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Research Article

Keywords: beef cattle, genetic correlation, heritability, Bayesian inference, SNP

Posted Date: September 3rd, 2026

DOI: https://doi.org/10.21203/rs.3.rs-10101152/v1

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Genomic parameters reveal favorable genetic associations among carcass traits in *Curraleiro Pé-Duro* cattle.

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Abstract: The objective of this study was to estimate genetic parameters for carcass traits and body size measurements in adult *Curraleiro Pé-Duro* cattle. Data were collected from 31 farms located across different regions of Brazil, and 1,889 animals were genotyped using a 100K SNP panel to construct the genomic kinship matrix (G matrix). Ribeye area (REA) and subcutaneous fat thickness (SFT) were measured by ultrasonography and adjusted to 100 kg of body weight. (Co)variance components were estimated using Bayesian inference implemented in GIBBSF90+, and convergence of the Gibbs chains was assessed using the Geweke criterion. Heritability estimates for REA (0.38), SFT (0.40), and body weight (0.45) were moderate to high, indicating potential for genetic selection. The adjusted traits also exhibited moderate heritabilities (REA100c: 0.30 and SFT100c: 0.33). Among the body size measurements, withers height (0.55) and thoracic depth (0.51) showed the highest heritability estimates. A strong positive genetic correlation was observed between REA and SFT (0.78). This finding contrasts with the antagonistic relationship commonly reported in the literature for other cattle breeds, suggesting a distinct genetic pattern in Curraleiro *Pé-Duro* cattle that warrants further investigation from evolutionary and adaptive perspectives. Additionally, a moderate positive genetic correlation (0.59) was found between SFT and adult body weight. The evaluated traits exhibited sufficient genetic variability to achieve genetic progress through selection in the *Curraleiro Pé-Duro* breed. The favorable genetic association between muscling and fat deposition allows simultaneous genetic gains without compromising the maintenance of energy reserves in adult animals.

Keywords: beef cattle, genetic correlation, heritability, Bayesian inference, SNP

Implications

The *Curraleiro Pé-Duro* cattle breed is valued for its hardiness and adaptability, although its potential for beef production remains underexplored. The results of this study indicate sufficient genetic variability to promote changes in carcass and body size traits through selection, as evidenced by moderate to high heritability estimates. The favorable genetic correlation between ribeye area and subcutaneous fat thickness demonstrates that simultaneous genetic gains in these traits can be achieved in adult *Curraleiro Pé-Duro* cattle. These findings provide support for the inclusion of this breed in breeding programs, reconciling the conservation of genetic resources with the enhancement of productive performance. The results are relevant to breeders, technical advisors, and policymakers involved in the conservation and sustainable use of native cattle breeds.

Introduction

The beef cattle industry faces the challenge of increasing production efficiency to meet the growing global demand for animal protein. In this context, animal breeding relies on the identification of animals with superior genetic merit for traits that influence carcass yield and biological efficiency, particularly carcass and body size traits (Evangelista et al. 2020; Reis et al. 2024). Animals that stand out for functionality within beef production systems are typically characterized by a well-developed skeletal structure, moderate frame size, evident carcass length and conformation, as well as adequate rib depth and spring (Soares et al. 2024).

Estimates of genetic parameters, such as heritability and genetic correlations, provide the foundation for predicting selection response, enabling the estimation of direct and indirect genetic gains, the calculation of breeding values, and the development of selection indices (Kluska et al. 2018). Therefore, obtaining these estimates using robust methodologies and reliable data is essential for the genetic characterization of populations undergoing selection.

Understanding the relationship between skeletal structure and indicators such as ribeye area (REA) and subcutaneous fat thickness (SFT) allows the identification of biological types that reach physiological maturity more efficiently. Without this knowledge, selection focused exclusively on body size may inadvertently increase maintenance nutritional requirements and delay fat deposition, resulting in less precocious animals and carcasses with insufficient finish to meet industry standards and the requirements for high-quality beef production.

In breeds with a long history of selection, the literature indicates that REA and SFT exhibit distinct associations with body size. In general, animals with larger skeletal structures tend to present greater REA values but may exhibit lower SFT at a given age due to differences in age, physiological stage, production systems (nutritional management), and breed characteristics (Suguisawa et al. 2013; McPhee et al. 2020).

The current scientific literature lacks genetic parameter estimates for native cattle populations such as the *Curraleiro Pé-Duro* breed. Although this breed possesses considerable adaptive value, no studies have reported genetic parameters for carcass and body size traits. This knowledge gap hinders the development of breed-specific selection indices as well as the prediction of breeding values that simultaneously account for the breed's inherent adaptability and its potential for high-quality beef production.

Knowledge of the genetic associations between carcass and body size traits makes it possible to determine whether selection for increased carcass yield can be achieved without altering the breed's average body structure, ensuring that genetic progress in carcass performance does not occur at the expense of hardiness and moderate body size, which are essential adaptive characteristics for survival in semi-arid environments. Understanding these relationships will provide valuable insights for identifying biological types that combine the breed's inherent resilience with competitive productive performance, thereby enhancing the value of this native genetic resource.

Therefore, the objective of this study was to estimate genomic-based genetic parameters (heritability values and genetic correlations) for carcass traits and body size measurements in adult *Curraleiro Pé-Duro* cattle in order to support the development of selection strategies capable of improving productive performance without compromising the breed's hardiness.

Materials and Methods

The data analyzed in this study were obtained from a database developed within the framework of the project "Conservation, Characterization, and Development of the *Curraleiro Pé-Duro* Breed", conducted by Embrapa Mid-North and Embrapa Genetic Resources and Biotechnology in partnership with the Brazilian Association of *Curraleiro Pé-Duro* Cattle Breeders (ABCPD) and the Federal University of Piauí (UFPI), with financial support from the National Council for Scientific and Technological Development (CNPq) through the project "Genetic Management of *Curraleiro Pé-Duro* Cattle Aimed at the Development and Selection of Economically Important Traits". The study was approved by the Animal Ethics Committees (CEUA) of Embrapa (Certificate No. 03/2023) and UFPI (Protocol No. 683/21).

The study was conducted between 2023 and 2025 through technical visits to 31 farms located in the North, Northeast, and Central-West regions of Brazil, covering the main breeding nuclei of the *Curraleiro Pé-Duro* breed affiliated with ABCPD. The final database included 2,895 registered animals, of which 1,663 had records for ribeye area (REA), 2,529 had body weight records, 2,149 had rump height records, and 1,653 had subcutaneous fat thickness (SFT) measurements. Additionally, 1,889 animals were genotyped using the GGP Bovine 100K SNP panel (Neogen).

Blood samples were collected in vacuum tubes containing EDTA. Samples were kept refrigerated on ice and transported to Embrapa Genetic Resources and Biotechnology, where they were processed and subsequently submitted for genotyping.

Carcass traits, namely ribeye area (REA) and subcutaneous fat thickness (SFT), were measured in the *Longissimus dorsi* muscle between the 12th and 13th ribs using an Aloka SSD-500 ultrasound scanner equipped with a 3.5-MHz linear-array transducer. To optimize image quality, a stand-off pad and vegetable oil were used as acoustic coupling media. Images were digitally stored and subsequently analyzed using ImageJ software version 1.54 (Rasband 2018), allowing precise determination of REA (cm²) and SFT (mm).

The body size traits evaluated were: withers height (WH, cm), defined as the vertical distance from the highest point of the withers to the ground, measured perpendicular to the floor using a measuring stick; rump height (RH, cm), defined as the vertical distance from the midpoint of the sacrum to the ground, measured perpendicular to the floor using a measuring stick; body length (BL, cm), measured as the horizontal distance between the point of the shoulder (scapulohumeral joint) and the pin bone using a non-elastic measuring tape kept parallel to the ground; thoracic circumference (TC, cm), measured immediately caudal to the scapula (approximately between the fourth and fifth intercostal spaces) using a non-elastic measuring tape; thoracic depth (TD, cm), defined as the vertical distance from the dorsal line at the level of the withers to the most ventral point of the sternum, measured perpendicular to the floor using a measuring stick; thoracic depth-to-withers height ratio (TD/WH, %), calculated as TD divided by WH and multiplied by 100; and rump angle (RA, degrees), measured using a goniometer between the last lumbar vertebra and the first sacral vertebra.

The REA and SFT measurements were adjusted to 100 kg of body weight, using equations developed by the authors and adapted from the methodology proposed by Marestone et al. (2022), considering the smaller body size of the *Curraleiro Pé-Duro* breed, as follows:

$$REA100c = REAx\left(\sqrt[3]{\frac{100}{Weight}}\right)^2, \quad SFT100c = SFTx\left(\sqrt[3]{\frac{100}{Weight}}\right)^2$$

where REA100c and SFT100c represent ribeye area (REA) and subcutaneous fat thickness (SFT) adjusted to a standard body weight of 100 kg, expressed in cm² and mm, respectively.

For phenotypic data editing and consistency, only animals with complete records for year of birth, farm, sex, and age at data collection were retained for subsequent analyses. Contemporary groups were defined based on the following fixed effects: animal sex (male or female), year of data collection (2023 to 2025), and farm (1 to 31). Animal age at the time of measurement was included in the model as a covariate (linear effect). Records with values exceeding ±3 standard deviations from the mean of their respective contemporary group were excluded.

Genomic quality control was performed using R software (version 4.5.2). Single nucleotide polymorphisms (SNPs) located on unknown genomic positions or non-autosomal chromosomes were removed (n = 1,192,401). Markers with a minor allele frequency (MAF) lower than 0.05 (n = 5,779), a call rate lower than 0.95 (n = 2,844), or extreme deviation from Hardy-Weinberg equilibrium ($P < 10^{-6}$; n = 1,999) were also excluded. After quality control, the final dataset used for analysis consisted of 78,335 SNPs and 1,853 animals.

Genetic parameters were estimated using a three-trait animal model under a Bayesian framework. The general model can be described in matrix notation as follows:

$$y = X\beta + Z\alpha + e$$

here **y** is the vector of phenotypic observations for each animal; $\boldsymbol{X}$ is the incidence matrix relating observations to fixed effects; β is the vector of fixed effects (contemporary group and animal age as a covariate); $\boldsymbol{Z}$ is the incidence matrix associated with genomic genetic effects; $\boldsymbol{\alpha}$ is the vector of genomic breeding values; and $\boldsymbol{e}$ is the vector of random residual effects.

The vectors $\boldsymbol{\alpha}$ and $\boldsymbol{e}$ were assumed to follow a multivariate normal distribution with mean zero and (co)variance matrices defined as follows:

$$Var(\boldsymbol{\alpha}) = \boldsymbol{G_0} \otimes \boldsymbol{G}$$

$$Var(\boldsymbol{e}) = \boldsymbol{R_0} \otimes \boldsymbol{I}$$

where $\boldsymbol{G_0}$ is the additive genetic (co)variance matrix among the three traits (3 x 3); $\boldsymbol{G}$ is the genomic relationship matrix (N x N); $\boldsymbol{R_0}$ is the residual (co)variance matrix among the three traits (3 x 3); $\boldsymbol{I}$ is an identity matrix of dimension $N \; x \; N$ corresponding to the number of observations; and $\otimes$ denotes the Kronecker product operator.

The genomic kinship matrix ($\boldsymbol{G}$) quantifies the genetic similarity among individuals based on SNP information and was constructed according to Method 1 proposed by Van Raden (2008):

$$G = \frac{ZZ'}{\mathrm{k}}$$

where Z is the centered genotype matrix, obtained as $Z = \boldsymbol{M} - \boldsymbol{2P}$; $\boldsymbol{M}$ is the genotype matrix, with genotypes coded as 0, 1, and 2 according to the number of reference alleles; $\boldsymbol{P}$ is the matrix containing allele frequencies expressed as 2pj; and k is the scaling factor, defined as $2\Sigma pj(1 - pj)$, corresponding to the sum of the expected variances across all loci. Because pedigree information was unavailable for the studied population, the genomic kinship matrix (G) was used as a complete replacement for the traditional numerator relationship matrix (A).

Genomic information was incorporated into the genetic evaluation model by replacing the inverse of the pedigree-based kinship matrix (A^{-1}) with the inverse of the genomic kinship matrix (G^{-1}). For the multi-trait model, the

mixed model equations incorporate the inverses of the additive genetic (co)variance matrix $\left(\boldsymbol{G_0^{-1}}\right)$ and the residual (co)variance matrix $\left(\boldsymbol{R_0^{-1}}\right)$, and can be expressed as follows:

$$\begin{bmatrix} \boldsymbol{X'R_0^{-1}X} & \boldsymbol{X'R_0^{-1}Z} \\ \boldsymbol{Z'R_0^{-1}X} & \boldsymbol{Z'R_0^{-1}Z + (G_0^{-1} \otimes G^{-1})} \end{bmatrix} \begin{bmatrix} \widehat{\boldsymbol{\beta}} \\ \widehat{\boldsymbol{\alpha}} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X'R_0^{-1}y} \\ \boldsymbol{Z'R_0^{-1}y} \end{bmatrix}$$

where $\boldsymbol{R_0^{-1}}$ *and* $\boldsymbol{G_0^{-1}}$ represent the inverses of the residual and additive genetic (co)variance matrices, respectively; $\widehat{\boldsymbol{\beta}}$ is the vector of estimated fixed effects; and $\widehat{\boldsymbol{\alpha}}$ is the vector of predicted genomic breeding values.

(Co)variance components were estimated using Bayesian inference implemented in GIBBSF90+ (Misztal et al. 2014). Three-trait analyses were performed using REA, REA100c, SFT, and SFT100c as anchor traits, each analyzed in combination with one of the body size traits (WH, RH, BL, TC, TD, TD/WH%, and RA). This procedure resulted in 42 different trait combinations, allowing the estimation of (co)variance components and the corresponding genetic parameters for all traits evaluated.

Markov chain Monte Carlo (MCMC) chains of 2,000,000 iterations were generated, with a burn-in period of 1,000,000 iterations and thinning every 20 cycles, resulting in 50,000 effective posterior samples. Convergence was assessed using the Geweke diagnostic and Monte Carlo error estimates through the POSTGIBBSF90 program (Misztal et al. 2014). Final estimates of heritability and genetic correlations were obtained from the posterior means across all analyses in which each trait was included.

Results

In adulthood, males exhibited a greater REA in absolute terms (46.6 ± 9.5 cm²) than females (31.6 ± 8.0 cm²), as shown in Table 1. However, after adjustment to 100 kg of body weight (REA100c), this relationship was reversed, with females exhibiting greater relative muscling (23.5 ± 5.4 cm²) compared with males (20.4 ± 4.0 cm²).

For SFT, females also presented a higher absolute mean value (2.5 ± 1.7 mm) than males (2.2 ± 1.1 mm). The same pattern was observed after adjustment for body weight (SFT100c), with mean values of 1.3 ± 0.8 mm for females and 0.9 ± 0.5 mm for males (Table 1). Variability in fat-related traits was high, with CV ranging from 51.9% to 67.8%.

Sexual dimorphism in ABW was evident, with males (367.4 ± 98.7 kg) averaging approximately 110 kg heavier than females (258.7 ± 56.9 kg). Body weight exhibited moderate variability, with CV values of 26.9% for males and 21.9% for females (Table 1).

Table 1. Descriptive statistics for carcass traits assessed by ultrasonography and adult body weight in *Curraleiro Pé-Duro* cattle.

Sex	Trait	N	Mena ± SD	Minimum	Maximum	CV (%)

Male	REA (cm²)	110	46.6 ± 9.5	22.8	74.5	20.3
	REA100c (cm²)	110	20.4 ± 4.0	8.9	39.6	20.4
	SFT (mm)	110	2.2 ± 1.1	0.8	6.6	51.9
	SFT100c (mm)	110	0.9 ± 0.5	0.3	3.2	57.4
	ABW (Kg)	156	367.4 ± 98.7	159.0	640.0	26.9
Female	REA (cm²)	798	31.6 ± 8.0	10.8	54.7	25.4
	REA100c (cm²)	798	23.5± 5.4	5.4	30.0	23.5
	SFT (mm)	798	2.5 ± 1.7	0.1	20.2	67.8
	SFT100c (mm)	798	1.3 ± 0.8	0.1	11.5	63.9
	ABW (Kg)	1019	258.7 ± 56.9	101.5	450.0	21.9

REA = ribeye area; REA100c = ribeye area adjusted to 100 kg of body weight; SFT = subcutaneous fat thickness; SFT100c = subcutaneous fat thickness adjusted to 100 kg of body weight; ABW = adult body weight.

Descriptive statistics for body size traits in adult *Curraleiro Pé-Duro* cattle are presented in Table 2. For height measurements, males exhibited mean WH and RH values of 116.2 cm and 119.5 cm, respectively. In females, the corresponding means were 110.1 cm for WH and 112.9 cm for RH.

Mean BL was 123.2 cm in males, ranging from 98 to 167 cm (Table 2). In females, the average BL was 113.6 cm, with values ranging from 85 to 147 cm. TC averaged approximately 170.9 cm in males and 152.8 cm in females. Mean TD was 63.0 cm and 58.0 cm for males and females, respectively.

TD/WH ratio averaged approximately 54.6% in males and 52.6% in females. For RA, males presented a mean value of 105.5°, ranging from 85.0° to 146.4°, whereas females exhibited a mean value of 97.2° (Table 2).

CV for body size traits, represented by the morphometric measurements, were all below 10% in the overall population, ranging from 4.7% to 9.7% (Table 2), indicating relatively low phenotypic variability for these traits.

Table 2 - Descriptive statistics of body size traits in adult *Curraleiro Pé-Duro* cattle.

Sex	Trait	N	Mean ± SD	Minimum	Maximum	CV (%)
Male	WH (cm)	142	116.2 ± 7.2	97.0	135.0	6.2
	RH (cm)	143	119.5 ± 6.6	100.0	136.0	5.5
	BL (cm)	142	123.2 ± 11.9	98.0	167.0	9.7
	TC (cm)	142	170.9 ± 16.2	131.0	216.0	9.5
	TD (cm)	142	63.0 ± 5.8	49.5	76.0	9.0
	TD/WH (%)	142	54.6 ± 2.9	47.6	63.9	5.2
	RA (degrees)	142	105.5 ± 9.4	85.0	146.4	8.9
Female	WH (cm)	951	110.1 ± 5.6	92.0	126.0	5.1
	RH (cm)	954	112.9 ± 5.5	95.0	135.0	4.7
	BL (cm)	951	113.6 ± 8.8	85.0	147.0	4.7
	TC (cm)	951	152.8 ± 11.9	106.0	186.6	4.7

TD (cm)	951	58.0 ± 4.5	42.0	74.0	7.8
TD/WH (%)	951	52.6 ± 2.8	44.7	63.8	5.3
RA (degrees)	951	97.2± 7.5	75.1	139.0	7.7

WH = withers height; RH = rump height; BL = body length; TC = thoracic circumference; TD = thoracic depth; TD/WH = thoracic depth-to-withers height ratio; RA = rump angle.

Ultrasound-measured carcass traits exhibited moderate heritability (Table 3), with values of 0.38 for REA and 0.40 for SFT, which indicate that a substantial proportion of the phenotypic variation observed in these traits is attributable to additive genetic effects, demonstrating their potential for genetic improvement through selection. After adjustment to 100 kg of body weight (REA100c and SFT100c), heritability estimates remained moderate, with values of 0.30 and 0.33, respectively. ABW exhibited a high heritability estimate of 0.45.

Table 3 - Posterior mean estimates of additive genetic, residual, and phenotypic variances, and heritability for carcass and body size traits in *Curraleiro Pé-Duro* cattle.

Trait	σ_α^2	σ_e^2	σ_p^2	h^2
REA	12.0	19.6	31.8	0.38
REA100c	2.4	5.7	8.1	0.30
SFT	0.4	0.7	1.1	0.40
SFT100c	0.3	0.6	0.9	0.33
ABW	619.0	768.8	1387.8	0.45
WH	12.9	10.6	23.4	0.55
RH	9.9	9.3	19.2	0.51
BL	10.3	23.2	33.6	0.31
TC	23.3	46.8	70.1	0.33
TD	4.6	4.3	8.9	0.51
TD/WH	1.8	5.3	7.1	0.25
RA	5.7	31.5	37.1	0.15

REA = ribeye area; REA100c = ribeye area adjusted to 100 kg of body weight; SFT = subcutaneous fat thickness; SFT100c = subcutaneous fat thickness adjusted to 100 kg of body weight; ABW = adult body weight; WH = withers height; RH = rump height; BL = body length; TC = thoracic circumference; TD = thoracic depth; TD/WH = thoracic depth-to-withers height ratio; RA = rump angle.

For body size traits, heritability estimates ranged from moderate to high (Table 3). Height-related measurements exhibited the highest estimates, with WH showing the greatest heritability (0.55), followed by RH (0.51). TD also displayed a high heritability estimate (0.51). TC and BL showed moderate heritability estimates of 0.33 and 0.31, respectively. The lowest estimates were observed for the TD/WH ratio (0.25) and RA (0.15).

Genetic correlations revealed distinct and informative patterns, as shown in Table 4. The correlation between REA and SFT was positive and strong (0.78), contrasting with the antagonistic relationship frequently reported in other

beef cattle breeds. This finding suggests a potentially unique adaptive strategy in *Curraleiro Pé-Duro* cattle, in which muscle development and energy reserve deposition may occur simultaneously in adult animals.

Muscling, represented by REA, exhibited strong positive genetic associations with measures of body volume and weight (Table 4), including TC (0.84), ABW (0.65), TD (0.65), and BL (0.54). In contrast, its genetic correlation with WH was essentially null (0.05). A similar pattern was observed for REA100c, which was strongly correlated with TD (0.88) and moderately correlated with BL (0.40), while exhibiting weak or negative associations with height-related traits (RH: 0.03; WH: −0.30).

Regarding carcass finish, SFT showed a positive moderate genetic correlation with ABW (0.59) (Table 4), indicating that body weight may serve as a useful predictor of energy reserves. SFT was also positively associated with body volume traits, particularly BL (0.63) and TD (0.54), as well as with rump conformation, represented by RA (0.80). After adjustment for body weight (SFT100c), correlations with body volume traits decreased to low-to-moderate magnitudes, ranging from 0.15 to 0.40.

ABW exhibited very strong positive genetic correlations with the principal measures of body volume and structural development (Table 4), particularly TC (0.90) and TD (0.87), reflecting its close relationship with overall body size. As expected, height traits (WH and RH) were almost perfectly genetically correlated (0.97) and showed strong associations with TC (0.82 and 0.70, respectively) and TD (0.90 and 0.80, respectively).

A detailed examination of the genetic correlations (Table 4) revealed additional structural relationships of interest. The carcass traits adjusted for body weight, REA100c and SFT100c, showed a strong positive genetic correlation (0.80), reinforcing the notion that relative muscling and carcass finish may be jointly expressed traits in this breed at the adult stage. In addition to its strong genetic association with SFT (0.80), RA also exhibited moderate genetic correlations with muscling (REA; 0.57) and ABW (0.65), highlighting its potential as an easily measured morphological indicator of productive performance.

Evidence of biological trade-offs was also observed. Body length showed negative genetic correlations with TC (−0.42) and RA (−0.30), suggesting the existence of distinct biological types within the breed. These relationships indicate that selection focused solely on increasing body length could inadvertently reduce thoracic circumference, an important trait associated with respiratory capacity and visceral volume.

The favorable, non-antagonistic genetic association between muscling and carcass finish, together with the observed correlation patterns involving body size traits, suggests that selection for improved beef production in *Curraleiro Pé-Duro* cattle can be achieved without compromising key adaptive characteristics, such as the maintenance of adequate body energy reserves (Table 4).

Phenotypic correlations presented in Table 4 generally reflected the same trends observed for genetic correlations, although with lower magnitudes. REA showed moderate phenotypic correlations with WH, ABW, and TC, ranging from 0.30 to 0.40. Notably, REA100c exhibited phenotypic correlations close to zero or slightly negative with most body size traits, particularly RH (−0.16), ABW (−0.14), and WH (−0.11), indicating that adjustment for body weight effectively removed much of the influence of body size on muscling. SFT displayed a strong phenotypic correlation with TD (0.70) and moderate correlations with ABW (0.52) and TC (0.43). In contrast, SFT100c showed a moderate negative phenotypic correlation with BL (−0.60).

Table 4 - Genetic correlations (above the diagonal) and phenotypic correlations (below the diagonal) among carcass and body size traits in adult *Curraleiro Pé-Duro* cattle.

Trait	REA	REA100c	SFT	SFT100c	ABW	WH	RH	BL	TC	TD	TD/WH	RA
REA	-	0.92	0.78	0.25	0.65	0.05	0.37	0.54	0.84	0.65	0.57	0.57
REA100c	0.50	-	0.90	0.80	0.30	-0.30	0.00	0.40	0.66	0.88	0.41	0.49
SFT	0.30	0.40	-	0.96	0.59	0.10	0.43	0.63	0.28	0.54	0.31	0.80
SFT100c	0.40	0.27	0.98	-	0.35	-0.18	-0.12	0.15	0.15	0.40	0.30	0.50
ABW	0.30	-0.14	0.52	0.20	-	0.80	0.60	-0.56	0.90	0.87	0.40	0.65
WH	0.40	-0.11	0.09	-0.15	0.03	-	0.97	0.62	0.82	0.90	0.18	-0.05
RH	0.18	-0.16	0.30	0.13	0.59	0.39	-	0.60	0.7	0.80	0.42	0.14
BL	0.10	-0.10	0.18	-0.60	0.40	0.39	0.34	-	-0.42	0.50	-0.26	-0.30
TC	0.40	-0.01	0.43	0.18	0.26	0.57	0.13	0.17	-	0.78	0.21	0.40
TD	0.10	0.06	0.70	0.24	0.74	0.45	0.60	0.21	0.20	-	0.40	0.16
TD/WH	0.12	0.05	0.30	0.23	0.50	0.06	0.42	0.17	0.36	0.7	-	0.70
RA	0.10	0.07	0.38	0.06	0.17	0.17	0.08	0.14	0.26	0.13	0.17	-

REA = ribeye area; REA100c = ribeye area adjusted to 100 kg of body weight; SFT = subcutaneous fat thickness; SFT100c = subcutaneous fat thickness adjusted to 100 kg of body weight; ABW = adult body weight; WH = withers height; RH = rump height; BL = body length; TC = thoracic circumference; TD = thoracic depth; TD/WH = thoracic depth-to-withers height ratio; RA = rump angle.

Discussion

The superiority of males for absolute ribeye area and adult body weight (Table 1) can be attributed to the anabolic effects of testosterone, which enhances protein synthesis and retention even at advanced ages (Berg and Butterfield 1976). However, the reversal observed after adjustment for body weight (REA100c), with females exhibiting higher values (23.5 cm^2) than males (20.4 cm^2), indicates that adult females displayed greater relative muscling when evaluated on a body weight-adjusted basis.

The REA values observed in the present study (Table 1) were lower than those commonly reported for specialized beef breeds, whose mean values often exceed 50 cm^2 at younger ages (Suguisawa et al. 2006; Climaco et al. 2011). This difference in absolute values is likely attributable to the smaller body size and lower mature weight characteristic of the *Curraleiro Pé-Duro* breed.

Because REA is inherently associated with body weight, animals with smaller skeletal structures and lower body weights tend to exhibit lower absolute REA values (Yokoo et al. 2015). However, when muscling was evaluated using the body weight-adjusted measure (REA100c), the values observed in this study (20.4 cm^2 for males and 23.5 cm^2 for females) were consistent with those reported in the literature. Nevertheless, the adjustment applied in the present study differs from previously reported approaches (Yokoo et al. 2015; Marestone et al. 2022). From a biological standpoint, this finding highlights that standardized carcass indices developed for larger-framed breeds may not be directly applicable to smaller genetic groups, emphasizing the need to account for breed-specific biometric characteristics when defining reference standards (Yokoo et al. 2015).

In absolute terms, SFT values were below the thresholds generally recommended by the beef industry (Pacheco et al. 2023). This result is likely associated with the production systems adopted on the evaluated farms, where animals were predominantly raised under grazing conditions. Fat deposition is the final major tissue accretion event during growth and requires a positive energy balance that is seldom achieved in extensive systems without intensive supplementation (Lawrie and Ledward, 2006). Similarly, De Faria et al. (2015) reported SFT values in polled Nellore cattle (2.3 mm) that were comparable to those observed in the present study.

Adjustment of SFT to a standardized body weight was performed to isolate the effects of body size and absolute weight. This approach enables the identification of animals capable of depositing adipose tissue despite having lower body weights and smaller body frames, while also reducing the influence of body weight and potential environmental or management differences among animals (Rosanova et al. 2025).

The high coefficients of variation observed for SFT indicate that fat deposition is likely the trait most sensitive to grazing management conditions. At the same time, this variability reveals the existence of individuals within the breed

306 possessing substantial genetic potential for carcass fat cover deposition (Yokoo et al. 2008). In contrast, the low
307 coefficients of variation observed for morphometric traits (CV < 10%) suggest remarkable uniformity in body structure
308 across the breed, despite differences in environmental and management conditions. These findings support the premise
309 that body size has not undergone substantial directional selection over time. Increasing body size may lead to greater
310 maintenance requirements and, consequently, reduce adaptability under tropical production conditions (Marestone et al.
311 2022).

312 Heritability estimates for REA100c and SFT100c remained moderate, although slightly lower than those
313 obtained for the corresponding unadjusted traits (Table 3). These results indicate that the capacity to deposit muscle and
314 fat tissue relative to body weight is itself a heritable characteristic rather than merely a consequence of increased body
315 size. Adjustments to a standardized body weight are important for carcass evaluation because they allow comparisons of
316 tissue deposition efficiency among animals of different ages and weights (Luchiari Filho 2000), facilitating the
317 identification of individuals capable of producing greater yields of high-value cuts and subcutaneous fat deposition at
318 lighter body weights (Suguisawa et al. 2013).

319 The heritability estimate for ABW (0.45) was classified as high (Table 3), indicating that 45% of the observed
320 phenotypic variation is attributable to additive genetic effects. From a production standpoint, direct selection for body
321 weight is expected to result in rapid genetic progress. However, selection focused exclusively on body weight may
322 increase maintenance requirements because of larger mature size (Marcondes et al. 2010). Menezes et al. (2022) reported
323 lower heritability estimates for adult weight in Caracu cattle (0.26), whereas Pedrosa et al. (2010) reported estimates
324 similar to those obtained in the present study (0.43).

325 The heritability estimates obtained for height traits (WH and RH) indicate that these characteristics are less
326 affected by environmental and nutritional fluctuations (Table 3). Pedrosa et al. (2010) reported lower heritability estimates
327 for rump height (0.35) than those observed here. Height traits generally exhibit substantial genetic variability in cattle
328 populations, allowing breeders to achieve rapid genetic progress when adjusting body size to meet the nutritional demands
329 of different production systems.

330 Because TC reflects both skeletal structure (rib cage development) and soft tissue deposition (muscle and fat), it
331 tends to exhibit greater residual variance than height measurements (Table 3). Boligon et al. (2008) reported that thoracic
332 circumference is a reliable indicator of body weight and overall body volume; however, its phenotypic expression is more
333 strongly influenced by nutritional status, which explains the larger environmental variance component observed (σ_e^2 =
334 46.8).

Thoracic depth is associated with animal vigor as well as cardiorespiratory and digestive capacity (Table 3). The high heritability estimate observed ($h^2 = 0.51$) suggests that selection for greater thoracic depth may favor animals with enhanced forage intake capacity (Rebouças et al. 2024).

The heritability estimate obtained for body length indicates that direct selection for this trait would result in moderate genetic gains (Table 3). According to Pacheco et al. (2005), traits associated with body length tend to be more sensitive to nutritional fluctuations during the post-weaning growth phase.

The genetic correlations between REA and body size traits (TC, TD, BL, and ABW) indicate that genes involved in growth also exert positive effects on muscling (Table 4). Consequently, direct selection for muscling is expected to result in animals with greater thoracic capacity and body length. The positive association with body weight further suggests that increases in muscle mass contribute directly to greater REA values.

The genetic correlations observed between muscling and stature traits revealed an interesting biological pattern, particularly for the relationships between REA and WH and between REA and RH (Table 4). The divergence in correlation estimates suggests that increased muscle deposition is largely independent of anterior skeletal growth. Furthermore, the correlation between REA and RH indicates that hindquarter height may be modestly associated with muscle development, possibly reflecting coordinated growth of the hindquarters, where rump structure provides support for the musculature associated with the most valuable commercial cuts.

The genetic correlation between REA100c and RH demonstrates that improvements in relative muscling can be achieved without increasing animal stature (Table 4). This relationship supports the possibility of increasing muscle density while maintaining moderate frame size. Such a strategy would help preserve production efficiency without increasing mature body size. Moreover, the use of adjusted traits contributes to the identification of animals capable of producing heavier carcasses while maintaining skeletal structures suited to their production environment (Suguisawa et al. 2006; Yokoo et al. 2008).

The strong positive genetic correlation observed between REA and SFT (0.78) suggests that some genes involved in muscle development may act concomitantly with those regulating subcutaneous fat deposition in adult animals (Table 4). This finding contrasts with studies reporting antagonistic genetic relationships between muscle and fat deposition (Suguisawa et al. 2013). Importantly, however, most reports of antagonism are based on evaluations conducted in younger animals, typically at yearling age. This discrepancy suggests that tissue deposition dynamics may change with physiological maturity and highlights the need for future studies evaluating these traits at standardized ages, such as weaning and yearling stages, in *Curraleiro Pé-Duro* cattle.

The genetic correlation observed between the adjusted carcass traits, REA100c and SFT100c, was also positive and strong (0.80) (Table 4). Animals adapted to resource-limited environments tend to exhibit a more balanced pattern of tissue deposition. In this context, subcutaneous fat deposition functions not only as thermal insulation or a late-stage energy reserve but also as a mechanism of metabolic homeostasis that accompanies muscle growth and serves as a dynamic thermoregulatory tissue (Schmidt-Nielsen 1997).

The genetic correlation between REA and RA (0.57) suggests that selection for increased muscling is associated with changes in rump conformation (Table 4). From a morpho-functional perspective, this result indicates that animals with greater muscular development tend to possess a skeletal structure capable of supporting increased tissue deposition, representing a favorable characteristic for carcass conformation and meat production.

SFT also exhibited a strong positive genetic correlation with RA (Table 4). This finding indicates that genes associated with a more pronounced rump structure are closely linked to the capacity for subcutaneous fat deposition. Although RA showed low heritability, making direct selection for this trait relatively inefficient, its strong positive genetic correlation with SFT, which exhibited moderate heritability (Table 4), suggests that indirect genetic progress can be achieved through selection for carcass finish.

These results may reflect pleiotropic genetic effects, whereby genes influencing rump conformation are also involved in regulating fat deposition. Consequently, selection aimed at increasing SFT is expected to promote favorable correlated responses in RA. Moreover, from a practical standpoint, RA assessment may serve as a useful phenotypic indicator of carcass finish and body condition (Pfeifer et al. 2018).

The analysis presented in Table 4 further revealed a moderate-to-strong positive genetic correlation (0.50) between SFT100c and RA. The persistence of this association after adjustment for body weight suggests that the relationship between rump conformation and carcass finish is largely independent of overall body size. Genetically, this finding indicates that genes associated with greater rump angulation may also influence finishing precocity and the animal's intrinsic efficiency in depositing energy reserves.

The genetic correlations observed between ABW and SFT indicate a favorable association between these traits (Table 4). Direct selection for increased body weight is therefore expected to result in correlated genetic gains in fat thickness among adult animals. Once the metabolic demands associated with muscle growth decline, nutrient partitioning shifts toward lipogenesis, making body weight a useful predictor of fat cover. Unlike younger animals, in which body weight is primarily associated with carcass growth and slaughter performance, the relationship between body weight and fatness in adults reflects the status of body energy reserves (Ojo et al. 2025). Accordingly, animals with superior genetic merit for fat deposition are likely to maintain adult body weight more consistently under periods of nutritional restriction.

In mature animals, tissue dynamics are largely associated with physiological finishing rather than growth. Therefore, breeding objectives should not focus exclusively on maximizing mature body weight but rather on identifying animals capable of maintaining adequate subcutaneous fat thickness while retaining moderate mature size, thereby improving efficiency under pasture-based production systems (Hickson et al. 2021; Honig et al. 2022; Ojo et al. 2025).

The genetic correlations between height traits (WH and RH) and SFT were low in magnitude (Table 4). Larger-framed animals tend to be later maturing with respect to fat deposition because nutrients are preferentially allocated to skeletal and muscular growth. Consequently, selection focused exclusively on increased stature may increase the age required to achieve adequate carcass finish, potentially reducing production efficiency (Yokoo et al. 2009).

The strong genetic correlation between TD/WH ratio and RA (0.70) indicates a close genetic association between these traits, suggesting that they are largely influenced by additive genetic effects (Table 4). The height-to-depth relationship is commonly associated with biological precocity and functional efficiency in beef cattle (Montagner 2010; Sanches et al. 2021).

Phenotypic correlations between carcass and body size traits generally followed the same pattern observed for genetic correlations, although with lower magnitudes (Table 4). These results suggest that the biological processes underlying phenotypic expression are largely governed by the same factors responsible for the genetic associations; however, environmental variation attenuates the observable relationships among traits. The moderate-to-high heritability estimates and favorable genetic correlations observed in this study reinforce the value of incorporating genetic information into selection decisions aimed at improving productive performance in *Curraleiro Pé-Duro* cattle (Ojo et al. 2025).

Conclusions

The carcass and body size traits evaluated in *Curraleiro Pé-Duro* cattle exhibited sufficient additive genetic variability to support their inclusion in breding programs. The favorable positive association observed between muscling and carcass finish indicates that selection can effectively promote simultaneous genetic gains in these economically important traits. From a breeding perspective, this finding demonstrates that muscle development and fat deposition occur concomitantly in adult animals, enabling balanced genetic progress in both carcass yield and body energy reserves.

The genetic correlation patterns identified in this study reveal a coherent and informative morphological architecture for the *Curraleiro Pé-Duro* breed. The observation that muscling (REA) is genetically associated with body volume and weight, but not with stature (WH), provides a practical guideline for selection programs, indicating that greater muscularity can be achieved without necessarily increasing animal height.

The negative genetic correlation between body length and thoracic circumference suggests the existence of distinct biological types within the breed (long-bodied and compact animals), which should be strategically considered when developing multidimensional selection indices, which by exploiting the favorable association between muscling and fat deposition, can simultaneously direct body conformation preserving the adaptive attributes and biological efficiency that constitute the unique genetic heritage of the *Curraleiro Pé-Duro* breed.

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Statements and Declarations

Funding

This work was supported by National Council for Scientific and Technological Development (CNPq), CNPq/MCTI No. 10/2023 - Category B.

The Article Processing Charge (APC) for this publication was funded by the Coordination for the Improvement of Higher Education Personnel - CAPES (ROR identifier: 00x0ma614). For the purpose of open access, the authors have applied a Creative Commons Attribution (CC BY) license to any Author Accepted Manuscript version arising from this submission.

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Alan Oliveira do Ó, Geraldo Magela Cortes Carvalho, Alexandre Floriani Ramos, Natanael Pereira dos Santos, Gleyson Vieira dos Santos, Luiz Antonio Silva Figueiredo Filho, Natália Pereira de Morais and José Lindenberg Rocha Sarmento. The first draft of the manuscript was written by Alan Oliveira do Ó and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.