also restores the fibrolytic activity of ruminal bacteria, promoting dry matter intake and the degradation of carbohydrates for energy production (Lazzarini et al., 2009; Martinez et al., 2022). In this context, both protein and protein-energy supplementation strategies aim to meet the nutritional requirements of pregnant cows according to forage seasonality.

It is important to acknowledge that the sample size (n = 14 per group) was limited by the availability of dams within the experimental system. Although this constraint may have reduced the statistical power to detect subtle differences between treatments, the consistent biological trends observed across multiple performance and reproductive variables lend credibility to the findings. Thus, these results provide a meaningful foundation for future studies with larger cohorts designed to validate and expand on these initial observations.

Some studies have shown that maternal supplementation during gestation can positively affect the productive performance and/or carcass traits of the offspring (Stalker et al., 2007; Cracco et al., 2021; Polizel et al., 2021). On the other hand, there are reports in which maternal supplementation had no significant effect on productive or carcass variables in the offspring (Larson et al., 2009; Maresca et al., 2019; Ramírez-Zamudio et al., 2022; Nascimento et al., 2024), which aligns with the results of the present study. This suggests that the effects of maternal supplementation may vary depending on the basal nutritional conditions to which the dams were exposed (Rodrigues et al., 2021) or on the nutritional management of the offspring during the postnatal period (Picard and Gagaoua, 2020).

In the present study, the pasture composition where the dams were maintained showed mean crude protein (CP) contents of 7.42% and 7.53% for the NP and FP groups, respectively. Considering an average body weight (BW) of 456 kg for the dams, nutritional requirements were estimated using the BR-Corte system (Valadares Filho et al., 2016) at 90, 180, and 270 days of gestation. The estimated CP requirements were 573, 698, and 1030 g/day, while total digestible nutrient (TDN) requirements were 3.60, 3.85, and 4.61 kg/day, respectively. Predicted dry matter intake (DMI) was 9.52, 8.72, and 7.92 kg/day at the same stages. Based on these estimates and the pasture chemical composition, cows receiving only mineral supplementation (NP group) experienced a progressive reduction in dietary protein supply, with an estimated CP deficit of approximately 42.2% during the final third of gestation, despite meeting energy requirements. In contrast, cows receiving protein-energy supplementation (FP group; 5 g/kg BW) met both protein and energy requirements throughout gestation, indicating a clear nutritional divergence between treatments during late pregnancy.

Previous research with pregnant Nellore cows receiving 1 kg/day of protein supplement from the second trimester until calving (Rodrigues et al., 2021) showed no subsequent differences in offspring performance either up to weaning or during the finishing phase (Ramírez-Zamudio et al., 2022). The authors suggested that the nutritional value of the forage was sufficient to prevent severe restriction in cows receiving only mineral supplement, resulting in no significant differences in offspring performance. In our study, it is also likely that the nutritional restriction during the final trimester of gestation was not severe enough to compromise postnatal development. During this period, muscle fiber hyperplasia is already complete, with muscle hypertrophy and the development of intramuscular adipose tissue being the predominant processes (Bonnet et al., 2010; Du et al., 2015). Consequently, potential effects of maternal nutritional restriction on these developmental processes may be at least partially compensated for during early postnatal life.

Skeletal muscle and the gastrointestinal tract exhibit high plasticity, enabling animals exposed to prenatal nutritional restriction to develop compensatory adaptations that enhance postnatal energy utilization (Cruz et al., 2019; Ramírez-Zamudio et al., 2022).

Although no statistically significant differences were observed in carcass fat deposition between groups, the SFT and RFT values were numerically greater in bulls from the FP group, with averages of approximately 1.6 mm and 1.8 mm, respectively. These numerical differences may reflect a biologically relevant response that was not statistically detected because of the limited sample size. Maternal supplementation may have contributed to earlier physiological maturity, thereby favoring

subcutaneous fat deposition during the feedlot phase. This interpretation is consistent with the onset of subcutaneous adipose tissue development during the late second trimester of gestation (Santos et al., 2022). On the other hand, as previously discussed, the nutritional data indicate that the dams in the NP group experienced a more pronounced protein limitation during late gestation. Consequently, their offspring may have entered the feedlot finishing phase at a less advanced stage of physiological maturity, potentially favoring nutrient partitioning toward muscle rather than fat deposition. This process is metabolically more efficient for weight gain compared to lipogenesis. Classic studies indicate that lean tissue gain is approximately four times more efficient than fat gain (Owens et al., 1993, 1995), and it also requires less net energy per unit of BW gained. Therefore, despite lower values of fat deposition, NP bulls may have directed a greater proportion of nutrients toward compensatory muscle hypertrophy. Although prenatal nutritional restriction may have impaired subcutaneous adipose tissue development, muscle growth, which occurs predominantly through hypertrophy during late gestation, may have greater potential for postnatal compensation (Santos et al., 2022). Such physiological plasticity of skeletal muscle may help explain the similarity in average daily gain, final body weight, and feed efficiency between groups, despite numerical differences in fat deposition.

Regarding reproductive traits, testicular consistency, and scrotal circumference were not affected by the prenatal nutritional management to which the offspring were subjected. In cattle, scrotal circumference is associated with testicular parenchymal volume, which is directly related to the production of androgens (Lunstra et al., 1978) and spermatozoa (Amann, 1962). Testicular development in bovine fetuses begins around 41 days after conception and extends until approximately the fourth month of gestation, during which sexual differentiation takes place (Hyttel et al., 2009). In tropical regions, early gestation typically coincides with periods of good forage availability and quality (Nascimento et al., 2024), likely ensuring that the nutritional requirements of pregnant cows were met during the critical window of sexual differentiation and early fetal testicular development (from ~41 days to the fourth month of gestation). This likely explains the absence of differences in testicular characteristics between bulls from NP and FP groups (Rae et al., 2002; Jafariahangari et al., 2012; Mossa et al., 2018), consistent with previous findings from our laboratory in cattle (Polizel et al., 2021, 2023).

In cattle, puberty is considered to be reached when the ejaculate contains at least 10% progressively motile sperm and 70% morphologically normal spermatozoa (Wolf et al., 1965). In the present study, both groups exhibited more than 30% motility from 16 months of age, with 18–21% total sperm defects, corresponding to approximately 80% normal sperm. Additionally, scrotal circumference is recognized as a more accurate predictor of puberty than age or body weight (Bollwein et al., 2016).

Metabolic hormones such as leptin, insulin, growth hormone (GH), and insulin-like growth factor 1 (IGF-I), which undergo characteristic changes during puberty, may have distinct effects on sexual development in bulls (Brito et al., 2007). IGF-I stimulates the proliferation of Leydig cell precursors in immature animals and promotes their differentiation when combined with LH (Bollwein et al., 2016). Furthermore, both insulin and IGF-I increase basal and stimulated testosterone secretion in a dose-dependent manner *in vitro* (Bernier et al., 1986; Spiteri-Grech and Nieschlag, 1992; Lin, 1995). Studies in ewes have shown that nutritional restriction during late gestation can increase GH levels and reduce IGF-I, glucose, and insulin concentrations, indicating that the fetal somatotropic axis is nutritionally regulated during this period (Bauer et al., 1995). Additionally, maternal nutrition at this stage affects the offspring's insulin sensitivity (Gardner et al., 2005).

Although metabolic hormones were not measured in the offspring in the present study, it is possible that the endocrine profile of NP bulls was altered. Studies in buffaloes and zebu cattle have identified leptin in seminal plasma (Souza et al., 2012; Kumar et al., 2016). Despite the lack of a direct correlation with serum concentrations (Ellithy et al., 2014), elevated seminal leptin levels have been associated with an increased incidence of sperm abnormalities (Kumar et al., 2016). To date, the effects of fetal programming on sperm morphology have been poorly explored, with limited data indicating increases in major defects (Polizel et al., 2021, 2023). Considering that NP bulls were exposed to a high-energy diet during the finishing phase, it is plausible that this stimulus induced an increase in leptin production, which may have contributed to the greater incidence of minor sperm defects observed at 20 months of

age, but not at 16 months, since the latter preceded the feedlot period. It has been suggested that leptin may act directly on sperm cells or interfere with the testicular tissues responsible for their nourishment and maturation, thereby promoting the occurrence of morphological abnormalities (Haron et al., 2010).

From a practical standpoint, maternal protein-energy supplementation throughout gestation is worth prioritizing for its effect on offspring reproductive development, given the reduction in sperm defects, even when no gains in growth or carcass traits are expected. Where pasture already provides adequate nutrition, supplementation levels can be reduced without affecting productive outcomes. Adjusting supplementation to forage conditions is therefore a reasonable way to use resources more efficiently without sacrificing offspring performance or reproductive potential.

5. Conclusions

Protein-energy supplementation during gestation did not influence the feedlot performance or carcass traits assessed by ultrasound in Nellore bulls. However, affected specific reproductive traits, reducing minor and total sperm defects at 20 months of age. Despite a tendency for reduced sperm motility in the FP group, the overall findings suggest that fetal programming may enhance specific aspects of male reproductive function without altering growth-related phenotypes under intensive production conditions.

Data availability

The original contributions presented in the study are included in the article, further inquiries can be directed to the corresponding author.

Author contributions

Conceptualization: Santana, M. H. A. **Formal analysis:** Furlan, E. and Polizel, G. H. G. **Funding acquisition:** Santana, M. H. A. **Investigation:** Furlan, E.; Fernandes, A. C.; Prati, B. C. T.; Pombo, G. V. and Fantinato-Neto, P. **Methodology:** Polizel, G. H. G. and Fernandes, A. C. **Project administration:** Santana, M. H. A. **Supervision:** Santana, M. H. A. **Writing – original draft:** Furlan, E. **Writing – review & editing:** Furlan, E.; Polizel, G. H. G. and Ramírez-Zamudio, G. D.

Conflict of interest

The authors declare no conflict of interest.

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