



## Genotype by environment interaction in ultrasound carcass traits and growth of Hereford and Braford cattle

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**ABSTRACT:** In beef cattle breeding programs, various selection criteria have been proposed and employed with the aim of improving traits related to carcass composition and the quality of the final product, meat. However, the importance of genotype by environment interaction (G×E) for such traits is still not well understood. Our objectives were: 1) to investigate the importance of G×E on ultrasound carcass traits, growth and visual scores and 2) to estimate the genetic correlation of ultrasound carcass traits with growth and visual scores taking into account the G×E in Hereford and Braford cattle. A multiple-trait reaction norm model was fitted to the field records of 37,948 animals. With the exception of postweaning average daily weight gain (ADG), the G×E can lead to important changes in the ranking of estimated breeding values of sires across environments for all traits. Thus, models that consider heterogeneity of genetic variances along an environmental gradient may be considered more appropriate for genetic evaluations of animals reared under conditions similar to the present study. Based on estimates of genetic correlation, the quality of visual scores or ADG as indicators of carcass quality assessed by ultrasonography is dependent on the production environment.

**Key words:** beef cattle, fat thickness, genetic correlation, *longissimus dorsi*, reaction norm, visual score.

### Interação genótipo x ambiente sobre as características de carcaça e crescimento de bovinos das raças Hereford e Braford

**RESUMO:** Nos programas de melhoramento de bovinos de corte, diversos critérios de seleção têm sido propostos e utilizados com o objetivo de melhorar as características relacionadas à composição da carcaça e a qualidade da carne. Por outro lado, a importância da interação genótipo ambiente (G×E) para tais características ainda é pouco conhecida. Nossos objetivos foram: 1) investigar a importância da G×E nas características de carcaça avaliadas por ultrassonografia, crescimento e escores visuais e 2) estimar a correlação genética de características de carcaça com crescimento e escores visuais levando em consideração a G×E para bovinos Hereford e Braford. Um modelo de norma de reação multivariadas foi ajustado aos dados de 37.948 animais. Com exceção do ganho de peso diário médio pós-desmama (GMD), a G×E pode levar a mudanças importantes na classificação dos valores genéticos estimados de touros nos diferentes ambientes para todas as características. Assim, modelos que consideram a heterogeneidade de variâncias genéticas ao longo do gradiente ambiental podem ser considerados mais apropriados para avaliações genéticas de animais criados em condições semelhantes às do presente estudo. Com base nas estimativas de correlação genética, a qualidade dos escores visuais ou GMD como indicadores de qualidade de carcaça avaliados por ultrassonografia é dependente do ambiente de produção.

**Palavras-chave:** bovinos de corte, correlação genética, escore visual, espessura de gordura, *longissimus dorsi*, norma de reação.

## INTRODUCTION

In beef cattle breeding, various selection criteria have been proposed and utilized to enhance traits related to carcass composition and the quality of the final product, meat. The literature reports a significant genetic association between visual scores and ultrasound carcass traits (YOKOO et al., 2009; TORAL et al., 2011). Visual scores are considered

a cost-effective and straightforward, though less precise, alternative for incorporating carcass composition measurements into genetic evaluation schemes (JOHNSTON et al., 2003).

Favorable genetic associations have been observed among traits related to carcass composition, such as longissimus muscle area and backfat thickness, with growth traits like body weight, weight gain, and scrotal circumference (MOSER et al.,

1998; YOKOO et al., 2010; CAETANO et al., 2013). However, there is a wide range of genetic correlation estimates reported in the mentioned studies. This variation is likely due to differences in management practices, nutrition, production environments, and gene-environment interactions. The latter, commonly referred to as genotype by environment interaction (G×E), signifies that genotypes and environments interact mechanistically throughout an organism's development to shape its phenotype. At the population level, it indicates the degree of non-parallelism among reaction norms, resulting in a statistical G×E effect (PIGLIUCCI, 2005).

The G×E is a crucial factor to consider in genetic evaluations of beef cattle since the genetic merit of animals can change based on environmental variations. However, little is known about the effects of G×E on traits related to beef cattle carcass composition. In large countries like Brazil, which exhibit a wide range of climates, landscapes, and production systems, significant G×E effects are likely to occur, as documented by CARDOSO et al. (2011), SANTANA et al. (2014), and CARVALHO FILHO et al. (2022). Therefore, our objectives were as follows: 1) to investigate the importance of G×E on ultrasound carcass traits, growth, and visual scores, and 2) to estimate the genetic relationship of ultrasound carcass traits with growth and visual scores, accounting for G×E in Hereford and Braford cattle.

## MATERIALS AND METHODS

Animal Care Committee approval was not obtained for this study as all the analyses were performed using pre-existing databases. All the animals included in this study were managed in accordance with the Recommended Code of Practice for the Care and Handling of Farm Animals from the Brazilian Ministry of Agriculture and Livestock (MAPA, Brasília, DF, Brazil).

## Data

The traits considered in this study were longissimus muscle area (LMA), backfat thickness (BFT), postweaning average daily weight gain (ADG), scrotal circumference (SC), visual scores of conformation (CON), precocity (PRE), muscling (MUS), and size (SIZ) of Hereford and Braford cattle. The dataset comprised field records of 37,948 animals (Table 1), encompassing purebred animals (24,174 purebred Hereford and no purebred Nelore with records), Bradford cattle (36,314 animals with breed composition close to 5/8 Hereford), and other Hereford-Nelore crossbred animals (25,432). These animals were born between 1991 and 2013 and were raised in 37 distinct Brazilian herds situated in tropical and subtropical regions (latitude between 19°S and 31°S). They were reared under heterogeneous production systems primarily based on pasture.

The LMA (cm<sup>2</sup>) and BFT (mm) were assessed with the use of ultrasound and specific software equipment in the region between the 12th and 13th ribs of the animals at yearling age (at around 550 days). ADG was measured as the weight gain per day (kg/day) from the weaning (at around 205 days of age) to yearling age. Yearling scrotal circumference (SC) was measured at the widest point of the scrotum using an appropriate metric tape in centimeters. The CON is an estimate of the amount of meat in the carcass based on muscling, depth and especially on body length. The PRE is a measure of the animal's ability to reach a minimum level of finishing with a non-elevated body weight. MUS represents the development of muscle mass as a whole. SIZ is mainly determined by body length, depth of ribs and height of the animal. The visual scores were individually attributed to each animal using a method that evaluates animals in relation to their herd management group, i.e., animals of similar age (yearling) and reared under the same environmental

Table 1 - Description of the data set for longissimus muscle area (LMA), backfat thickness (BFT), postweaning average daily weight gain (ADG), scrotal circumference (SC), visual scores of conformation (CON), precocity (PRE), muscling (MUS) and size (SIZ) of Hereford and Braford cattle.

	LMA (cm <sup>2</sup> )	BFT (mm)	ADG (kg/day)	SC (cm)	CON (un <sup>*</sup> )	PRE (un <sup>*</sup> )	MUS (un <sup>*</sup> )	SIZ (un <sup>*</sup> )
Animals in the pedigree file, n	17,503	17,322	55,887	27,829	57,626	57,652	57,646	47,881
Animals with record, n	8,514	8,403	32,498	11,620	33,660	33,682	33,679	27,790
Sires with progeny record, n	255	253	884	602	895	895	895	764
Dams with progeny record, n	6,075	6,001	21,740	9,544	22,417	22,427	22,425	18,326
Contemporary groups, n	510	510	2,203	830	2,055	2,055	2,055	1,774
Mean of the trait	53.19	2.44	0.43	31.12	3.36	3.34	3.29	3.27
Standard deviation of the trait	20.38	1.14	0.20	3.88	0.97	1.00	1.01	0.97

\* visual scores on a scale of 1 to 5.

conditions. Scores ranging from 1 to 5 were attributed to animals by trained personnel.

#### Contemporary groups and quality control of data

The contemporary groups (CG) were formed by the herd (at weaning and yearling), management groups at yearling, year of birth, and sex. Records of animals in CG with fewer than 5 animals, CG with all progeny of a single sire, sires with fewer than 3 progeny records, records of animals with unknown sire and dam, and data exceeding 3.5 standard deviations above or below the mean of the respective CG were excluded (Table 1).

#### Environmental gradient

The environmental gradient was defined based on solutions of CG (without the effect of sex) for the ADG. At this stage of the study, sex was considered as a simple and individual classificatory effect in the model. The CG solutions for ADG were chosen because they represent the conditions of management, nutrition and climate to which the animals of the present study were submitted. The CG solutions were obtained in a previous analysis through a single-trait standard animal model. Descriptive statistics of the traits and distribution of records according to the environmental gradient are shown in table 2. Some results were presented using

the terms unfavorable, intermediate and favorable, which corresponded to environments where the CG solutions of ADG were < 0.15, between 0.30 and 0.45, and > 0.60 kg/day, respectively.

#### Model

The model for all traits included the respective fixed effects of CG, age of dam at calving in years (2 to 12), and the linear covariates: age of animal at recording (in days), individual and maternal breed composition (percentage of Hereford genes), individual and maternal heterozygosis. For ADG, the model additionally included the age of animal at weaning and age of animal at yearling as linear covariates. Five four-trait analyzes were carried out (LMA, BFT, and ADG were included in all analyzes together with SC, PRE, CON, MUS or SIZ). The estimated parameters of the traits were calculated as the average of the five analyzes. The multiple-trait random regression animal model (reaction norm model) adopted can be described as follows:

$$y_{ijkm} = \mu + SF, h_k + l_i + S_j, h_k + fixed_m + e_{ijkm}$$

where  $y_{ijkm}$  is the record for the trait  $i$  of animal  $j$  in environment  $k$  of systematic environmental effects  $m$ ;  $\mu$  is the intercept for the "fixed" regression;  $SF$ ,  $h_k$  is the fixed coefficient of a regression of  $y$  on  $h_k$  (environment  $j$ , defined to be CG solutions of ADG);  $l_i$  is the random intercept (level) of the reaction norm

Table 2 - Mean (standard deviation) [number of records] for longissimus muscle area (LMA), backfat thickness (BFT), postweaning average daily weight gain (ADG), scrotal circumference (SC), visual scores of conformation (CON), precocity (PRE), muscling (MUS) and size (SIZ) of Hereford and Braford cattle according to the environment gradient.

Trait	-----Environment gradient (kg/day) <sup>#</sup> -----				
	< 0.15	≥ 0.15 to < 0.30	≥ 0.30 to < 0.45	≥ 0.45 to < 0.60	> 0.60
LMA (cm <sup>2</sup> )	35.78 (6.44) [867]	41.91 (7.66) [2,461]	49.98 (9.63) [2,518]	61.15 (13.92) [1,871]	66.66 (11.01) [797]
BFT (mm)	1.83 (0.62) [866]	2.17 (0.97) [2,404]	2.56 (1.17) [2,512]	2.83 (1.33) [1,863]	2.70 (1.09) [758]
ADG (kg/day)	0.22 (0.06) [6,974]	0.35 (0.09) [11,239]	0.51 (0.09) [7,854]	0.65 (0.10) [4,737]	0.81 (0.14) [1,694]
SC (cm)	25.92 (3.11) [641]	28.74 (3.44) [2,407]	30.93 (3.28) [3,567]	32.61 (3.20) [3,530]	34.19 (3.01) [1,475]
CON (un <sup>*</sup> )	3.26 (1.01) [7,876]	3.35 (0.96) [11,415]	3.38 (0.97) [7,912]	3.44 (0.97) [4,753]	3.54 (0.93) [1,704]
PRE (un <sup>*</sup> )	3.19 (1.00) [7,877]	3.34 (0.97) [11,416]	3.40 (1.02) [7,912]	3.41 (1.03) [4,773]	3.48 (0.96) [1,704]
MUS (un <sup>*</sup> )	3.11 (1.03) [7,875]	3.28 (0.98) [11,415]	3.37 (1.03) [7,913]	3.42 (1.04) [4,773]	3.54 (0.94) [1,703]
SIZ (un <sup>*</sup> )	3.17 (0.99) [6,007]	3.26 (0.96) [9,338]	3.29 (0.98) [6,920]	3.36 (0.99) [4,070]	3.46 (0.88) [1,455]

\*visual scores on a scale of 1 to 5; <sup>#</sup>Contemporary group solutions of ADG.

of animal  $i$ ;  $S_j$ ,  $h_k$  is the random linear coefficient (slope) of a random regression of  $y$  on  $h_k$ ;  $fixed_m$  is the set of systematic environmental effects (CG and covariates described above);  $e_{ijkm}$  is the random residual effect. Residual variance was assumed to be homogeneous across the environmental gradient. The fixed and random regressions on  $h_k$  were modeled with orthogonal Legendre polynomials. The general model can be written in matrix form as:

$$y = Xb + Za + e,$$

where  $y$  is the vector of observations;  $b$  is the vector of systematic environmental effects (CG and covariates);  $a$  is the vector of random regression coefficients for additive genetic effects;  $e$  is the vector of random residual effects, and  $X$  and  $Z$  are incidence matrices corresponding to the observations for fixed effects and random additive genetic effects, respectively. The model adopted was based on the following assumption:

$$V \begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} K_a \otimes A & 0 \\ 0 & R \otimes I_n \end{bmatrix},$$

where  $K_a$ , is a  $8 \times 8$  (co)variance matrix between random regression coefficients for additive genetic effects;  $\otimes$  is the Kronecker product between matrices;  $A$  is the relationship matrix;  $R$  is a  $4 \times 4$  (co)variance matrix containing the residual variances, and  $I$  is an identity matrix for  $n$  records.

The (co)variance components were obtained using Gibbs sampling. The analyzes were performed with the GIBBS2F90 program (MISZTAL et al., 2002). The analyzes consisted of single chains of 300,000 cycles, with a burn-in period of 50,000 cycles and a thinning interval of 25 cycles. Thus, 10,000 samples were effectively used for final inferences. To assess the importance of incorporation G×E effects in the genetic evaluation model, we compared the reaction norm model to a standard animal model (maintaining the same model effects as the reaction norm model, except for the CG regressions). The deviance information criterion (DIC) was adopted for this purpose. The DIC comprises a measure of model fit to the data and the corresponding complexity of the model, referred to as the effective number of parameters (pD) (SPIEGELHALTER et al., 2002). Smaller DIC values indicated a better-fitting model.

## RESULTS AND DISCUSSION

The phenotypic mean of all traits increased as the environmental gradient became more favorable (Table 2). Based on the data presented in tables 1 and 2, ADG, LMA, and BFT exhibited increases in response

to the environmental gradient, with increments in relation to the overall mean of the trait of up to 88, 25, and 16%, respectively. In contrast, SC and visual scores showed an increase in performance along the environmental gradient, relative to the overall mean of each trait, ranging from 4 to 10%.

Despite the greater complexity of the reaction norm model, it has been demonstrated to be a better fit for the data when compared to the regular animal model, as shown in table 3. In this regard, models considering the genotype-environment interaction G×E effect can be considered more suitable for genetic evaluations of Hereford and Braford cattle raised under the conditions of the present study. This finding agrees with the results reported by CARDOSO et al. (2011) for post-weaning gain of Hereford cattle.

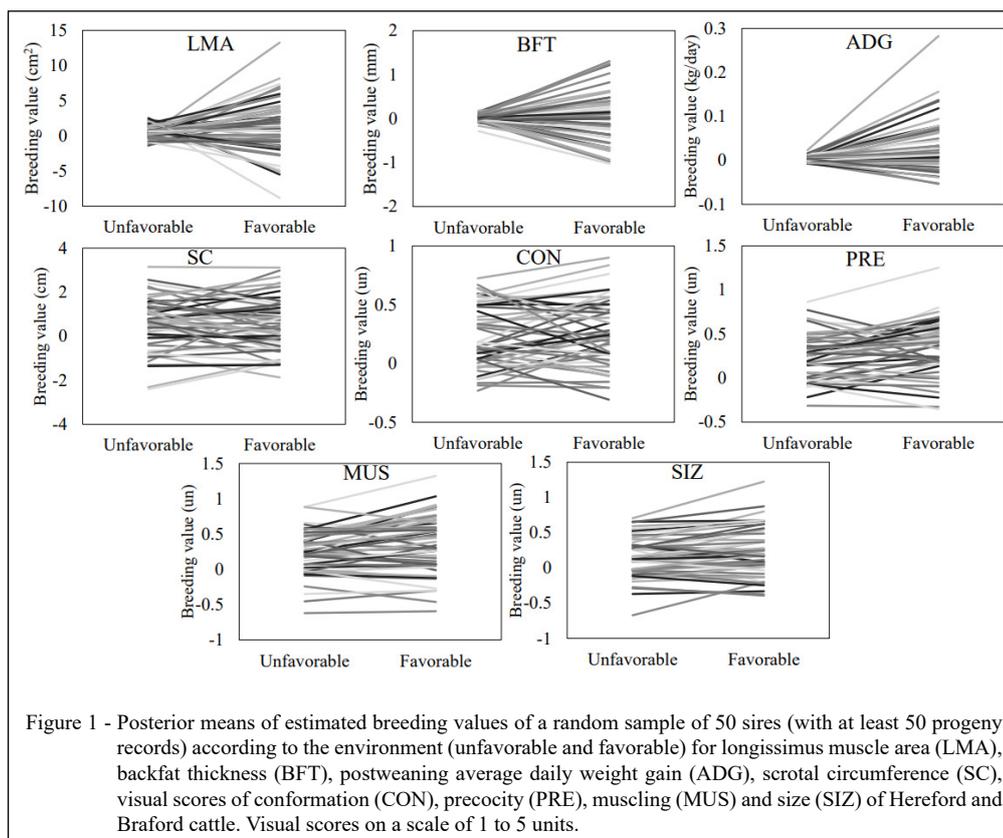
The magnitude of the G×E effect, quantified as the slope/intercept ratio, was higher for LMA, BFT, and ADG with values of 0.56, 0.31, and 0.31, respectively. For SC, CON, MUS, PRE, and SIZ, the magnitude of G×E was equal to 0.21, 0.19, 0.12, 0.14, and 0.09, respectively. The genetic correlation between the slope and intercept of the reaction norms was strong and positive for LMA, BFT, and ADG (0.82, 0.94, and 0.99, respectively) and weak or even negative for SC, CON, MUS, PRE, and SIZ (-0.16, 0.12, 0.35, 0.40, and 0.29, respectively). In general, high genetic correlations between the intercept and slope of reaction norms are commonly associated with a scale effect for G×E. In contrast, low correlations are associated with a reranking of estimated breeding values along the environmental gradient. The reaction norms of the animals for the studied traits illustrate this scenario (Figure 1).

The overall mean of heritability estimates and corresponding standard deviation (SD) for the

Table 3 - Comparison of the reaction norm model (RN) with a regular animal model (MA). The comparison was made through the difference between the deviance information criterion (DIC) and the effective number of parameters (pD) in multi-trait analyses.

Traits considered in the analysis	DIC (RN - MA)	pD (RN - MA)
LMA, BFT, ADG, SC	-24147.2	+1913.6
LMA, BFT, ADG, C	-22390.2	+5182.1
LMA, BFT, ADG, P	-19022.3	+5596.6
LMA, BFT, ADG, M	-19955.8	+4083.7
LMA, BFT, ADG, S	-21318.6	+4773.4

LMA = longissimus muscle area, BFT = backfat thickness, ADG = postweaning average daily weight gain, SC = scrotal circumference, CON = visual scores of conformation, PRE = precocity, MUS = muscling, SIZ = size.

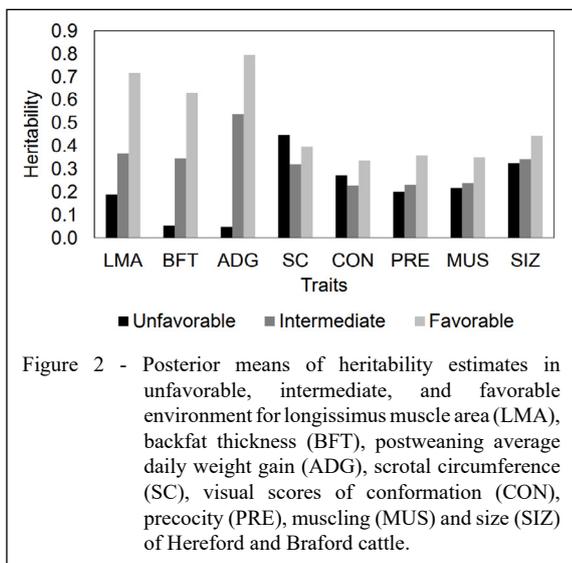


environmental gradient was 0.39 (0.20), 0.34 (0.18), 0.49 (0.13), 0.36 (0.19), 0.26 (0.09), 0.25 (0.09), 0.25 (0.08), and 0.36 (0.10) for LMA, BFT, ADG, SC, CON, PRE, MUS and SIZ, respectively. Heritability estimates displayed substantial variation along the environmental gradient, especially for LMA, BFT, and ADG (Figure 2). For all the traits, except SC, higher heritability estimates were obtained in favorable environments.

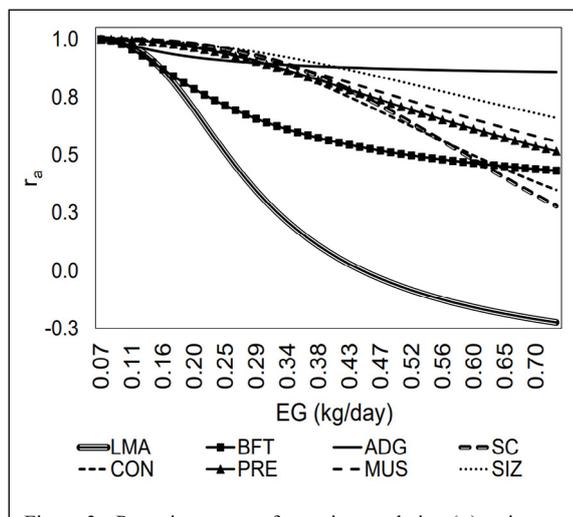
The genetic correlation between performance in an unfavorable environment and the other environments are illustrated for each trait in figure 3. In general, ultrasound carcass traits exhibited lower genetic correlation along the environmental gradient compared to the other traits. The genetic correlation between extreme opposite environments for LMA reached an estimate of -0.22 (SD = 0.12). Estimates of genetic correlations between performance in extreme opposite environments reached values between 0.28 (SD = 0.15) e 0.43 (SD = 0.22) for SC and CON, between 0.50 (SD = 0.23) and 0.65 (SD = 0.21) for PRE, MUS and SIZ and of 0.86 (SD = 0.27) for ADG. On average, the genetic correlations within traits among environments were 0.24 (SD =

0.36), 0.62 (SD = 0.18), 0.90 (SD = 0.04), 0.75 (SD = 0.12), 0.75 (SD = 0.22), 0.79 (SD = 0.16), 0.82 (SD = 0.14), and 0.66 (SD = 0.11) for LMA, BFT, ADG, SC, CON, PRE, MUS and SIZ, respectively. In agreement with the findings presented here, HAY & ROBERTS (2018) observed genetic correlations below unity for ADG, BFT, and intramuscular fat percentage at the 12th rib in composite beef cattle subjected to different nutritional environments during gestation.

The overall mean (minimum - maximum) of the genetic correlation estimates across environments between LMA and ADG, SC, CON, PRE, MUS and SIZ were 0.22 (-0.03 - 0.27), 0.15 (0.07 - 0.34), 0.43 (0.25 - 0.60), 0.37 (0.24 - 0.50), 0.51 (0.28 - 0.78) e 0.30 (0.19 - 0.53), respectively (Figure 4). For BFT, these estimates were 0.17 (0.11 - 0.31), -0.07 (-0.19 - 0.29), 0.03 (-0.10 - 0.10), 0.26 (0.21 - 0.38), 0.08 (-0.04 - 0.53) and 0.02 (0.01 - 0.19), respectively. In general, visual scores were more genetically associated with LMA than with BFT. As depicted in figure 4, the strongest genetic associations were observed between LMA and CON, especially between LMA and MUS along the environmental gradient. BFT showed a stronger genetic correlation



with PRE throughout the environmental gradient. For BFT, a strong genetic correlation was also observed with MUS, but primarily in unfavorable environments. While the genetic correlation between ADG and LMA tended to be stronger and reached an asymptotic value in intermediate and favorable environments, the genetic correlation between ADG and BFT tended to be weaker in these environments.

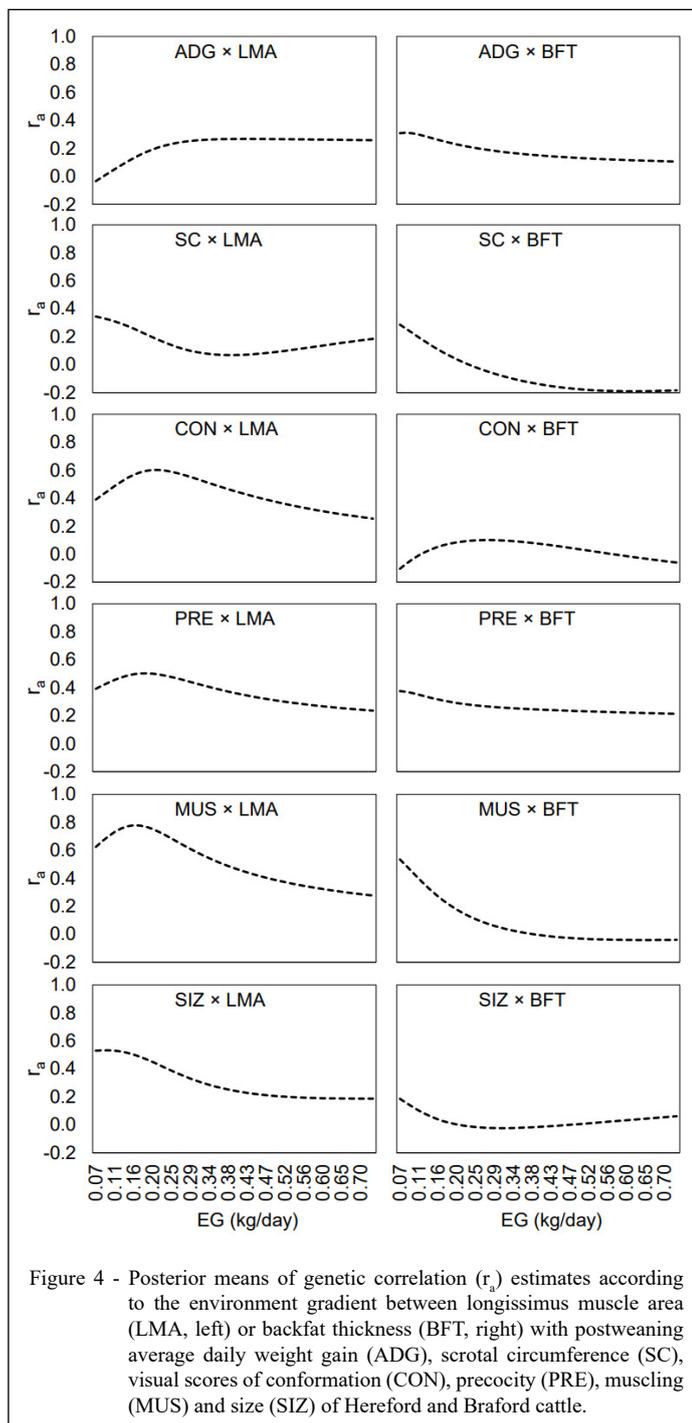


The genetic correlation between LMA and SC was stronger in extreme environments and lower in intermediate environments. The correlation between BFT and SC tended to be weaker or close to zero as the environment became more favorable. In general, the genetic correlation between LMA or BFT and visual scores followed a similar trend of reduction in favorable environments.

This study has demonstrated significant phenotypic and genetic variation for most of the traits along the environmental gradient. LMA, BFT, and ADG exhibited a greater magnitude of  $G \times E$  effect compared to the visual scores or SC. However, especially for ADG, the genetic correlations between environments were consistently above 0.9 (Figure 3), indicating minimal reranking of animals along the environmental gradient (Figure 1).

For LMA, BFT, and ADG, the  $G \times E$  effect was primarily of the scale type, aligning with the findings of CARDOSO et al. (2011) for adjusted postweaning weight gain of Hereford cattle raised in production environments like those in this study. Despite the high correlation between the intercept and slope of reaction norms for LMA,  $G \times E$  may still result in some reranking of sires between environments. Therefore, the impact of  $G \times E$  on carcass traits of Hereford and Braford cattle should not be overlooked in genetic evaluations. In contrast, Ibi et al. (2005) found no evidence of  $G \times E$  on LMA, rib thickness, subcutaneous fat thickness, and marbling score at the 6th- to 7th-rib of Japanese Black cattle between regions or management systems, with genetic correlations within traits higher than 0.84. JEYARUBAN et al. (2009) also found no evidence of  $G \times E$  on ultrasound carcass traits of Angus cattle raised in Australia. It's worth noting that in the study by JEYARUBAN et al. (2009), animals from only two Australian states (Victoria and Queensland) were considered, which may indicate more homogeneous management practices, nutrition, and climatic conditions compared to those in Brazil. In a study involving temperate and tropically adapted beef cattle breeds in Australia, JOHNSTON et al. (2003) reported high genetic correlations for carcass traits measured by ultrasound in different rearing conditions (market weight, finishing regime, or geographic region), suggesting that  $G \times E$  had no major impact on bull rankings.

The differences in the observed  $G \times E$  effects for carcass traits in this study compared to other studies can be partly attributed to variations in population backgrounds, data structures, production environments, and  $G \times E$  modeling approaches.



Despite the relatively lower magnitude of the G×E effect, it should be considered important in the genetic evaluations of visual scores for Hereford and Braford cattle. This importance is underscored by the low genetic correlations observed between opposing environments and the significant crossing

of reaction norms of sires along the environmental gradient (Figure 1). JOHNSTON et al. (2003) found a genetic correlation of muscle score for temperate breeds in Australia that depended on the finishing regime. SANTANA et al. (2014) obtained genetic correlations ranging from 0.18 to 0.80 for yearling

muscling scores of Tropical composite cattle in different regions of Brazil. Based on these results, SANTANA et al. (2014) recommended conducting genetic analyses on a regional basis or incorporating the G×E effect into the statistical model to enable the appropriate evaluation and comparison of animals. HAY & ROBERTS (2018) found genetic correlations of up to 0.65 for ADG, yearling weight, and BFT in composite beef cattle and concluded that G×E can impact the genetic parameters of that population. The effects of G×E on carcass traits measured by ultrasound and on visual scores in beef cattle have not been extensively documented in the literature, making it challenging to draw direct comparisons with existing studies. This highlighted the need for more research in this area to better understand the extent and implications of G×E on these traits in beef cattle.

The posterior means of heritability estimates for ADG and visual scores (CARDOSO et al., 2011; TORAL et al., 2011; CARVALHEIRO et al., 2019), SC (JEYARUBAN et al., 2009; YOKOO et al., 2010) and BFT and LMA (YOKOO et al., 2009; TORAL et al., 2011; GORDO et al., 2012) reported in this study align with values found in the literature for beef cattle raised under similar environmental conditions. The heritability estimates for all traits in most environments exhibited moderate to high magnitudes, indicating the potential for satisfactory responses to selection (Figure 2). However, it's evident that there is heterogeneity in the additive genetic variances along the environmental gradient. In practical terms, this discovery suggested that the responses to selection may vary depending on the production environment of the animals. This emphasized the importance of considering G×E in genetic evaluations and selection strategies for beef cattle.

Genetic correlations between LMA and BFT with other traits exhibited notable variation across the environmental gradient. In most environments, ADG can be considered a modest indicator of carcass quality in terms of both LMA and BFT. ADG is one of the most common selection criteria in beef cattle breeding programs. Selecting for ADG is expected to produce modest but favorable selection responses in both LMA and BFT across the majority of environments. HIROOKA et al. (1996) reported a genetic correlation of 0.24, similar to the one found in this study, between ADG and LMA in Japanese Brown cattle. TORAL et al. (2011) noted genetic correlations near zero between LMA or BFT and ADG in Hereford and Braford cattle. It is worth

mentioning that both HIROOKA et al. (1996) and TORAL et al. (2011) employed a standard animal or sire model for their analyses, overlooking G×E effect.

The genetic association between LMA or BFT and SC remained relatively weak across the environmental gradient, particularly between BFT and SC. Only in unfavorable environments did the genetic relationship between these traits strengthen. YOKOO et al. (2010) also reported weak genetic correlations (below 0.28) between LMA or BFT and SC measured at 365, 450, and 550 days of age in Nelore cattle. These authors concluded that selecting for carcass traits should not result in important alterations in the SC of the animals.

The visual scores CON, PRE, MUS, and SIZ have demonstrated themselves as modest or reasonable indicators of carcass quality in Hereford and Braford cattle. Consequently, it is expected that, in many instances, the direct response to selection for LMA or BFT will be more substantial than the indirect selection through visual scores. While ultrasound carcass traits offer objective measurements of carcass quality, they are specific and precise. Conversely, visual scores involved an assessment of various areas of the animal carcass, providing a broader selection criterion. From this perspective, visual scores and ultrasound carcass traits could be viewed as distinct yet complementary selection criteria.

Consistent with the findings of the present study, BONIN et al. (2015) observed genetic correlations between LMA and BFT with visual scores CON, PRE, MUS, and frame ranging from 0.16 to 0.39 for Nelore cattle. These authors concluded that selecting for carcass visual scores may result in lower genetic progress compared to selection based on ultrasound carcass traits. YOKOO et al. (2009) reported genetic correlations of LMA and BFT with PRE and MUS between 0.38 and 0.61 in Nelore cattle. Based on these estimates, YOKOO et al. (2009) suggested that selecting for PRE and MUS should promote genetic changes in the same direction for LMA and BFT. TORAL et al. (2011) provided genetic correlation estimates between LMA or BFT with CON, PRE, and MUS ranging from 0.04 to 0.48 for Hereford and Braford cattle. In Nelore cattle, GORDO et al. (2012) obtained genetic correlations similar to those found in this study for LMA or BFT with PRE and MUS (0.33 to 0.44). Based on these estimates, GORDO et al. (2012) reported that selecting for MUS should lead to an increase in LMA without compromising BFT.

The posterior mean estimates of genetic correlations between LMA or BFT and visual scores or growth traits exhibited significant variation along

the environmental gradient. This variability highlights how the production environment significantly affects the utility of visual scores or ADG as genetic indicators of carcass quality. To illustrate this environmental dependence, consider the genetic correlation estimate between BFT and MUS, which was 0.04 as reported by TORAL et al. (2011) when employing a standard animal model for the same population studied here. In contrast, the estimates in the present study ranged from -0.03 to 0.53, demonstrating the substantial impact of G×E on carcass traits. These findings emphasized the importance of models that account for heterogeneity in additive genetic variances across the environmental gradient, particularly in the context of genetic evaluations for animals raised under conditions similar to the present study.

## CONCLUSION

Except for ADG, G×E can result in shifts in the rankings of estimated breeding values of sires across environments for all studied traits.

Models that consider heterogeneity of genetic variances along an environmental gradient may be considered more appropriate for genetic evaluations of animals raised in conditions resembling the present study.

The quality of visual scores and ADG as indicators of carcass quality, assessed through ultrasonography, is dependent upon the production environment.

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## DECLARATION OF CONFLICT OF INTEREST

The authors declare that there is no conflict of interest associated with this publication.

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