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Sex and environment-biased maternal investment in cattle

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ABSTRACT - Mothers must allocate limited resources between raising their offspring and maintaining their own biological functions. In both wild and livestock populations, food availability fluctuates with climate, soil fertility, and rainfall, challenging mothers and calves when environmental quality declines. This study evaluated whether maternal investment is influenced by progeny sex and environmental conditions, using coefficients of variation as a measure of evolvability. We analyzed three pre-weaning growth traits in cattle: birth weight (BW), body weight at 120 days (BW120), and at 210 days (BW210). Environmental conditions were classified as low or high quality based on whether the cohort mean was below or above the overall mean. Environmental quality did not affect the maternal coefficient of variation for BW, but values for BW120 and BW210 were significantly higher in the low-quality environment, suggesting increased maternal investment under resource limitation. Additive genetic coefficients of variation for body weights were consistently higher in females than in males (BW: 6.74 vs. 5.98; BW120: 6.21 vs. 5.38; BW210: 6.07 vs. 4.90). In contrast, maternal effect coefficients were lower in females than in males from birth (3.21 vs. 3.92) to 120 days (5.52 vs. 6.09), but not at weaning (5.30 vs. 5.64). Overall, maternal investment in cattle appears sex-biased until 120 days and is modulated by environmental quality, with cows adjusting allocation to ensure stronger calves at weaning despite challenging conditions.

Keywords: adaptation, calf, coefficient of variation, evolvability, offspring, weight

1. Introduction

The cow plays a crucial role in calf development from birth to weaning. It contributes half of the calf's genes, influencing its development throughout life, and certain maternal phenotypes directly affect calf development, a phenomenon known as the maternal effect. Key maternal phenotypes include physical contact time (Toledo et al., 2013), suckling facilitation (Castanheira et al., 2013), and milk production (Calegare et al., 2007; Calegare et al., 2009).

Milk production is essential for calf growth, supplying around 70% of the calf's metabolizable energy until weaning (Calegare et al., 2007; Calegare et al., 2009). This trait is shaped by genetics,

environment, and their interactions across species, including beef cattle (MacNeil and Mott, 2006), dairy cattle (Kearney et al., 2004), buffalo (Flores and Werf, 2015), goats (Castañeda-Bustos et al., 2014), and sheep (Haile et al., 2019). Both calf sex and cow rearing conditions are non-genetic factors affecting milk yield. Some studies report that beef cows nursing males produce more milk than those nursing females (Daley et al., 1987; Albertini et al., 2012), whereas others find no sex effect (Cruz et al., 1997; Espasandin et al., 2001; Minick et al., 2001; Cerdótes et al., 2004a). A seminal large-scale study in dairy cattle further demonstrated that fetal sex can program maternal physiology, with Holstein cows producing significantly more milk for daughters than for sons (Hinde et al., 2014). This work provided the first evidence that sex-biased maternal investment may be initiated in utero through fetal signaling mechanisms that shape mammary gland development and resource allocation. Environmental conditions also influence milk yield, with cows in low-quality environments producing less milk and weaning lighter calves (Lalman et al., 2000; Cerdótes et al., 2004a,b).

The heritability of milk yield in beef cows is moderate (0.25 ± 0.06) (MacNeil and Mott, 2006). Due to the challenge of direct measurement, breeders use maternal genetic effects as an indicator of milk production (Minick et al., 2001; MacNeil and Mott, 2006). Additionally, maternal permanent environmental effects can be included to account for environmental factors shared by multiple offspring of the same cow (Kruuk and Hadfield, 2007). Maternal genetic and permanent environmental effects explain 17% to 35% of the phenotypic variance in pre-weaning growth traits in beef cattle (Lee et al., 1997; Mattos et al., 2000a; Diaz et al., 2011; Abreu et al., 2018). Greater variance in maternal effects suggests differences among cows in providing optimal conditions, which is crucial for adaptation to changing environments.

Total maternal effects, including genetic and environmental components, show no consistent evidence of sex-biased investment in beef cattle (Lee et al., 1997; Diaz et al., 2011). However, comparing milk production between cows nursing male or female calves is complicated by the lack of body weight standardization. Variance is influenced by scale, as variables having higher means generally exhibiting higher variances (Toral et al., 2019). Moreover, heritability is often an inadequate measure for comparing evolvability and variability. Instead, standardized measures of variation, such as the additive genetic coefficient of variation, are more appropriate for these purposes (Houle, 1992).

Current evidence does not definitively show that maternal investment in milk production or total maternal effects is influenced by sex or environment, as many studies lack comprehensive data. Therefore, this study aims to evaluate whether maternal investment in pre-weaning growth traits is affected by sex and environmental conditions, using indirect indicators to assess cow behavior and milk production adjustments according to environmental conditions and calf sex.

2. Material and methods

2.1. Animals and traits evaluated

The data used in this study were obtained from retrospective weight records collected from a private beef cattle company. These weight measurements were routinely performed as part of the farm's standard management practices, and therefore, ethical committee approval was not required.

Growth and pedigree records of Nellore calves born between 1994 and 2018 were utilized. Initially, the animals were raised on a commercial farm located in Brotas, São Paulo, Brazil (22°10'44.69" S, 48°01'20.9" W, altitude of 647 meters), classified under the Cfa climate according to the Köppen-Geiger classification. In 2001, the animals were relocated to another farm in Uberaba, Minas Gerais, Brazil (19°24'33.3" S, 48°06'34.5" W, altitude of 840 meters), classified under the Aw climate according to the same classification system.

Pregnant cows were maintained on pastures with year-round access to water, shade, and mineral supplements. The predominant grass species (>80%) on both farms belonged to the *Urochloa genus*, and the stocking rate was approximately 0.98 animal units per hectare (one animal unit is equivalent to

a 450 kg animal). After calving, newborn calves were identified, weighed, and received umbilical care. Subsequently, groups of approximately 30 cows and their calves were moved to 30-hectare paddocks. Calves remained with their dams and were weaned at approximately 210 days of age.

The calves were weighed at birth and again at approximately 120 days (ranging from 75 to 165 days) and 210 days (ranging from 165 to 255 days) of age. Average daily gain from birth to 120 days of age (ADG120) and from birth to 210 days of age (ADG210) were calculated as the difference between body weight at 120 and 210 days of age and birth weight, divided by the age of the calf at weighing, respectively. Body weight at 120 days of age (BW120) and body weight at 210 days of age (BW210) were computed using the following formulas:

$$BW120 = BW + 120 \times ADG120 \quad (1)$$

in which BW120 is the body weight at 120 days of age, BW is the birth weight, and ADG120 is the average daily gain from birth to 120 days of age.

$$BW210 = BW + 210 \times ADG210 \quad (2)$$

in which BW210 is the body weight at 210 days of age, BW is the birth weight, and ADG210 is the average daily gain from birth to 210 days of age.

Therefore, we analyzed three pre-weaning growth traits: birth weight (BW), body weight at 120 days of age (BW120) and body weight at 210 days of age (BW210).

2.2. Management group

A management group is a fundamental concept that accounts for environmental conditions influencing phenotypes. Animals within the same management group are expected to experience similar climatic, nutritional, sanitary, and management conditions. Consequently, phenotypic differences within a management group are primarily attributed to individual additive genetic effects, maternal effects (including cow age, maternal additive genetic effects, and maternal permanent environmental effects), and other unknown factors. For BW, management groups consisted of calves of the same sex born in the same year and month. For other traits, management groups comprised calves of the same sex that were kept in the same paddock from birth until weighing and were weighed on the same day. To ensure reliable statistical analysis, phenotypes from management groups with fewer than five individuals were excluded.

2.3. Complete datafiles and pedigree

The complete dataset comprised 21,242 BW records, 18,036 BW120 records, and 18,290 BW210 records. There were 305 management groups for BW, 1,298 management groups for BW120, and 1,358 management groups for BW210. Since the herd's establishment in 1978, its breeding management has been closely monitored, providing extensive pedigree information. We pruned the pedigree to include only animals with recorded phenotypes, along with their sires and dams. This process resulted in a total of 21,402 calves, 344 bulls, and 5,463 cows. The final pruned pedigree contained 25,929 individuals, including animals, their sires, dams, and older ancestors.

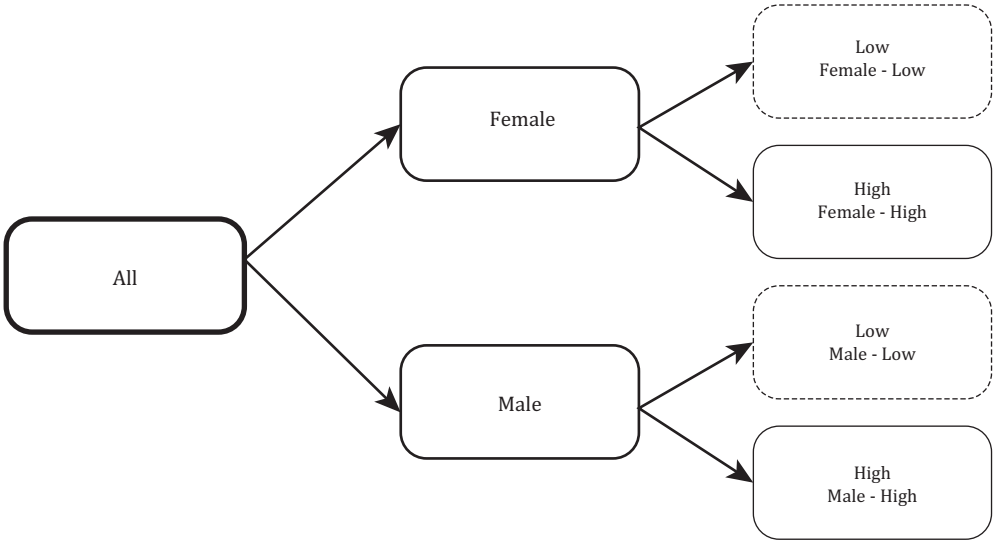
2.4. Statistical analysis

We fitted mixed animal models to estimate quantitative genetic and environmental parameters (variances and covariances) for pre-weaning growth traits. Bayesian analysis was performed using the GIBBS3F90 software (Misztal et al., 2015), which employs the Gibbs sampler algorithm to generate samples from the posterior distribution of genetic and environmental parameters. The animal models included fixed effects for the management group and accounted for the linear and quadratic effects of cow age at calving as covariates. The random effects comprised direct additive genetic, maternal additive genetic, maternal permanent environmental, and residual effects. Consequently,

the phenotypic variance (V_P) was partitioned into components attributed to direct additive genetic variance (V_A), maternal additive genetic variance (V_{MA}), maternal permanent environmental variance (V_{MP}), and residual variance (V_R). To simplify the model, maternal additive genetic and permanent environmental variances were combined into a single component (VM = VMA + VMP), referred to as maternal variance (or maternal effect). We observed that fitting animal models with maternal additive genetic + maternal permanent environmental effects, maternal additive genetic alone, or maternal permanent environmental effects alone did not significantly alter estimates of direct additive genetic and maternal variances (Kassahun et al., 2022). Furthermore, the main objective of this study was to evaluate maternal investment regardless of its origin (genetic or non-genetic).

Initially, three single-trait analyses were conducted, each corresponding to one of the pre-weaning growth traits. Subsequently, two sets of two-trait analyses and one set of four-trait analyses were performed. In the first set of two-trait analyses, each pre-weaning growth trait measured in females was considered as trait 1, while the corresponding trait measured in male calves was considered as trait 2 (one analysis for each trait). Female management groups were classified based on their phenotypic means relative to the overall female mean: groups with means below the overall female mean were classified as "Female – Low Quality," while those with means above the overall female mean were classified as "Female – High Quality." A similar classification procedure was applied to male management groups, resulting in the categories "Male – Low Quality" and "Male – High Quality."

In the second set of two-trait analyses, a pre-weaning growth trait measured in the "Female – Low Quality" and "Male – Low Quality" groups was considered as trait 1, while the corresponding trait measured in the "Female – High Quality" and "Male – High Quality" groups was considered as trait 2 (one analysis for each trait). Finally, in the four-trait analysis, a pre-weaning growth trait measured in the "Female – Low Quality," "Female – High Quality," "Male – Low Quality," and "Male – High Quality" groups was designated as traits 1, 2, 3, and 4, respectively. A schematic representation of the data files and the analyses is presented in Figure 1.



First, all the records were analyzed with single trait models ("All" files contain records from females and males). Second, a pre-weaning growth trait measured in females was designated as trait 1 and the corresponding trait measured in male calves was designated as trait 2 ("Female" and "Male" files). Third, a pre-weaning growth trait measured in Female – Low and Male – Low groups was designated as trait 1 and the corresponding trait measured in Female – High and Male – High groups was designated as trait 2 ("Low" and "High" files). Finally, a pre-weaning growth trait designated in the Female – Low, Female – High, Male – Low and Male – High groups was designated as trait 1, 2, 3 and 4, respectively ("Female – Low", "Female – High", "Male – Low", and "Male – High" files). These procedures were performed for each pre-weaning growth traits separately.

Figure 1 - Schematic representation of data files for single, two-trait and four-trait mixed-model analyses.

Unfortunately, it was not possible to directly evaluate pasture production and quality in this experiment. Instead, we used the management group mean of pre-weaning growth traits as a proxy for environmental quality. Calves from management groups whose phenotypic means were below the overall mean of the trait were classified as being raised in a low-quality environment, whereas calves from management groups with phenotypic means above the overall mean were classified as being raised in a high-quality environment.

Furthermore, the samples of conditional distributions for variances and covariances were used to compute additional parameters, including additive genetic coefficient of variation (CV_A), maternal coefficient of variation (CV_M), residual coefficient of variation (CV_R), and phenotypic coefficient of variation (CV_P). Additionally, we calculated heritability (h^2), the proportion of phenotypic variation attributable to maternal effects (m^2), and genetic (r_A) and maternal (r_M) correlations as follows:

$$CV_i = \frac{\sqrt{V_i}}{\bar{X}_i} \times 100\% \quad (3)$$

in which CV_i is the coefficient of variation of the trait i, V_i is the variance of the trait i, and $\bar{X}_i$ is the phenotypic mean of the trait i.

$$h^2 = \frac{V_A}{V_P} \text{ and } m^2 = \frac{V_M}{V_P} \quad (4)$$

in which h^2 is the heritability, V_A is the additive genetic variance, V_P is the phenotypic variance, m^2 is the phenotypic variation due to maternal effects, and V_M is the maternal variance.

$$r_{A_{X,Y}} = \frac{COV_{A_{X,Y}}}{\sqrt{V_{A_X} \times V_{A_Y}}} \text{ and } r_{M_{X,Y}} = \frac{COV_{M_{X,Y}}}{\sqrt{V_{M_X} \times V_{M_Y}}} \quad (5)$$

in which $COV_{A_{X,Y}}$ and $COV_{M_{X,Y}}$ represent the additive genetic and maternal covariances between traits X and Y, respectively.

2.5. Summary statistics

The Gibbs sampler was employed to obtain samples from the posterior distributions of the parameters of interest, including variances, coefficients of variation, heritabilities, and correlations. These posterior distributions were derived from prior distributions and observed data, representing an updated estimate of the parameters after incorporating the data. Given the space constraints and the inherent complexity of posterior distributions, presenting all of them would be impractical. Instead, we provide statistical summaries following the guidelines of Sorensen and Gianola (2002). These summaries include the posterior mean, standard deviation, and the lower and upper limits (LL and UL) of the highest posterior density (HPD) interval with 95% credibility for each parameter or contrast. To enhance interpretability, we also report posterior summaries of contrasts (differences between parameters). For example, the difference between additive genetic variances of two traits ($\sigma^2_{\alpha_1} - \sigma^2_{\alpha_2}$) can offer more insight than the individual variances alone. These contrasts were calculated from the posterior samples of the corresponding parameters.

For hypothesis testing, we employed a 95% region of practical equivalence (ROPE), allowing for a probabilistic interpretation of the practical significance of differences between parameters. The ROPE was defined by the lower and upper limits of the 95% highest posterior density (HPD) interval for each contrast. By incorporating the ROPE, we established a criterion for identifying meaningful differences between contrasts. If zero fell within the ROPE, the difference between the parameters was considered practically equivalent to zero, indicating no statistically significant difference.

To investigate the effects of sex and environment on the parameters of interest, we designed contrasts specifically to evaluate differences in variances and coefficients of variation between sexes and environmental conditions. These contrasts provided insights into how these factors influenced genetic parameters, enabling us to assess maternal investment regardless of its genetic or non-genetic origin. This approach allowed us to indirectly assess whether maternal investment in milk production was influenced by environmental conditions and calf sex, providing a more nuanced interpretation of maternal effects.

3. Results

3.1. Phenotypic means

Differences between sexes and environmental levels (Table 1) were consistently statistically significant (Tukey test, P<0.001). Females were consistently lighter than males at all evaluated ages: 4.87% lighter at birth, 6.49% lighter at 120 days, and 6.98% lighter at 210 days. Furthermore, calves raised in low-quality environments were significantly lighter compared to those raised in high-quality environments: 4.31% lighter at birth, 12.45% lighter at 120 days, and 15.92% lighter at 210 days. These differences remained statistically significant (Tukey test, P<0.001) even when Tukey's tests were performed to compare sex differences within environmental levels and environmental differences within sex classes.

Table 1 - Summary statistics[1] for birth weight (BW), body weight at 120 (BW120) and body weight at 210 (BW210) days of age of Nellore calves in the complete datafile and according to calf sex, environmental quality, and sex by environment subclasses

Sex	Environment	BW (kg)			BW120 (kg)			BW210 (kg)		
		n	Mean	SD	n	Mean	SD	n	Mean	SD
All	All	21,242	30.88	3.70	18,036	124.44	18.60	18,290	183.08	28.71
Female	All	10,428	30.09b	3.54	8,876	120.20b	16.97	8,985	176.34b	25.87
Male	All	10,814	31.63a	3.69	9,160	128.55a	19.18	9,305	189.59a	29.80
All	Low	10,778	30.21B	3.52	8,584	115.81B	17.10	8,208	165.78B	23.80
All	High	10,464	31.57A	3.76	9,452	132.28A	16.29	10,082	197.16A	24.33
Female	Low	5,321	29.47bB	3,47	4,272	112.39bB	15.67	4,054	160.76bB	22.28
Female	High	5,107	30.74bA	3.50	4,604	127.44bA	14.77	4,931	189.15bA	21.15
Male	Low	5,457	30.93aB	3.42	4,312	119.19aB	17.78	4,154	170.68aB	24.21
Male	High	5,357	32.35aA	3.82	4,848	136.89aA	16.33	5,151	204.83aA	24.71

[1] n and SD = number of records and standard deviation, respectively.
Lowercase letters indicate comparisons between sexes, while uppercase letters represent comparisons between environments, according to Tukey's test (P<0.05).

3.2. Variances

The posterior summary of contrasts (mean of the difference) and the ROPE allowed us to evaluate differences between sexes and environmental conditions. Sex did not represent a significant source of variation for additive genetic variance, either on average or within specific environments (Tables S1, S2, and S3). The only exception occurred for BW in the low-quality environment, where the additive genetic variance was significantly higher in females compared to males (mean of the difference =

1.32; LL95 = 0.24; UL95 = 2.39). On the other hand, sex was a significant source of variation for maternal variance in both average and specific environments. Maternal variances for pre-weaning growth traits were consistently lower in female calves compared to male calves (Tables S1, S2, and S3).

In general, the posterior means of residual and phenotypic variances were significantly lower in female calves compared to male calves, both on average and within specific environments (Tables S1, S2, and S3). The only exception was observed for BW in the low-quality environment, where no significant difference between sexes was detected (Table S1).

Although the variance was lower in females, the difference was not statistically significant. Additive genetic variances for BW were significantly lower in the low-quality environment compared to the high-quality environment, both when considering females and males together (mean difference = −1.36; LL95 = −2.21; UL95 = −0.49) and when analyzing male calves separately (mean difference = −2.23; LL95 = −3.52; UL95 = −0.90) (Table S1). However, the environment did not significantly affect additive genetic variances for BW120 (Table S2) or BW210 (Table S3).

Environmental quality did not significantly influence maternal variances across any of the pre-weaning growth traits (Tables S1, S2, and S3). However, residual and phenotypic variances for BW were significantly lower in the low-quality environment compared to the high-quality environment, both when considering females and males together (residual variance: mean difference = −0.65; LL95 = −1.29, UL95 = −0.03; phenotypic variance: mean difference = −1.77; LL95 = −2.31, UL95 = −1.21) and when analyzing male calves separately (residual variance: mean difference = −1.05; LL95 = −2.05, UL95 = −0.04; phenotypic variance: mean difference = −3.29; LL95 = −4.18, UL95 = −2.48) (Table S1). In general, residual and phenotypic variances for BW120 were not significantly affected by environmental quality (Table S2). Regarding BW210, residual variances were not influenced by the environment, but phenotypic variances were significantly lower in the low-quality environment compared to the high-quality environment. This pattern was observed both when considering females and males together (mean difference = −33.21; LL95 = −53.54, UL95 = −13.40) and when analyzing male calves separately (mean difference = −41.31; LL95 = −71.65, UL95 = −8.28) (Table S3).

3.3. Coefficients of variation

The posterior means of the additive genetic coefficient of variation remained relatively stable from birth to weaning: 6.40% for BW, 5.66% for BW120, and 5.25% for BW210. In contrast, the maternal coefficient of variation increased over time, rising from 3.38% at birth to 5.72% at 120 days and 5.37% at 210 days (Tables 2, 3, and 4). The posterior means of the residual coefficients of variation were 9.24% for BW, 9.11% for BW120, and 8.55% for BW210, while the phenotypic coefficients of variation were 11.74% for BW, 12.16% for BW120, and 11.38% for BW210. Neither the residual nor the phenotypic coefficients of variation showed significant changes across the evaluated ages (Tables 2, 3, and 4).

Similarly, to the variances, the posteriori summary of contrasts and the ROPE allowed us to compare the differences between sex and environment. The posterior means of additive genetic coefficients of variation for pre-weaning growth traits were significantly higher in female calves than in male calves when data from both environmental levels were considered together (BW – mean of the difference = 0.77; LL95 = 0.08; UL95 = 1.40; BW120 – mean of the difference = 0.84; LL95 = 0.03; UL95 = 1.62; BW210 – mean of the difference = 1.16; LL95 = 0.29; UL95 = 2.00) (Tables 2, 3, and 4). These results reflect the similar additive genetic variances observed in both female and male calves (Tables S1, S2, and S3), combined with the lower body weights of females compared to males (Table 1).

Maternal coefficients of variation for females were lower than those for males for both BW and BW120 when considering both environments together or specifically in the high-quality environment. The mean difference for BW was −0.71 (LL95 = −1.31; UL95 = −0.15), and for BW120, it was −0.57 (LL95 = −1.05; UL95 = −0.09). Specifically, in the high-quality environment, the mean difference for BW was −1.07 (LL95 = −1.83; UL95 = −0.19), and for BW120, it was -0.69 (LL95 = −1.31; UL95 = −0.09).

Conversely, sex was not a significant source of variation for maternal coefficients of variation for BW210 (Table 4). Sex did not significantly affect the residual coefficient of variation for BW. However, residual coefficients of variation for BW120 and BW210 were significantly lower in female calves compared to male calves, regardless of environmental quality. Regarding the phenotypic coefficient of variation for BW, female calves exhibited higher values than male calves in the low-quality environment, but lower values in the high-quality environment (Table 2). For BW120, phenotypic coefficients of variation were lower in females compared to males when data from both environments were analyzed together or when considering only the low-quality environment (Table 3). Finally, sex was not a significant source of variation for the phenotypic coefficient of variation for BW210 (Table 4).

Additive genetic coefficients of variation for BW were significantly lower in the low-quality environment when considering calves of both sexes combined (mean difference = −0.82; LL95 = −1.50, UL95 = −0.13) and when analyzing males separately (mean difference = −1.55; LL95 = −2.53, UL95 = −0.51) (Table 2). For BW120, additive genetic coefficients of variation were significantly higher in calves raised in the low-quality environment compared to those raised in the high-quality environment. This pattern was observed when data from both female and male calves were combined (mean difference = 0.89; LL95 = 0.03, UL95 = 1.77) and when analyzing females separately (mean difference = 1.37; LL95 = 0.13, UL95 = 2.55) (Table 3). Environmental quality was not a significant source of variation for the additive genetic coefficient of variation for BW210 (Table 4).

Environmental quality did not significantly affect the maternal coefficient of variation for BW (Table 2). However, maternal coefficients of variation for BW120 and BW210 were significantly higher in the low-quality environment compared to the high-quality environment (Tables 3 and 4). Residual coefficients of variation for BW were not significantly affected by environmental quality. However, phenotypic coefficients of variation for BW were significantly lower in the low-quality environment compared to the high-quality environment when data from both female and male calves were analyzed together (mean difference = −0.27; LL95 = −0.50, UL95 = −0.01) and when data from male calves were analyzed separately (mean difference = −0.87; LL95 = −1.25, UL95 = −0.53) (Table 2). In general, residual and phenotypic coefficients of variation for BW120 and BW210 were higher in the low-quality environment compared to the high-quality environment (Tables 3 and 4).

3.4. Heritability

The posterior means of heritability from single-trait analyses were 0.30 for BW, 0.22 for BW120, and 0.21 for BW210 (Tables 2, 3, and 4). These values indicate that additive genetic differences between animals accounted for a moderate proportion of the total variability. Furthermore, the posterior means of heritability for pre-weaning growth traits were consistently higher in female calves compared to male calves (Tables 2, 3, and 4).

The posterior means of heritability for BW were significantly lower in the low-quality environment compared to the high-quality environment. This difference was observed when data from both female and male calves were analyzed together (mean difference = −0.06; LL95 = −0.13, UL95 = −0.01) and when analyzed separately for males (mean difference = −0.10; LL95 = −0.18, UL95 = −0.02) (Table 2). Environmental quality did not significantly affect the heritability estimates for BW120 and BW210 (Tables 3 and 4).

The posterior means of the proportions of phenotypic variance due to maternal effects were low at birth (0.08 for BW) and moderate at 120 (0.22) and 210 (0.22) days of age (Tables 2, 3, and 4). For BW, the proportions of phenotypic variation attributed to maternal effects were significantly lower in female calves compared to male calves (mean difference = −0.04; LL95 = −0.07, UL95 = −0.01). In contrast, calf sex did not significantly affect the proportions of phenotypic variation due to maternal effects for BW120 and BW210. Overall, environmental quality did not significantly influence the proportions of phenotypic variance attributable to maternal effects (Tables 2, 3, and 4).

Table 2 - Summary statistics[1] of posterior distributions of additive genetic, maternal, residual and phenotypic coefficients of variation, heritability, proportions of phenotypic variance due to maternal effects and their contrasts, for birth weight of Nellore calves in the full dataset and according to sex (F – female, M – male), environmental quality (L – low, H – high) and sex by environment subclasses

Sex	Environment	Additive genetic			Maternal			Residual			Phenotypic			h^2			c^2		
		Mean	LL95	UL95	Mean	LL95	UL95	Mean	LL95	UL95	Mean	LL95	UL95	Mean	LL95	UL95	Mean	LL95	UL95
All	All	6.40*	5.88	6.94	3.38*	3.01	3.71	9.24*	9.03	9.46	11.74*	11.58	11.90	0.30*	0.25	0.34	0.08*	0.07	0.10
F	All	6.74*	6.15	7.32	3.21*	2.76	3.65	9.18*	8.90	9.47	11.84*	11.65	12.04	0.32*	0.28	0.38	0.07*	0.05	0.09
M	All	5.98*	5.36	6.57	3.92*	3.50	4.35	9.20*	8.94	9.47	11.66*	11.47	11.85	0.26*	0.22	0.31	0.11*	0.09	0.14
All	L	6.01*	5.44	6.61	3.83*	3.43	4.26	9.17*	8.91	9.44	11.62*	11.43	11.81	0.27*	0.22	0.32	0.11*	0.09	0.13
All	H	6.83*	6.19	7.48	3.32*	2.85	3.79	9.14*	8.84	9.46	11.89*	11.70	12.11	0.33*	0.28	0.39	0.08*	0.06	0.10
F	L	6.79*	6.00	7.58	4.00*	3.42	4.63	9.16*	8.77	9.57	12.10*	11.81	12.38	0.32*	0.25	0.38	0.11*	0.08	0.14
F	H	6.93*	6.09	7.79	3.33*	2.74	3.95	8.80*	8.35	9.24	11.70*	11.43	11.99	0.35*	0.28	0.43	0.08*	0.06	0.11
M	L	5.30*	4.57	6.09	4.58*	4.06	5.07	8.84*	8.49	9.18	11.29*	11.04	11.54	0.22*	0.16	0.28	0.17*	0.13	0.20
M	H	6.85*	5.92	7.67	4.40*	3.78	5.00	9.02*	8.54	9.46	12.16*	11.90	12.45	0.32*	0.25	0.39	0.13*	0.10	0.17
F – M	All	0.77*	0.08	1.40	−0.71*	−1.31	−0.15	−0.02	−0.36	0.33	0.19	−0.05	0.42	0.06*	0.00	0.11	−0.04*	−0.07	−0.01
F – M	L	1.49*	0.50	2.44	−0.58	−1.31	0.17	0.32	−0.16	0.84	0.81*	0.46	1.17	0.09*	0.01	0.17	−0.06*	−0.10	−0.01
F – M	H	0.09	−1.00	1.17	−1.07*	−1.83	−0.19	−0.22	−0.82	0.39	−0.46*	−0.81	−0.08	0.03	−0.06	0.13	−0.05	−0.09	0.00
All	L – H	−0.82*	−1.50	−0.13	0.51*	−0.09	1.07	0.03	−0.33	0.39	−0.27*	−0.50	−0.01	−0.06*	−0.13	−0.01	0.03	0.00	0.06
F	L – H	−0.14	−1.30	0.92	0.68	−0.15	1.51	0.36	−0.24	0.94	0.40*	0.02	0.78	−0.04	−0.14	0.06	0.03	−0.01	0.07
M	L – H	−1.55*	−2.53	−0.51	0.18	−0.57	0.93	−0.18	−0.74	0.36	−0.87*	−1.25	−0.53	−0.10*	−0.18	−0.02	0.03	−0.01	0.08

[1] LL95 and UL95 = lower and upper limits of the highest posterior density interval with 95% of posterior samples, respectively.
Asterisk (*) indicates that the 95% Bayesian credible interval does not include zero.

Table 3 - Summary statistics[1] of posterior distributions of additive genetic, maternal, residual and phenotypic coefficients of variation, heritability, proportions of phenotypic variance due to maternal effects and their contrasts, for body weight at 120 days of Nellore calves in the full dataset and according to sex (F – female, M – male), environmental quality (L – low, H – high) and sex by environment subclasses

Sex	Environment	Additive genetic			Maternal			Residual			Phenotypic			h^2			c^2		
		Mean	LL95	UL95	Mean	LL95	UL95	Mean	LL95	UL95	Mean	LL95	UL95	Mean	LL95	UL95	Mean	LL95	UL95
All	All	5.66*	4.98	6.32	5.72*	5.40	6.00	9.11*	8.86	9.38	12.16*	11.98	12.34	0.22*	0.17	0.26	0.22*	0.20	0.24
F	All	6.21*	5.41	6.96	5.52*	5.11	5.88	8.65*	8.31	9.00	12.00*	11.76	12.24	0.27*	0.20	0.32	0.21*	0.18	0.24
M	All	5.38*	4.65	6.14	6.09*	5.68	6.47	9.28*	8.99	9.60	12.34*	12.11	12.57	0.19*	0.14	0.24	0.24*	0.22	0.27
All	L	6.25*	5.37	7.11	6.52*	6.07	6.95	9.57*	9.21	9.95	13.17*	12.91	13.42	0.23*	0.17	0.29	0.25*	0.21	0.28
All	H	5.36*	4.63	6.08	5.35*	4.99	5.73	8.54*	8.23	8.83	11.42*	11.21	11.64	0.22*	0.16	0.27	0.22*	0.19	0.25
F	L	7.17*	6.09	8.22	6.59*	6.05	7.13	8.55*	7.94	9.16	12.97*	12.63	13.33	0.31*	0.23	0.39	0.26*	0.22	0.30
F	H	5.80*	4.92	6.64	5.26*	4.77	5.73	8.21*	7.76	8.64	11.36*	11.07	11.64	0.26*	0.19	0.33	0.22*	0.18	0.25
M	L	5.98*	4.90	7.00	7.14*	6.53	7.75	9.83*	9.32	10.30	13.55*	13.21	13.91	0.20*	0.13	0.26	0.28*	0.24	0.32
M	H	5.33*	4.45	6.15	5.95*	5.47	6.43	8.41*	8.02	8.80	11.61*	11.35	11.91	0.21*	0.15	0.28	0.26*	0.22	0.30
F – M	All	0.84*	0.03	1.62	−0.57*	−1.05	−0.09	−0.64*	−1.04	−0.22	−0.34*	−0.62	−0.07	0.08*	0.02	0.14	−0.03	−0.07	0.00
F – M	L	1.19	−0.14	2.57	−0.55	−1.31	0.18	−1.28*	−2.05	−0.54	−0.58*	−1.02	−0.11	0.11*	0.03	0.22	−0.02	−0.08	0.03
F – M	H	0.47	−0.54	1.51	−0.69*	−1.31	−0.09	−0.20	−0.76	0.33	−0.25	−0.62	0.13	0.05	−0.03	0.13	−0.05	−0.10	0.00
All	L – H	0.89*	0.03	1.77	1.17*	0.66	1.67	1.03*	0.60	1.44	1.75*	1.46	2.03	0.00	−0.05	0.07	0.03	−0.01	0.06
F	L – H	1.37*	0.13	2.55	1.33*	0.65	1.93	0.33	−0.42	0.98	1.61*	1.22	2.03	0.05	−0.05	0.14	0.04	0.00	0.09
M	L – H	0.65	−0.40	1.85	1.19*	0.46	1.93	1.41*	0.81	1.99	1.94*	1.54	2.36	−0.02	−0.09	0.06	0.02	−0.04	0.07

[1] LL95 and UL95 = lower and upper limits of the highest posterior density interval with 95% of posterior samples, respectively.
Asterisk (*) indicates that the 95% Bayesian credible interval does not include zero.

Table 4 - Summary statistics[1] of posterior distributions of additive genetic, maternal, residual and phenotypic coefficients of variation, heritability, proportions of phenotypic variance due to maternal effects and their contrasts, for body weight at 210 days of Nellore calves in the full dataset and according to sex (F – female, M – male), environmental quality (L – low, H – high) and sex by environment subclasses

Sex	Environment	Additive genetic			Maternal			Residual			Phenotypic			h^2			c^2		
		Mean	LL95	UL95	Mean	LL95	UL95	Mean	LL95	UL95	Mean	LL95	UL95	Mean	LL95	UL95	Mean	LL95	UL95
All	All	5.25*	4.61	5.90	5.37*	5.07	5.64	8.55*	8.32	8.79	11.38*	11.22	11.56	0.21*	0.17	0.27	0.22*	0.20	0.24
F	All	6.07*	5.29	6.83	5.30*	4.95	5.69	7.97*	7.61	8.33	11.34*	11.13	11.59	0.29*	0.22	0.36	0.22*	0.19	0.25
M	All	4.90*	4.16	5.64	5.64*	5.28	6.03	8.72*	8.42	9.01	11.50*	11.29	11.71	0.18*	0.13	0.24	0.24*	0.21	0.27
All	L	5.45*	4.67	6.27	6.09*	5.67	6.52	9.24*	8.91	9.58	12.34*	12.10	12.58	0.20*	0.14	0.25	0.24*	0.21	0.28
All	H	5.19*	4.50	5.94	5.15*	4.80	5.49	7.92*	7.62	8.22	10.78*	10.59	10.99	0.23*	0.17	0.29	0.23*	0.20	0.26
F	L	6.41*	5.36	7.47	6.37*	5.78	6.90	8.41*	7.85	8.95	12.36*	12.03	12.72	0.27*	0.19	0.35	0.27*	0.23	0.31
F	H	5.87*	4.98	6.69	5.18*	4.76	5.61	7.33*	6.90	7.78	10.73*	10.45	10.99	0.30*	0.23	0.38	0.23*	0.20	0.27
M	L	5.27*	4.24	6.23	6.71*	6.11	7.28	9.24*	8.75	9.67	12.59*	12.28	12.93	0.18*	0.11	0.24	0.28*	0.24	0.33
M	H	5.06*	4.26	5.92	5.57*	5.14	6.00	7.94*	7.58	8.32	10.95*	10.68	11.21	0.22*	0.15	0.28	0.26*	0.22	0.30
F – M	All	1.16*	0.29	2.00	−0.34	−0.79	0.12	−0.75*	−1.17	−0.33	−0.16	−0.41	0.13	0.10*	0.03	0.17	−0.02	−0.06	0.01
F – M	L	1.14	−0.17	2.28	−0.34	−1.10	0.44	−0.83*	−1.49	−0.14	−0.23	−0.66	0.22	0.09	0.00	0.18	−0.02	−0.08	0.04
F – M	H	0.81	−0.21	1.77	−0.40	−0.94	0.12	−0.61*	−1.15	−0.11	−0.21	−0.56	0.13	0.09	0.00	0.17	−0.03	−0.07	0.02
All	L – H	0.27	−0.57	1.11	0.94*	0.48	1.45	1.32*	0.95	1.73	1.56*	1.31	1.84	−0.04	−0.10	0.03	0.02	−0.02	0.05
F	L – H	0.54	−0.55	1.64	1.19*	0.51	1.84	1.08*	0.46	1.70	1.62*	1.24	2.03	−0.03	−0.13	0.05	0.03	−0.02	0.09
M	L – H	0.21	−0.96	1.33	1.14*	0.47	1.83	1.30*	0.75	1.89	1.64*	1.25	2.03	−0.04	−0.12	0.04	0.03	−0.03	0.08

[1] LL95 and UL95 = lower and upper limits of the highest posterior density interval with 95% of posterior samples, respectively.
Asterisk (*) indicates that the 95% Bayesian credible interval does not include zero.

3.5. Genetic and maternal correlations

The posterior means of additive genetic and maternal correlations between pre-weaning growth traits in females and the corresponding traits in male calves were high and positive (≥ 0.94 and ≥ 0.86, respectively; Table 5). These high correlations indicate that the traits tend to evolve in the same direction in both sexes. Although slightly lower correlations between traits in females and males were observed within both low and high-quality environments, this difference could not be conclusively attributed to environmental factors. The highest posterior density intervals obtained from analyses that included all environments together, as well as from separate analyses for each environment level, overlapped. This overlap suggests that the observed differences were not statistically significant.

The posterior means of additive genetic and maternal correlations between pre-weaning growth traits in calves raised in low-quality environments and the corresponding traits in calves raised in high-quality environments were high and positive (≥ 0.95 and ≥ 0.82, respectively; Table 6). These high correlations suggest that the traits tend to evolve in the same direction regardless of environmental conditions. Although the correlations were slightly lower within each sex compared to the combined sex data, this effect could not be significantly attributed to sex differences. The highest posterior density intervals obtained from analyses of combined data and separate analyses for each sex overlapped, indicating that the observed differences were not statistically significant.

Table 5 - Summary statistics[1] of posterior distributions of additive genetic and maternal correlations between birth weight (BW), body weight at 120 (BW120) and body weight at 210 (BW210) days of age in female with the corresponding trait in male Nellore calves according to environmental quality

Trait	Environment	Additive genetic correlation			Maternal correlation		
		Mean	LL95	UL95	Mean	LL95	UL95
BW	All	0.98*	0.96	1.00	0.86*	0.76	0.96
BW	Low	0.94*	0.89	0.99	0.73*	0.59	0.85
BW	High	0.89*	0.80	0.98	0.65*	0.49	0.82
BW120	All	0.95*	0.90	1.00	0.95*	0.90	0.98
BW120	Low	0.89*	0.79	0.97	0.84*	0.76	0.92
BW120	High	0.89*	0.78	0.99	0.87*	0.80	0.94
BW210	All	0.94*	0.87	1.00	0.94*	0.89	0.98
BW210	Low	0.87*	0.74	0.99	0.80*	0.69	0.89
BW210	High	0.87*	0.77	0.97	0.90*	0.85	0.96

[1] LL95 and UL95 = lower and upper limits of the highest posterior density interval with 95% of posterior samples, respectively.
Asterisk (*) indicates that the 95% Bayesian credible interval does not include zero.

Table 6 - Summary statistics[1] of posterior distributions of additive genetic and maternal correlations between birth weight (BW), body weight at 120 (BW120) and body weight at 210 (BW210) days of age in Nellore calves under low quality environment with the corresponding trait in calves under high quality environment according to sex

Trait	Sex	Additive genetic correlation			Maternal correlation		
		Mean	LL95	UL95	Mean	LL95	UL95
BW	All	0.97*	0.93	1.00	0.82*	0.69	0.94
BW	Female	0.90*	0.82	0.97	0.57*	0.37	0.77
BW	Male	0.88*	0.79	0.97	0.68*	0.55	0.82
BW120	All	0.95*	0.90	1.00	0.92*	0.86	0.97
BW120	Female	0.86*	0.74	0.97	0.86*	0.77	0.93
BW120	Male	0.88*	0.76	0.97	0.83*	0.75	0.91
BW210	All	0.97*	0.92	1.00	0.91*	0.84	0.97
BW210	Female	0.94*	0.87	0.99	0.79*	0.68	0.89
BW210	Male	0.86*	0.73	0.96	0.81*	0.73	0.90

[1] LL95 and UL95 = lower and upper limits of the highest posterior density interval with 95% of posterior samples, respectively.
Asterisk (*) indicates that the 95% Bayesian credible interval does not include zero.

4. Discussion

This study presents the results of a 25-year experiment conducted under natural conditions, involving cattle with an average of 3.58 to 3.92 calves per cow, depending on the trait analyzed. The animals were consistently pasture-fed throughout the study period, and variations in climate and soil likely influenced the quality and quantity of available grass. Pre-weaning growth traits were analyzed using animal models, and posterior distributions of variances for additive genetic, maternal, and residual effects were obtained through Gibbs sampling. The analysis of these posterior distributions, including the posterior mean, standard deviation, and the lower and upper limits of the highest posterior density, has proven effective in testing hypotheses related to genotype-by-environment interactions (Raidan et al., 2015) and maternal investment (Abreu et al., 2018). The use of Bayesian inference and Gibbs sampling allowed for robust estimation of variance components, making it possible to investigate the impact of environmental changes on genetic parameters. Such an approach is essential when analyzing long-term data obtained under variable natural conditions, as it accounts for uncertainties and provides credible intervals for parameter estimates.

The pre-weaning growth of calves observed in this experiment closely resembles that of Nellore calves reported in the literature (Associação Brasileira dos Criadores de Zebu, 2024), suggesting that the genetic base and environmental conditions of this study are representative of typical Nellore cattle management. Females were consistently 4.87% to 6.98% lighter than males from birth to 210 days of age. Such differences are common in Nellore cattle (Associação Brasileira dos Criadores de Zebu, 2024; Toral et al., 2004) and have been reported in other cattle breeds as well (Lee et al., 1997; Van Vleck and Cundiff, 1998; Diaz et al., 2011), indicating a pronounced male-biased sexual size dimorphism. Strong evidence indicates that fetal sex can program maternal physiology and resource allocation. Hinde et al. (2014), who analyzed more than two million lactation records from dairy cows, showed that dams consistently produced greater milk yields for daughters than for sons, regardless of parity. Importantly, the sex of the fetus carried during the first parity had lasting consequences, increasing milk production in subsequent lactations. These results reveal a sustained programming of mammary gland function by offspring in utero and demonstrate that sex-biased maternal investment arises not only from differences in postnatal calf demand, but also from fetal signaling mechanisms that shape maternal endocrine and metabolic pathways. Therefore, this dimorphism may be partially explained by lower milk production in beef cows nursing female calves compared to those nursing male calves (Daley et al., 1987; Albertini et al., 2012).

Additionally, this dimorphism could result from sex-specific genes located on the sex chromosomes (Connallon and Clark, 2011) or from the differential expression of genes that are present in both sexes (Pointer et al., 2013). Gionbelli et al. (2018) showed that maternal nutrition during mid-gestation alters the expression of genes related to muscle, adipose, and connective tissue development, with males exhibiting greater skeletal muscle growth than females, regardless of diet. These effects were modulated across gestation, indicating that part of the sex-specific growth trajectories is programmed in utero. Similarly, Gionbelli et al. (2016) reported that female fetuses developed greater intestinal mass, density, and villi length than males, suggesting intrinsic sex-based differences in gastrointestinal development. Together, these findings reinforce that sexual dimorphism in bovines emerges early in fetal life and involves multiple physiological systems. Lower mean values were observed for BW (4.31%), BW120 (12.45%), and BW210 (15.92%) in animals from groups raised in low-quality environments compared to those raised in high-quality environments. These differences were detected even among groups of animals raised on the same farm and were as pronounced as those reported between groups raised on different farms (Toral et al., 2004) or in different countries (Mattos et al., 2000b). These findings reflect the impact of the methods used to characterize environmental quality, emphasizing the considerable natural variation in environmental conditions and its influence on pre-weaning growth in beef cattle. Consistent with this, Meneses et al. (2024) demonstrated that protein supplementation during mid-gestation in Zebu cows improved maternal body condition, nutrient digestibility, and uterine blood flow, which in turn increased calf birthweight. Although no

significant sex × nutrition interaction was detected for maternal traits, these results provide biological evidence that the intrauterine environment, shaped by maternal nutrition, represents a key pathway through which environmental variation translates into differences in offspring performance.

The mean value of a trait influences its variability, thereby affecting its response to selection. However, because the mean is scale-dependent, relying solely on it can lead to biased conclusions due to scale effects (Tatliyer et al., 2019). In animal breeding, understanding a trait's selection potential is essential, and given that the additive genetic component (V_A) is linked to the mean, using metrics such as coefficients of variation (CVs) is more informative than relying solely on variances (Houle, 1992; Cheung, 2020). To mitigate bias when evaluating the interactions between sex and environment on pre-weaning growth and selection capacity, we focused on the coefficients of additive (CV_A), maternal (CV_M), residual (CV_R), and phenotypic (CV_P) variation.

When analyzing sexes separately across both environments, the CV_A estimates for females were consistently higher than those for males. Specifically, for BW, females had a CV_A of 6.74%, compared to 5.98% for males; for BW120, the CV_A was 6.21% for females versus 5.38% for males; and for BW210, females exhibited a CV_A of 6.07%, compared to 4.90% for males. Furthermore, when data from both low and high-quality environments were combined, the differences between sexes remained evident, with CV_A estimates for females being 0.77%, 0.84%, and 1.16% higher for BW, BW120, and BW210, respectively. According to Ehsaninia (2023), traits with high heritability and a high CV_A are expected to exhibit the greatest genetic improvement through selection. However, it is important to note that these differences did not reach statistical significance when data from low and high-quality environments were analyzed separately.

Unlike CV_A, CV_M values were lower for females compared to males when considering both sexes separately and across both environments. Specifically, females exhibited lower CV_M for BW (3.21% vs. 3.92%), BW120 (5.52% vs. 6.09%), and BW210 (5.30% vs. 5.64%). In Nellore cattle, there is a significant maternal influence on calf development up to weaning (Boligon et al., 2010), but this influence tends to decrease as the animal ages. Ferreira et al. (2015), using reaction norms, investigated genotype-environment interactions on weights at 120 and 210 days of age in Nellore cattle. When comparing maternal effects between these traits, the authors found that weight at 120 days exhibited a greater maternal influence, both for maternal and permanent maternal effects. Despite these maternal influences, investment varies according to the offspring's sex. The Trivers-Willard (TW) hypothesis (Trivers and Willard, 1973) suggests that dams in favorable environmental conditions will invest more in male offspring to maximize their fitness returns. Conversely, in unfavorable conditions, dams are likely to invest more in females, as they are more likely to achieve reproductive success despite being smaller and less competitive than males. This hypothesis suggests that in polygynous species, where a limited number of males mate with many females, greater investment is directed towards males. Our results partially align with the TW hypothesis. Although the environment plays an important role as a source of variation, changes in maternal investment are also influenced by the age of the calf. Consistent with this perspective, Santos et al. (2022) reviewed the role of fetal programming and highlighted that gestational nutrition effects on offspring performance and meat quality are not uniform, but strongly dependent on fetal sex, gestational timing, and nutritional intensity. These findings provide mechanistic support for the sex- and environment-biased allocation patterns predicted by the TW hypothesis, reinforcing the idea that maternal investment strategies are shaped by both external conditions and intrauterine signals.

Our results indicated that dams invested more in male calves at specific ages, particularly when data from both environments were analyzed together or when data from the high-quality environment were considered separately. In beef cattle, maternal investment is generally biased toward males up to 120 days of age. However, from 210 days of age onward, calf performance tends to be more influenced by the individual genetic component (direct effect) rather than by maternal factors. The influence of calf age on maternal weaning investment changes over time, as documented in the literature. Kour et al. (2021) investigated the suckling behavior of beef calves at 1 and 4 months of age and confirmed this pattern. They observed that the average duration of suckling was shorter at 1 month than at 4 months, whereas

the frequency of suckling was higher at 1 month than at 4 months. The authors suggested that as calves grow older, they suckle less frequently but for longer periods during each session. Consequently, as the calf gradually reduces its dependence on milk, maternal investment decreases, leading to a reduction in maternal effects as the animal ages. Therefore, our findings support the hypothesis that, in general, maternal investment in beef cattle is biased toward males up to 120 days of age.

CV_R and CV_P for BW, BW120, and BW210 are generally expected to be higher in low-quality environments, where limited or poor-quality resources, such as food, impose significant challenges on individuals. This pattern was observed for BW120 and BW210, which typically exhibited higher CV_R and CV_P in low-quality environments (Tables 3 and 4). However, for BW, environmental quality did not significantly affect CV_R, and CV_P was lower in low-quality environments. We hypothesize that the intrauterine environment may act as a protective factor, shielding the calf from potential environmental fluctuations. This protective effect is likely mediated by physiological mechanisms that prioritize nutrient allocation to the fetus, such as the maintenance of uteroplacental blood flow, the mobilization of maternal body reserves, and endocrine adjustments that favor fetal nutrient supply. In this way, even under challenging external conditions, cows may buffer fetal development against short-term environmental stressors (Hinde et al., 2014; Meneses et al., 2024).

Previous studies have shown that nutrient restrictions and exposure to challenging environments during gestation can significantly impair calf development and performance throughout the productive life (Monteiro et al., 2016; Noya et al., 2022). The increase in residual variance is primarily attributed to the greater influence of random or unpredictable factors, as described by Meyer (1992). These environmental stressors amplify differences between animals, leading to a greater expression of residual and phenotypic variances. In adverse environments, non-genetic factors such as nutrition, management, and exposure to disease exert a more pronounced impact on animal performance, resulting in increased heterogeneity in individual responses (Rebbeck et al., 1997). The heightened phenotypic variability in these contexts reflects the challenges that individuals face in adapting to suboptimal conditions, which accentuates differences among them and increases the phenotypic coefficient of variation. In this context, recent studies have shown that maternal nutrition during gestation not only shapes fetal growth but also programs postnatal physiology in a sex-dependent manner. Nascimento et al. (2022) demonstrated that calves born to protein-supplemented or restricted dams exhibited distinct patterns of nutrient digestibility and intake efficiency depending on sex, indicating that prenatal nutritional status induces long-term adjustments in nutrient utilization and feeding behavior. More recently, Nascimento et al. (2024) showed that protein supplementation during mid-gestation enhanced offspring growth and promoted favorable metabolic responses, particularly in females, with clear sex-specific differences in gene expression related to muscle development and lipogenesis. Together, these findings reinforce that maternal nutrition acts as a programming signal that differentially shapes offspring growth, metabolism, and feeding strategies according to fetal sex.

Additive genetic and maternal correlations between female and male pre-weaning growth traits in Nellore were high, resembling the correlations observed in other cattle breeds (Lee et al., 1997; Diaz et al., 2011). We hypothesize that pre-weaning growth in both female and male calves is predominantly controlled by similar sets of genes, despite the potential influence of sex chromosomes. Additionally, maternal effects on growth appear to be consistent in direction for both sexes, suggesting a shared genetic basis underlying these traits.

Correlations between the same trait evaluated in different environments are often related to the degree of disparity between those environments. As the difference between environments increases, the correlation between traits typically decreases (Kearney et al., 2004; Santana et al., 2013). In our study, we categorized environments into two levels—low quality and high quality—whereas other studies have used more refined categorizations, such as quartiles (Kearney et al., 2004) or linear reaction norms (Santana et al., 2013). We chose to use only two levels to maximize the number of records within each category, thereby enhancing the precision of parameter and correlation estimates. Positive correlations between different traits indicate that both genetic and non-genetic effects influencing one trait also affect the other in the same direction. Our results suggest that additive

and maternal effects on pre-weaning growth traits evolve similarly in both female and male calves, as well as in calves raised in low-quality and high-quality environments. This pattern likely results from natural or artificial selection acting in a consistent direction different environmental conditions.

The findings of this study have important practical implications for beef production systems, particularly regarding the management of maternal investment to optimize pre-weaning growth. Since maternal investment in beef cattle tends to favor higher growth rates in male calves up to 120 days of age and given that the maternal coefficient of variation is consistently higher for males, selection strategies could prioritize enhancing maternal traits related to milk production and calf-rearing efficiency. Furthermore, understanding the impact of environmental quality on maternal investment enables producers to implement targeted management practices. By ensuring that cows adjust their maternal efforts when resources are limited, producers can optimize calf development under varying conditions. Applying these insights can help make informed decisions that improve beef production efficiency and sustain productivity across diverse environmental contexts.

Nonetheless, it is important to acknowledge some methodological limitations of this study. Environmental classification was based on the phenotypic mean of contemporary groups, which, while practical for field applications, may not precisely capture actual environmental variation. Additionally, the absence of physiological data from the dams, such as milk yield or body condition score, limits our ability to interpret the biological mechanisms underlying maternal allocation. Future studies should aim to incorporate objective environmental indicators and direct maternal measurements, thereby offering a more comprehensive understanding of maternal investment dynamics. These refinements may strengthen the link between biological processes and productive outcomes, ultimately supporting more precise decision-making in breeding and management programs.

5. Conclusions

Altogether, this study provides a contribution by jointly evaluating environmental quality and offspring sex as modulators of maternal investment in beef cattle, using evolvability-based indicators under real conditions of extensive commercial production. Sex and environmental quality were identified as significant sources of variation in pre-weaning growth traits in beef cattle. Assessing maternal investment requires considering differences in trait means based on offspring sex and environmental quality. Our findings indicate that maternal investment in beef cattle is sex-biased up to 120 days of age, favoring higher growth rates in male calves. Additionally, cows tend to increase their maternal investment when environmental resources are limited, with the aim of weaning more robust calves despite challenging conditions.

Supplementary material

The supplementary material of this article can be found online at: https://www.rbz.org.br/wp-content/uploads/articles_xml/1806-9290-rbz-55-e20250090/1806-9290-rbz-55-e20250090-suppl01.pdf

Data availability

The data used in this study are from a commercial farm and they might be available under request.

Author contributions

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Conflict of interest

The authors declare that they have no conflict of interests. The author Eduardo Penteado Cardoso is the owner of the Mundo Novo farm, where the data was collected. Author Daniel Resende Gonçalves was employed by the company Mundo Novo farm.

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