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# Genotype × environment interaction in milk traits of Guzerá cattle using reaction norm models

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**ABSTRACT -** This study aimed to evaluate genotype × environment (G×E) interactions in Guzerá breed animals for 305-day first-lactation cumulative yields (kg) of milk (MY305), fat (FY305), and protein (PY305). We used 6823 records of MY305, 2466 records of FY305, and 1870 records of PY305. The contemporary groups (CG) were created considering herd and year of calving. The analyses were performed in two steps. In the first step, environmental effects on phenotypes were estimated by using a multi-trait model ignoring G×E interactions. In the second step, G×E interactions were evaluated by using single-trait analyses with the reaction norm model and considering heterogeneous residual variance divided into five classes. The CG solutions obtained in step 1 were used as an environmental gradient in step 2, representing low to high management environments. We observed increasing genetic variance estimates along the environmental gradient for all evaluated traits. Residual variance showed the same pattern, except with class 5 of FY305 and class 4 of PY305. Heritability estimates increased slightly as the management level increased. The correlation estimates between the intercept and the slope of the reaction norm curve were 0.998 for MY305, 0.989 for FY305, and 0.987 for PY305. The genetic correlation among the low (5% quantile), medium (55% quantile), and high (95% quantile) management level environments was high, with values higher than 0.99, 0.97, and 0.70 for MY305, FY305, and PY305, respectively. The breeding values of the animals changed along the environmental gradient, even those classified as robust. These results demonstrate a G×E interaction with scale effect for the evaluated traits that affects the breeding values.

**Keywords:** cattle, contemporary group, environmental sensitivity, heritability, random regression, zebu

## 1. Introduction

Guzerá is a zebu breed known for its good zootechnical indexes when raised in tropical climates and under adverse conditions. In addition, the breed stands out for its dual purpose: it can be used to produce milk, meat, or both. Despite the rusticity of the breed, the performance of these animals can be negatively influenced, mainly due to the genotype × environment (G×E) interaction.

According to Falconer and Mackay (1996), G×E interactions represent changes in the performance of different genotypes under different environments. Consequently, those genotypes classified as better for one environment may not be so for others. Since the traditional genetic evaluation disregards the G×E interaction, the progenies may not present the expected productive performance when bred in environments that differ from those in which their parents were selected (Santos et al., 2019).

The reaction norm models obtained via random regression have been used to evaluate G×E interactions. This methodology considers that genotypes have different sensitivities to specific environmental changes (Kolmodin et al., 2002) and is efficient in analyzing traits that vary gradually and continuously over time and/or space (Fazel et al., 2018). With this approach, the breeding value is divided into two components—environment-independent (intercept) and environment-dependent (slope)—that are related to the sensitivity of animals to environmental changes (Sartori et al., 2022; Toro-Ospina et al., 2022).

Santana Jr. et al. (2020) evaluated heat stress in Guzerá animals, observing that a G×E interaction negatively influences milk yield at the initial (5 to 54 days) and intermediate (55 to 154 days) stages of lactation. This was the first study to consider the effect of a G×E interaction on milk production in the Guzerá breed. Further research should examine not only milk production but also its constituents and environmental gradients to direct individuals to suitable environments. Adapted individuals will have conditions to express their genetic potential and, consequently, to reach a better productive performance and a higher economic return.

Therefore, this study aimed to evaluate G×E interactions for the milk, fat, and protein yields of Guzerá breed animals using reaction norm models and assuming the solutions for the effects of contemporary groups as an environmental gradient.

## 2. Material and methods

This study used data from the database of the Programa Nacional de Melhoramento do Guzerá para Leite (National Program for the Improvement of Guzerá for Dairy Purposes), coordinated by Embrapa Gado de Leite in partnership with the Centro Brasileiro de Melhoramento Genético do Guzerá (Brazilian Center for Genetic Improvement of Guzerá). Data from primiparous females born between 1958 and 2016 were used. Individual information on genealogy, performance, birth date, calving date and order, and calving season was used. Traits of 305-day first-lactation cumulative yields (kg) of milk (MY305), fat (FY305), and protein (PY305) were evaluated. The pedigree file comprised 25,685 animals, being 2,669 sires and 12,367 dams.

The contemporary groups (CG) were defined by herd and calving year. The calving season was divided into dry (April to September) and rainy (October to March). We considered only the information of primiparous phenotypes within the range of ± 3 standard deviations from the mean and only CG with at least three records of daughters from at least two different sires. The descriptive analysis of the data is shown in Table 1.

**Table 1 -** Number of records (N), mean, standard deviation, minimum and maximum, and number of contemporary groups (CG) for 305-day first-lactation cumulative yields (kg) of milk (MY305), fat (FY305), and protein (PY305)

| Trait | N | Mean | Standard deviation | Minimum | Maximum | CG |
|---|---|---|---|---|---|---|
| MY305 | 6823 | 2033 | 1001 | 105 | 6487 | 421 |
| FY305 | 2466 | 85 | 38 | 3 | 281 | 150 |
| PY305 | 1870 | 61 | 29 | 4 | 242 | 84 |

The analyses were performed in two steps. The first estimated environmental effects (CG solutions) using a multi-trait animal model that ignores the existence of G×E interactions. The analyses were performed using the following model:

$$y = X\beta + Zu + e \qquad (1)$$

in which y is the vector of observations (MY305, FY305, or PY305); X and Z are the effect incidence matrices of β and u, respectively; β is the vector of fixed effects (calving season, CG, and linear covariate of cow age at calving); u is the additive genetic random effect vector; and e is the random residual effect vector. The additive genetic and residual effects assumed a normal distribution in which $u \sim N(0, G \otimes A)$ and $e \sim N(0, R \otimes I)$, wherein A is the numerator relationship matrix based on pedigree, I is an identity matrix, G is the genetic variance and covariance matrix, and R is the residual variance and covariance matrix.

The first step created a vector of corrected phenotypes for fixed effects ($y^*$):

$$y^* = y - (X\hat{\beta}) = Z\hat{u} + \hat{e}$$

The second step performed a single-trait analysis using the solutions for CG from the first step as the environmental gradient. The heterogeneous residual variance was divided into five classes according to the quantiles of the CG solutions estimated in the first step—(0, 20%), (20, 40%), (40, 60%), (60, 80%), and (80, 100%)—according to the recommendation of Zhang et al. (2019) and ensuring each class had a similar number of animals. Table 2 shows the number of animals and the range of CG solutions for each class of the evaluated traits. Linear Legendre polynomials were used to model the additive genetic effects.

**Table 2 -** Number of animals (N) and amplitude of the contemporary group solutions in each class of heterogeneous residual variance for 305-day first-lactation cumulative yields of milk (MY305), fat (FY305), and protein (PY305)

| Class | MY305 | | FY305 | | PY305 | |
|---|---|---|---|---|---|---|
| | N | Amplitude | N | Amplitude | N | Amplitude |
| 1 | 1672 | −366 : 752 | 572 | 4 : 35 | 446 | −1 : 27 |
| 2 | 1394 | 753 : 1111 | 457 | 36 : 50 | 379 | 28 : 36 |
| 3 | 1365 | 1112 : 1416 | 553 | 51 : 61 | 361 | 37 : 43 |
| 4 | 1361 | 1417 : 2034 | 510 | 62 : 82 | 381 | 44 : 52 |
| 5 | 1031 | 2035 : 4011 | 374 | 83 : 163 | 303 | 53 : 158 |

The reaction norm model was fitted for each trait as follows:

$$y^*_{ij} = \mu + a_i\phi_{0ij} + b_i\phi_{1ij} + \xi_{ij} \qquad (2)$$

in which $y^*_{ij}$ is the corrected phenotypic of animal *i* for level *j* of the estimated CG effects ($\hat{\beta}_{CG_{ij}}$); μ is the overall mean; $\phi_{0ij}$ and $\phi_{1ij}$ are the intercept and linear Legendre polynomial coefficients, respectively; $a_i$ and $b_i$ are the intercept and regression coefficients, respectively, for the regression of the additive genetic value of animal *i*; and $\xi_{ij}$ is the residual term. The joint distribution for $a_i = [a_1, a_2, ..., a_n]'$ and $b_i = [b_1, b_2, ..., b_n]'$ with $\theta = [a_i, b_i]'$ was given by $\theta \sim N(0, \Sigma_{ab} \otimes A)$, in which $\Sigma_{ab} = \begin{bmatrix} \sigma^2_a & \sigma_{ab} \\ \sigma_{ab} & \sigma^2_b \end{bmatrix}$.

The AIREMLF90 software was used to fit models 1 and 2, and PREDICTF90 software was used to obtain $y^*$ (Misztal et al., 2014). The breeding values of individual *i* at environmental level *j* were calculated using the equation $\hat{u}_{ij} = K'\hat{\theta}_i = \hat{a}_i\hat{\phi}_{0j} + \hat{b}_i\hat{\phi}_{1j}$, in which K' is the transposed matrix of Legendre coefficients and $\hat{\theta}_i$ is the vector of genetic values for the regression coefficients (linear and angular coefficients of the reaction norm). The estimates of genetic variance ($\hat{\sigma}^2_{uj}$) and heritability ($\hat{h}^2_j$) for the traits evaluated at environmental level *j* were calculated as [1] $\hat{\sigma}^2_{uj} = K'_j \sum_{ab} K_j = \hat{\sigma}^2_{aj} \hat{\phi}_{0j} + 2\hat{\sigma}_{abj} \hat{\phi}_{1j} + \hat{\sigma}^2_{bj} (\hat{\phi}_{1j})^2$, in which $\hat{\sigma}^2_{aj}$ is the genetic variance component for the linear coefficient, $\hat{\sigma}^2_{bj}$ is the variance component of the angular coefficient, and $\hat{\sigma}_{abj}$ is the covariance component between the linear and angular coefficient, and [2] $\hat{h}^2_j = \frac{\hat{\sigma}^2_{uj}}{\hat{\sigma}^2_{uj} + \hat{\sigma}^2_{ej}}$, in which $\hat{\sigma}^2_{ej}$ is the residual variance component.

The estimated genetic (co)variances and correlations between the trait at environmental levels *j* and *j'* were obtained by [3] $\hat{\sigma}_{u_{jj'}} = K'_j \sum_{abj} K_j = \hat{\sigma}^2_a \hat{\phi}_{0j} + \sigma_{ab} \hat{\phi}_{1j} + \sigma_{ab} \hat{\phi}_{1j'} + \hat{\sigma}^2_b \hat{\phi}_{1j} \hat{\phi}_{1j'}$, in which $\hat{\sigma}_{u_{jj'}}$ is the genetic covariance between the trait at levels *j* and *j'*, and [4] $\hat{r}g_{jj'} = \frac{\hat{\sigma}_{u_{jj'}}}{\sqrt{\hat{\sigma}^2_{uj} \hat{\sigma}^2_{uj'}}}$, in which $\hat{r}g_{jj'}$ is the genetic correlation for the trait at levels *j* and *j'*.

The genetic correlations among low (5% quantile), medium (55% quantile), and high (95% quantile) management-level environments were estimated. Sires were classified into robust ($|s_i| < 1\sigma_s$), sensitive ($1\sigma_s \geq |s_i| < 2\sigma_s$), and extremely sensitive ($|s_i| \geq 2\sigma_s$), admitting a plasticity scale based on the individual absolute value ($s_i$) and standard deviation ($\sigma_s$) of the slope.

## 3. Results

Genetic and residual variance estimates for the evaluated traits are shown in Figures 1 and 2, respectively. The CG solutions were defined as an environmental gradient. The ranges of the CG solutions were −366–4011 for MY305, 4–163 for FY305, and −1–158 for PY305, representing low to high management environments.

The additive genetic variance was observed to change the environmental gradient, with estimates increasing with the management level for all evaluated traits. For MY305, the residual variance behaved similarly to the genetic variance. For FY305, the residual variance increased until class 4, with class 5 showing similar values to class 3. For PY305, the residual variance increased until class 3, decreased in class 4, and increased again in class 5. The genetic variance estimates were lower than the residual variance estimates for all traits except in class 5 of FY305 and PY305.

Heritability estimates along the environmental gradient ranged from 0.17 to 0.36 for MY305, 0.22 to 0.65 for FY305, and 0.13 to 0.80 for PY305, with mean values of 0.27, 0.43, and 0.53 for MY305, FY305, and PY305, respectively. Despite their similar mean values, the heritability estimates (Figure 3) of the evaluated traits, except for class 5 of FY305 and PY305, increased slightly along the environmental gradient, with low to medium values. The heritability estimates were higher for class 5 of FY305 and PY305 than for the other classes, with medium to high values (0.43–0.65 and 0.39–0.80, respectively).

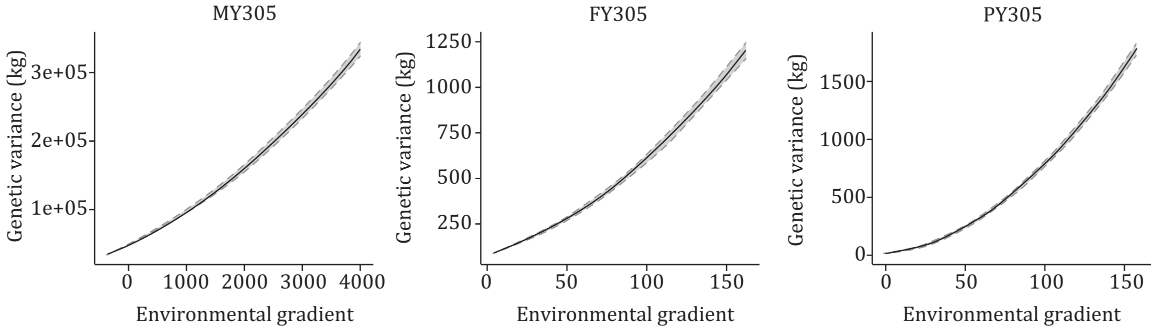

**Figure 1 -** Genetic variance with confidence interval for 305-day first-lactation cumulative yields of milk (MY305), fat (FY305), and protein (PY305) along the environmental gradient.

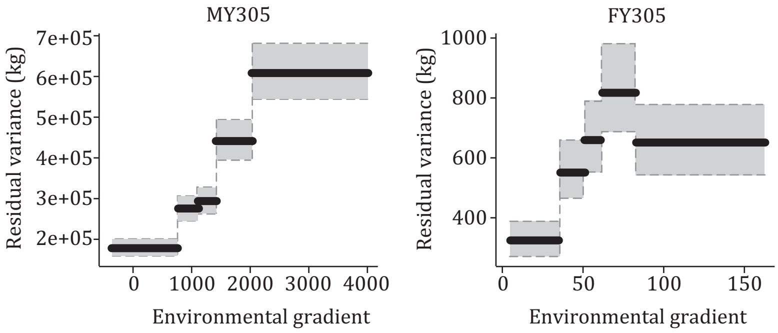

**Figure 2** - Residual variance with confidence interval for 305-day first-lactation cumulative yields of milk (MY305), fat (FY305), and protein (PY305) along the environmental gradient.

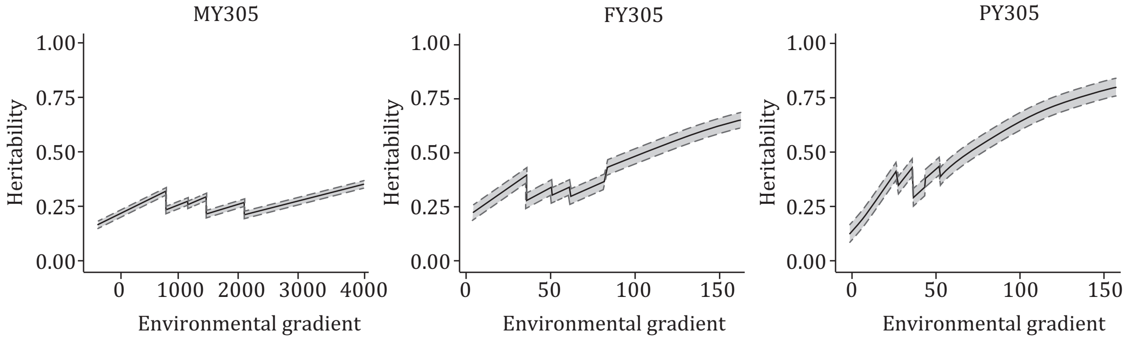

**Figure 3** - Heritability with confidence interval for 305-day first-lactation cumulative yields of milk (MY305), fat (FY305), and protein (PY305) along the environmental gradient.

The correlation estimates between the reaction norm intercept and slope were 0.998 for MY305, 0.989 for FY305, and 0.987 for PY305. The genetic correlations (Figure 4) among the low (5% quantile), medium (55% quantile), and high (95% quantile) management level environments were high for all traits, with values greater than 0.99, 0.97, and 0.70 for MY305, FY305, and PY305, respectively.

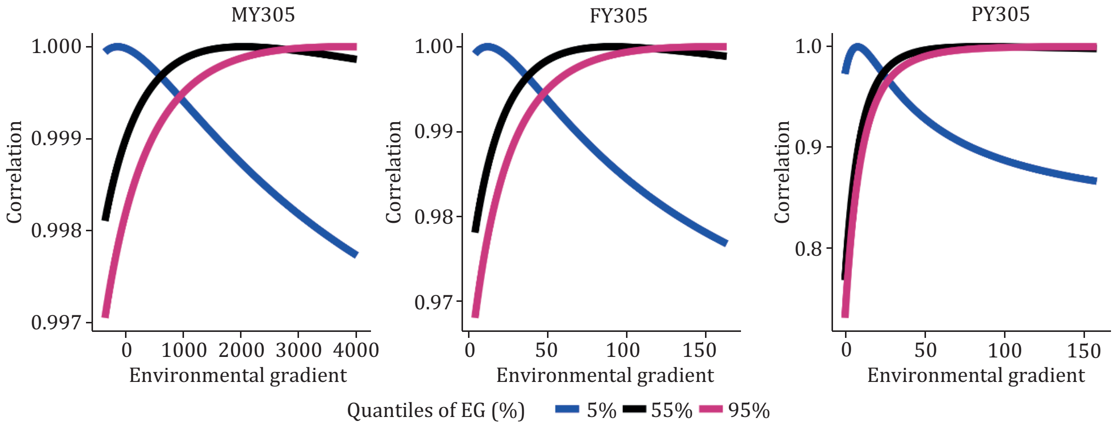

**Figure 4** - Genetic correlation among the low (5% quantile), intermediate (55% quantile), and high (95% quantile) values of the environmental gradient for 305-day first-lactation cumulative yields of milk (MY305), fat (FY305), and protein (PY305).

When evaluating the reaction norm of sires with at least 15 daughters (Figure 5), the breeding value variation was lower in environments with low management levels and higher in environments with high management levels. Few animals were classified as sensitive negative. There was no reranking of sires for MY305 and FY305. For PY305, there was little significant reranking of animals.

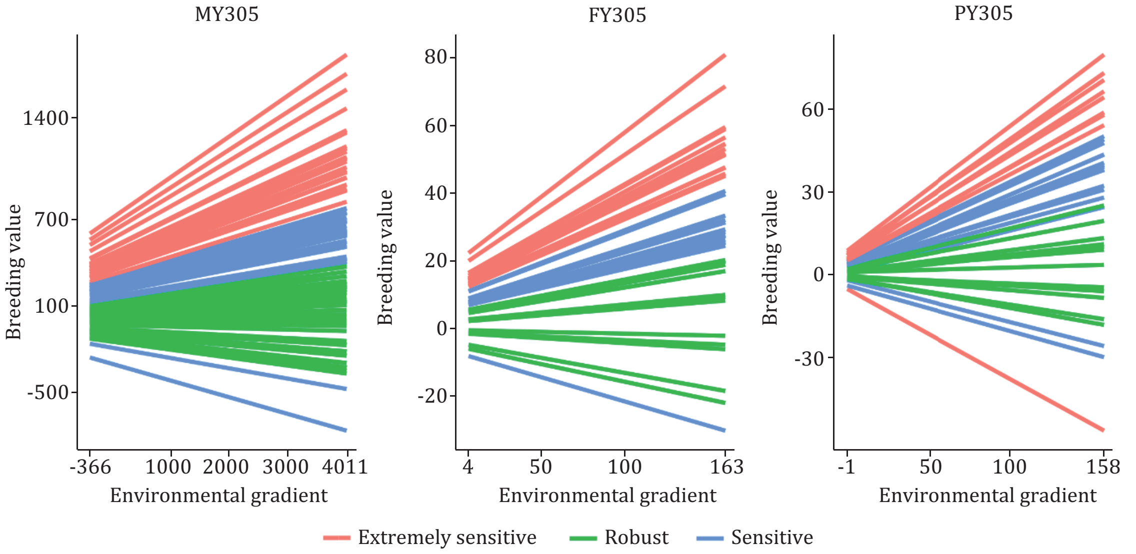

**Figure 5 -** Reaction norms along the environmental gradient for 305-day first-lactation cumulative yields of milk (MY305), fat (FY305), and protein (PY305) of sires with at least 15 daughters.

## 4. Discussion

Genetic variance estimates increased along the environmental gradient for all evaluated traits. The same pattern was observed with residual variance estimates, except for class 5 of FY305 and class 3 of PY305. The genetic variance was generally smaller than the residual variance, and both variances increased proportionally along the environmental gradient. Previous studies evaluating G×E interactions for milk, fat, and protein yields have also found variation in genetic and residual variance estimates along the environmental gradient (Gaia et al., 2018; Moreira et al., 2019; Santana Jr. et al., 2020; Bohlouli et al., 2021; Cheruiyot et al., 2020; Sartori et al., 2022).

Higher genetic variance estimates in environments with higher management levels can be explained by better management conditions allowing animals to express their genetic potential. The higher residual than genetic variance indicates that the phenotypic variability mainly results from environmental factors. The similar residual variances between FY305 classes 3 and 5 demonstrate that the environmental conditions for these classes contributed similarly to the residual variability. Oliveira et al. (2020) stated that changes in genetic and residual variances are an initial way to identify a G×E interaction. Even if it does not change the classification of genotypes, it can negatively influence the response to selection since genotypes can show lower breeding values in environments with lower variability.

Heritability values described in the literature are between 0.10 and 0.35 for MY305, 0.22 for FY305, and 0.29 for PY305 (Santana Jr. et al., 2020; Paiva et al., 2020; Brito et al., 2020; Carrara et al., 2022), generally corroborating the results found in our study. Heritability is the proportion of total variance attributed to additive genetic variance. Therefore, changes in variance estimates promote changes in heritability estimates. Heritability estimates showed similar values along the environmental gradient, except for class 5 of FY305 and PY305, since the genetic and residual variances changed proportionally along the environmental gradient. Since the heritability values found in our study indicate that the genetic variance contributed to the phenotypic variance, it is possible to obtain genetic gains through selection. Considering that the phenotypic variance was not constant along the environmental gradient, the evaluated traits are expected to respond differently to selection in different environments.

Most of the data was concentrated at the beginning and middle of the environmental gradient, and few data were observed at the end of the environmental gradient (Figure 6). The high heritability estimates found in class 5 of FY305 and PY305 may have been caused by the scarcity of data at the end of the environmental gradient. The observed range of the environmental gradient was also larger for this class. These factors may have influenced the estimates of variance components, overestimating the genetic variance and heritability.

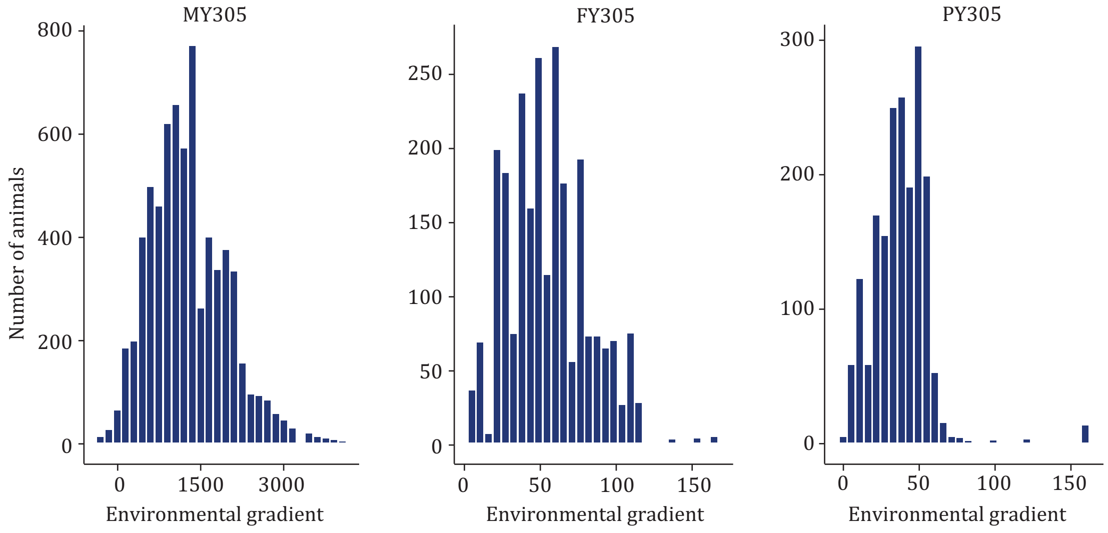

**Figure 6** - Distribution of the evaluated animals along the environmental gradient for 305-day first-lactation cumulative yields of milk (MY305), fat (FY305), and protein (PY305).

The correlations between the intercept and the slope were higher than 0.90 for all the evaluated traits. Kolmodin et al. (2002) reported high correlations between the intercept and slope for milk protein yield, which they attributed to genetically superior animals tending to be more sensitive to environmental changes. Ambrosini et al. (2016) stated that the high correlation between the reaction norm intercept and slope indicates that animals with higher average breeding values along the environmental gradient tend to show better responses in environments with high management.

High genetic correlations were observed among the low, medium, and high management level environments, indicating the absence of a complex G×E interaction. Streit et al. (2012) and Shariati et al. (2007) found similar results when evaluating dairy traits in Holstein cattle. They stated that high genetic correlations between distinct environments indicate low or no reranking of animals. Furthermore, our results indicate that groups of similar genes are involved in the control of the evaluated traits in different environments.

Regarding the reaction norms and reranking of sires, only PY305 showed a small reranking of animals. This result was already expected since the high genetic correlations between environments indicated little or no reranking of animals. Other studies have reported results that differ from ours. Despite evaluating different environments and breeds, they found complex G×E interactions for dairy cattle traits (Freitas et al., 2010; Santana Jr. et al., 2020; Santos et al., 2020).

A complex G×E interaction is observed when animals are reranked according to environmental changes. Consequently, the breeding value can be altered depending on the management level environment. Those animals considered better in a specific environmental condition may show inferior performances in others and vice-versa.

The G×E interaction with a scale effect is characterized by little or no reranking of animals in the different environments. However, the magnitude of variance does not remain constant across environments. Kolmodin et al. (2002) stated that the scale effect is observed when two or more genotypes show no changes in classification in different environments, but differences in phenotypic performance are greater in some than in others. When a G×E interaction with a scale effect is acting on the evaluated traits, the response to selection is lower in environments with low management levels and higher in environments with high management levels (Hammami et al., 2009).

The heterogeneous residual variance values, the high correlation between the intercept and slope, and the reaction norm of the bulls along the environmental gradient demonstrate that a G×E interaction with a scale effect exists for the traits evaluated in our study. The reaction norms (Figure 4) show that the difference between the breeding values of the bulls was smaller in environments with low management levels and increased with management levels. Therefore, it is difficult to quantify how much of the change in variance components is attributable to the G×E interaction (Streit et al., 2012), because the scale effect can be corrected by pre-adjusting the data or correcting the evaluation models. However, overlooking this effect can result in losses when traits are used to create an index (Hammami et al., 2009).

Calus and Veerkamp (2003) stated that the scale effect may not change the ranking of sires when only one trait is evaluated. However, if traits with different effects are combined into an economic index, reranking based on the index may occur, emphasizing the importance of including environmental sensitivity in genetic evaluations in breeding programs rather than only correcting for these effects in the statistical model. Toro-Ospina et al. (2022) stated that to make breeding values more accurate, it is vital to consider the effects of G×E interactions in the models of genetic evaluations to avoid inappropriate selection of genotypes.

## 5. Conclusions

No evidence was found to suggest that complex G×E interactions were present in the milk, fat, and protein yields in this population. However, the estimates of genetic and residual variance exhibited variation along the environmental gradient, indicating the presence of a G×E interaction with a scale effect. Given that selection indices are influenced by the scale effect, it is essential to investigate potential avenues for incorporating this phenomenon into animal breeding programs. Animals raised in favorable environments tend to demonstrate an increase in the expression of their genetic potential. However, when the environment is unfavorable, productivity is reduced, as the genetic potential of the animals is impaired. In environments with a significant scale effect, the response to selection may be constrained, thereby reducing the efficiency of genetic progress.

## Data availability

The dataset supporting the results of this study is not publicly available. The data do not belong to the institutions responsible for the research. Access to them was formalized in a technical cooperation agreement between the signatory parties, in this case Embrapa and CBMG$^2$ (Centro Brasileiro de Melhoramento Genético do Guzerá), which provides for confidentiality. Therefore, any access to this data must be requested from CBMG$^2$, under penalty of legal liability if the contract is broken.

## Author contributions

**Conceptualization:** Peixoto, M. G. D. and Lopes, P. S. **Data curation:** Peixoto, M. G. D.; Carrara, E. R. and Bruneli, F. A. T. **Formal analysis:** Soares, T. L. S.; Carrara, E. R.; Silva, D. A.; Santos, F. L. C. and Veroneze, R.

**Funding acquisition:** Lopes, P. S. **Writing – original draft:** Soares, T. L. S. **Writing – review & editing:** Peixoto, M. G. D.; Carrara, E. R.; Silva, D. A.; Veroneze, R. and Lopes, P. S.

## Conflict of interest

The authors declare no conflict of interest.

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