



Genotype by environment interaction in Nelore cattle from five Brazilian states

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Abstract

Records from 75,941 Nelore cattle were used to determine the importance of genotype by environment interaction (GEI) in five Brazilian states. (Co)variance components were estimated by single-trait analysis (with yearling weight, W450, considered to be the same trait in all states) and multiple-trait analysis (with the record from each state considered to be a different trait). The direct heritability estimates for yearling weight were 0.51, 0.39, 0.44, 0.37 and 0.41 in the states of Goiás, Mato Grosso, São Paulo, Mato Grosso do Sul and Minas Gerais, respectively. The across-state genetic correlation estimates between Goiás and Mato Grosso, Goiás and Minas Gerais, São Paulo and Minas Gerais, and Mato Grosso do Sul and Minas Gerais ranged from 0.67 to 0.75. These estimates indicate that GEIs are biologically important. No interactions were observed between Goiás and São Paulo, Goiás and Mato Grosso do Sul, Mato Grosso and São Paulo, Mato Grosso and Mato Grosso do Sul, Mato Grosso and Minas Gerais, or São Paulo and Mato Grosso do Sul (0.82 to 0.97). Comparison of single and multiple-trait analyses showed that selection based on the former was less efficient in the presence of GEI, with substantial losses (up to 10%) during selection.

Key words: Bayesian inference, beef cattle, genetic correlation.

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Introduction

Traits to be used in genetic evaluation programs are mainly chosen based on their economic importance in relation to current market trends. However, the emphasis given to each trait needs to be adjusted by taking into account not only specific market situations, but also ecoregional conditions. In the case of Brazil, which is characterized by vastly different environmental conditions among its various geographic regions, separate regional evaluations may be necessary so that differences between regions do not interfere with the genetic gain in animal breeding. In this context, genotype-environment interactions (GEI) are an important phenomenon in livestock breeding. The challenge is to identify the genotypes and environments in which GEI is large enough to be of economic and biological importance (Pégolo *et al.*, 2009).

Livestock production is influenced by the combined action of genetic and environmental factors. It is therefore

essential to evaluate the isolated effects and combination of factors that affect traits such as weight and weight gain measured at different ages in genetic breeding programs. Yearling weight is of particular importance in this regard since it is the last recording done by most breeders of selection herds before the sale of reproducers; yearling weight is also the weight closest to slaughter weight, and consequently shows the highest correlation with the latter.

Some investigators have used genetic correlations to compare the importance of GEI among regions in Nelore cattle. Genetic correlations ranged from 0.60 to 0.90 and heritability estimates for yearling weight ranged from 0.30 to 0.61 (Toral *et al.*, 2004; Ribeiro *et al.*, 2007; Lopes *et al.*, 2008). These values demonstrate the variability of this trait in GEI studies according to the environment investigated. However, few studies in the Brazilian literature have investigated the influence of GEI on economically important traits used in breeding programs.

In this study, single and multiple-trait analyses based on Bayesian inference were used to estimate heritabilities and genetic correlations for yearling weight in Nelore cattle. Specifically, we investigated GEI in five Brazilian

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states and assessed its effect on the average breeding value of selected animals.

Material and Methods

Records of yearling weight (W450) from 99,366 Nelore animals born between 1991 and 2006 were analyzed. The data were obtained from six Brazilian states (Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraná and São Paulo) participating in the Nelore Cattle Breeding Program (PMGRN) coordinated by the National Association of Breeders and Researchers (ANCP). However, only animals from five states (excluding Paraná) and raised exclusively on pasture were included in the analyses. Four birth or weight recording seasons were defined as follows: season 1 (January to March), season 2 (April to June), season 3 (July to September) and season 4 (October to December). The number of sires present in each state and the common number of sires in two states are shown in Table 1.

The GLM procedure (SAS, 2008) was used to form the contemporary groups. The contemporary group for which the model yielded the highest coefficient of determination for yearling weight consisted of the farm of weight recording, farm of origin, year of birth, season of birth, sex and management. Contemporary groups with fewer than nine observations and weight records that were outside the range given by the contemporary group mean plus or minus three standard deviations (SD) were excluded. The number of herds and structure after consistency of the data file for W450 per state analyzed are shown in Table 2.

(Co)variance components were estimated using the gibbs2f90 software (Miszta, 2008) by single-trait analysis

(in which W450 was considered to be the same trait in all states) and multiple-trait analysis (in which the record from each state was considered to be a different trait). The analysis model included contemporary groups as fixed effects, additive genetic effects and residual effects. The mathematical description of the general model used was:

$$y = X\beta + Zu + e$$

where y is the vector of observations, X and Z are incidence matrices relating β and u to the observations, β is the vector of fixed effects, u is the vector of direct genetic additive effects, and e is the vector of residual effects.

For the model, it was assumed that:

$$\begin{bmatrix} y \\ u \\ e \end{bmatrix} \sim MNV \left\{ \begin{bmatrix} X\beta \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} ZAZ' \otimes G + R \otimes I & G \otimes ZA & R \otimes I \\ AZ' \otimes G & G \otimes A & 0 \\ R \otimes I & 0 & R \otimes I \end{bmatrix} \right\}$$

where A is the additive numerator relationship matrix, I is an identity matrix, G is the additive genetic covariance matrix 5x5, R is a residual diagonal matrix, and \otimes denotes the direct product between matrices.

Vectors β and u are location parameters of a conditional distribution $y|\beta, u$. A uniform distribution was assumed as an *a priori* distribution for β , which reflects vague prior knowledge about this vector. A multivariate normal distribution was assumed as an *a priori* distribution for u , with a mean of 0 and variance $\sigma^2_a A$ and $G \otimes A$ for single- and multiple-trait analyses, respectively. For the other components, Wishart and inverted chi-square distributions were assumed as *a priori* distributions for multiple- and

Table 1 - Numbers of sires in each state (diagonal) and common in two states (above diagonal).

	W450_GO	W450_MT	W450_SP	W450_MS	W450_MG
W450_GO	582	148	246	220	175
W450_MT		379	237	236	147
W450_SP			937	334	253
W450_MS				871	217
W450_MG					360

GO - Goiás, MG - Minas Gerais, MS - Mato Grosso do Sul, MT - Mato Grosso, SP - São Paulo.

Table 2 - Number of herds, observations, average weight \pm standard deviations and coefficient of variation (CV) for yearling weight (W450) from five Brazilian states.

State	No. of herds	No. of observations	Average weight (kg)	CV (%)
Goiás	44	16,011	254 \pm 39	15.5
Mato Grosso	6	10,637	260 \pm 40	15.5
São Paulo	29	19,777	280 \pm 47	16.6
Mato Grosso do Sul	24	22,408	268 \pm 46	17.3
Minas Gerais	15	7,108	288 \pm 51	17.7
Total	118	75,941	269 \pm 46	17.1

single-trait analyses, respectively (Van Tassel and Van Vleck, 1996).

A pedigree file containing the identification of each animal, sire and dam was used in all analyses, with a total of 149,002 animals in the relationship matrix when all available relationships were considered (up to 11 generations).

Gibbs chains of 1,012,900 and 1,040,000 cycles were generated for single- and multiple-trait analyses, respectively, with a burn-in period of 50,000 cycles and a sampling interval of 100 cycles. The chains generated were then analyzed using the Gibanal software (Van Kaam, 1998) to determine the convergence of the chains and dependence among samples. GEI was estimated by genetic correlation between yearling weights in different states, with values < 0.80 indicating an important interaction.

On the basis of the mean (co)variance components obtained by single- and multiple-trait analyses, the animals were classified according to breeding values by best linear unbiased prediction (BLUP) using the blupf90 software developed by Misztal (2008). Thus, five breeding values were obtained for each animal, one for each state (BVGO, BVMT, BVSP, BVMS and BVMG). For single-trait analysis, breeding values in which yearling weight was considered to be the same trait (BVuni) were obtained, regardless of the state where the animal was reared.

To determine the influence of GEI on selection, the responses to selection were compared by considering the trait to be different or not different in the five states. Two selection scenarios were simulated, with the proportion of selected animals ranging from 1 to 10%. In the first scenario, the animals were selected based on breeding values obtained by single-trait analysis (BVuni). In the second scenario, the animals were selected based on the breeding value of each state (BVSP, BVMT, BVGO, BVMS and BVMG). The average breeding value of each state was then calculated for the selected animals and the mean values were compared. Only male animals born in 2005 (the last year during which the complete calving season was recorded) were used for this comparison.

Results and Discussion

Table 2 shows that there were wide variations in the mean yearling weight and standard deviation among the states. These differences may reflect the influence of factors such as genetic variation among herds, although most of the differences were probably attributable to the environment in which the animals were reared. This variation results in different estimates of the (co)variance components and, consequently, differences in the genetic parameter estimates (Carneiro *et al.*, 2008).

In Bayesian inference, when Monte Carlo Markov Chain methods are used to obtain the posterior distribution of the samples the convergence of the chains must be ensured since, if the samples are not generated from a stationary posterior distribution, the inferences will not be valid.

In the present study, the burn-in period (50,000 samples) used for the two analyses was adequate to ensure convergence of the chains.

The effective sample size was small, ranging from 81 to 268 (Table 3), despite the generation of 990,000 samples from the stationary distribution. This finding indicated a high dependence among samples. Although a small effective sample size impairs inferences at extreme values of parameter distributions, the measures of central tendency are generally reliable. In this study, similar measures of central tendency were obtained for the different states.

As indicated by the estimates shown in Table 3, Goiás was generally the only state in which the residual variance was lower than the additive genetic variance. With respect to additive genetic variance, São Paulo showed the highest estimate, followed by the states of Minas Gerais and Goiás. Figure 1 shows the posterior distributions of additive genetic variance for all of the states.

Examination of this graph allowed us to infer, based on the intersection of densities, that genetic variance was higher in the state of São Paulo than in Mato Grosso and Mato Grosso do Sul, whereas genetic variance was lower in Mato Grosso do Sul than in Goiás. The finding that genetic variance differed among states may indicate that genotypes react differently to different environments, a fact implying the existence of GEI. This is the case, for example, in states where the quality of pasture was on average better and the difference in animal weight was more evident. Barwick *et al.* (2009) also demonstrated a difference in the performance of beef cattle when the animals were exposed to different types and qualities of pasture. These differences in genetic variances among states may also reflect the fact that although there is a connection between the groups in all states there may be differences between states with regard to training of the breed. Practically all of the Nelore cattle in Brazil have been obtained through crossbreeding in a process that is ongoing, so it is likely that the proportion of herds is higher in those states where the absorption processes are more recent; this phenomenon may contribute to the differences in genetic variances.

In the present case, a GEI resulting from heterogeneity of variances would not alter the ranking of genotypes but would result in a difference in heritability. However, if higher variation were a consequence of differences in the level of genetic variation among herds within each state (possibly as a consequence of more intense selection for the trait in some herds and states) then the difference in genetic variation would not be the result of a GEI. The consequence of this on the genetic gain of herds under selection would be that, in the case of intense selection, states with a higher genetic variation would contribute proportionally more so that the genetic gain would be lower because the animals chosen from states with higher variation would not necessarily be genetically superior for all states.

Table 3 - Descriptive statistics of posterior distributions from variance components for yearling weight (W450) in five Brazilian states (multi-trait) and in five states together (single-trait).

Parameter	Multiple-trait analysis					
	Mean	Mode	Median	ES	SD	HDI 95%
Goiás (GO)						
σ_a^2	307.43	308.05	307.75	149	18.15	269.3-344.3
σ_c^2	291.86	289.45	291.00	214	13.11	265.4-316.2
Mato Grosso (MT)						
σ_a^2	264.94	275.94	265.60	102	14.63	215.4-311.9
σ_c^2	417.43	416.76	417.20	127	21.54	381.1-455.6
São Paulo (SP)						
σ_a^2	347.36	346.19	347.30	191	22.12	303.8-388.9
σ_c^2	438.40	432.37	437.70	198	15.86	409.4-468.4
Mato Grosso do Sul (MS)						
σ_a^2	246.59	254.08	246.90	149	15.60	216.5-275.2
σ_c^2	426.68	427.74	426.90	268	11.04	404.1-448.1
Minas Gerais (MG)						
σ_a^2	307.68	309.21	308.00	99	31.73	250.3-374.5
σ_c^2	439.96	438.80	438.80	81	24.17	396.8-488.4
Single-trait analysis						
σ_a^2	285.64	283.54	285.30	1,266	10.40	265.7-305.6
σ_c^2	408.35	407.57	408.40	1,266	7.43	394.1-422.0

σ_a^2 - additive genetic variance, σ_c^2 - residual variance, ES - effective samples, HDI - high density interval and SD - standard deviation.

The posterior distributions of residual variances and their descriptive statistics are shown in Figure 2 and Table 3, respectively. The lowest residual variances were observed for the state of Goiás, whereas the other states had similar distributions. A lower residual variance may indicate less environmental variation and greater care and reliability in data collection. On the other hand, lower residual variance may also be caused by an increased response of certain genotypes to some specific environment within the states, *i.e.*, there would be a GEI.

The heterogeneity of residual variance also reduces genetic gain when the selection intensity applied is high. A greater selection of animals from states with higher residual variance is not desirable since, in practice, animals from states with less “controlled” environmental effects would benefit.

In phenotype selection, when the heterogeneity of variance is ignored and the intensity of selection is high there is a tendency to select more animals from herds with greater variance since animals with more extreme values are found in these flocks. In the case of selection based on

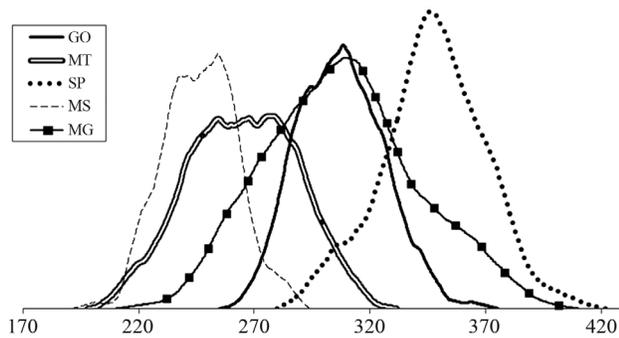


Figure 1 - Posterior densities of genetic additive estimates (σ_a^2) for yearling weight from Goiás (GO), Mato Grosso (MT), Mato Grosso do Sul (MS), Minas Gerais (MG) and São Paulo (SP).

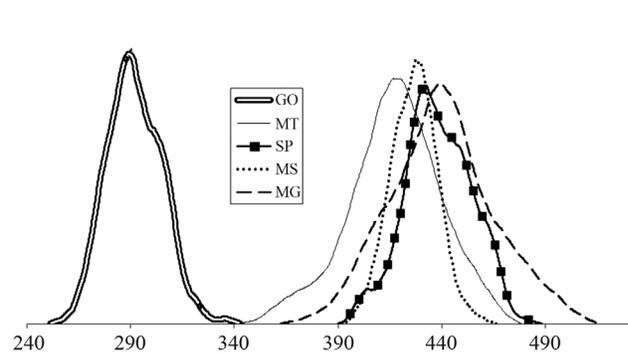


Figure 2 - Posterior densities of residual variance (σ_c^2) for yearling weight from Goiás (GO), Mato Grosso (MT), Mato Grosso do Sul (MS), Minas Gerais (MG) and São Paulo (SP).

parental information, data from herds with greater variation have greater weight in genetic evaluations.

The heritability estimates for yearling weight ranged from 0.37 to 0.51 in the regions analyzed (Table 4). These findings were consistent with the values reported for Nelore cattle as a whole, which range from 0.31 to 0.53 (Magnabosco *et al.*, 2000; Siqueira *et al.*, 2003; Faria *et al.*, 2007; Boligon *et al.*, 2009). The highest heritability estimate among the five states was observed for the state of Goiás (Figure 3) and was a direct consequence of the lower residual variance.

The heritability estimates obtained for weight in the different states were moderate to high, indicating that a substantial part of the variation in this trait among animals was attributable to differences in the genetic merit of the animals. Thus, yearling weight should respond efficiently to individual selection in any of the states studied.

In a study of GEIs in three states, Ferreira *et al.* (2001) reported a heritability estimate of 0.17 for yearling weight in a Nelore herd from Minas Gerais, a value much lower than that observed here. For the state of Mato Grosso do Sul, the estimated heritability (0.36) agreed with those of Toral *et al.* (2004) and Ribeiro (2006), who reported values ranging from 0.30 to 0.45 and from 0.31 to 0.48, respectively, for regions in Mato Grosso do Sul.

Although the different heritability estimates indicate variations in the genotype performance of animals from various regions, this difference only has practical consequences for selection when it changes the relative merit of the animals. This change will only occur when the interaction becomes important. In the present study, we applied the criterion of Robertson (1959), *i.e.*, an interaction has an important effect when the genetic correlation between the same trait in two environments is less than 0.80.

Genotype-environment interactions were observed between the states of Goiás and Mato Grosso, Goiás and Minas Gerais, São Paulo and Minas Gerais, and Mato Grosso do Sul and Minas Gerais. Based on the results obtained, the phenotypic expression of the trait will be different in states where the genetic correlation was lower than 0.80 and should therefore be considered a distinct trait. No interaction was observed between Goiás and São Paulo, Goiás and Mato Grosso do Sul, Mato Grosso and São

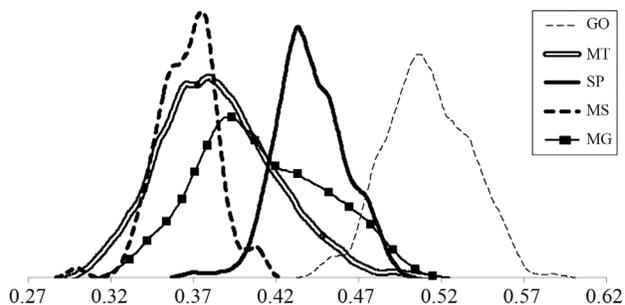


Figure 3 - Posterior densities of heritability estimates (h^2) for yearling weight from Goiás (GO), Mato Grosso (MT), Mato Grosso do Sul (MS), Minas Gerais (MG) and São Paulo (SP).

Paulo, Mato Grosso and Mato Grosso do Sul, Mato Grosso and Minas Gerais, or São Paulo and Mato Grosso do Sul. These results suggest that most of the genes responsible for the expression of yearling weight act in a similar fashion in two different environments and that the response to selection for the trait in one state will be similar to the response observed in another state.

For a more detailed analysis, Figure 4 shows the posterior densities of the genetic correlation estimates for yearling weight among the five states studied. The posterior distributions of the correlations involving the state of Minas Gerais showed a small probability of being above 0.80 (except for that involving the state of Mato Grosso), whereas for the state of Mato Grosso a good portion of the distribution of genetic correlations with the weights in other states was above 0.80 (except for the state of Goiás).

This finding indicates the existence of two groups of states where GEIs were more pronounced, namely, one including the states of Minas Gerais and Mato Grosso and the other including the states of Goiás, São Paulo and Mato Grosso do Sul. This finding also indicates that separate genetic evaluations of the two sets would be more interesting in terms of genetic progress. Within these groups, the correlations between states were high.

The lower genetic correlation estimates involving the state of Mato Grosso do Sul were consistent with the genetic correlations reported by Toral *et al.* (2004) for weights from birth to yearling in Nelore cattle among three homogeneous microregions in Mato Grosso do Sul. Simi-

Table 4 - Mean and standard deviations (in parentheses) of heritabilities (diagonal) and genetic correlations (above diagonal) for yearling weight in five Brazilian states.

	W450_GO	W450_MT	W450_SP	W450_MS	W450_MG
W450_GO	0.51(0.02)	0.74(0.07)	0.88(0.04)	0.89(0.01)	0.67(0.08)
W450_MT		0.38(0.03)	0.84(0.07)	0.82(0.05)	0.97(0.03)
W450_SP			0.44(0.02)	0.83(0.04)	0.75(0.08)
W450_MS				0.37(0.02)	0.73(0.06)
W450_MG					0.41(0.04)

GO - Goiás, MG - Minas Gerais, MS - Mato Grosso do Sul, MT - Mato Grosso, SP - São Paulo.

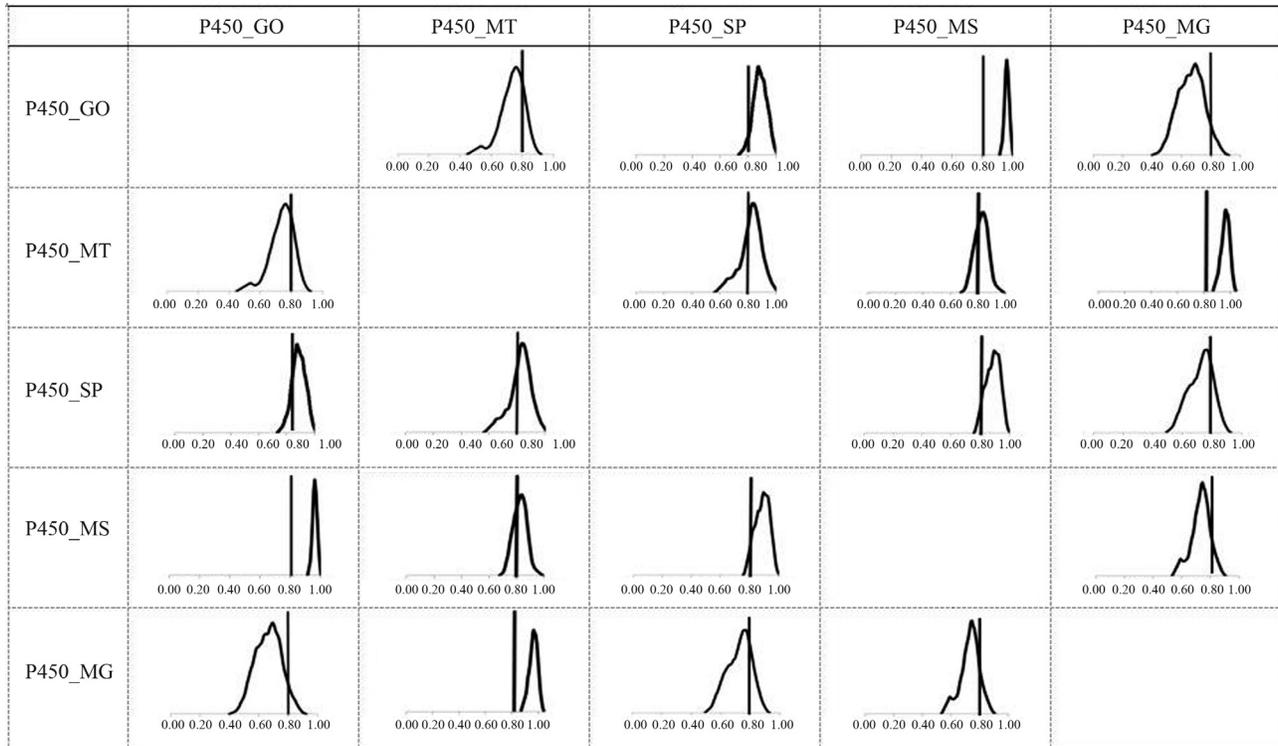


Figure 4 - Posterior densities of genetic correlation estimates (above and below the diagonal). The line in the distributions marks the threshold for the importance of GEI (0.80) for W450 in the five states studied.

larly, Souza *et al.* (2008) observed an effect of GEI only for postweaning traits between two regions in the state of Pará and Mato Grosso do Sul for Nelore animals.

Results similar to those of the present study have been reported by Ribeiro *et al.* (2007) who found no GEI between the western region of São Paulo and Mato Grosso do Sul (0.82 to 1.00). Eler *et al.* (2000) found GEIs for preweaning and postweaning weights in Nelore cattle reared on farms located in southeastern and midwestern Brazil, in agreement with the present study. However, Fridrich *et al.* (2005) observed no interaction between these states, with a mean genetic correlation of 0.92 in Tabapuã cattle.

It was important to quantify the effect of GEIs on the selection of animals in the states where this interaction was observed since GEIs are not included in most breeding programs. This was done by comparing the model that does not consider GEI (single-trait analysis) and with that which does (multiple-trait analysis) (Tables 5 and 6). The correlations between predicted breeding values obtained by single- and multiple-trait analyses were high for all states.

These correlations were higher than the genetic correlations between states since the data from all states were included in the single-trait model. This was a more realistic situation than the previous one since, if GEIs were ignored, data from all states would be collected and analyzed as a single trait. The genetic correlations reported above allowed prediction of the genetic gain in a state based on the

results of another state, in contrast to the situation studied previously using a model that considers GEI.

Table 6 shows the average breeding values of males born in 2005 when selected based on multiple-trait analysis (which considers GEI), and the percent reduction in these average values when selection was based on the results of single-trait analysis (which ignores GEI), according to the fraction selected. For animals from the state of Minas Gerais, the losses due to ignoring the effects of GEI may reach slightly more than 10% of the average breeding value of selected animals, whereas for the other states this loss was less important.

Table 5 - Pearson correlation coefficients for breeding values of males born in 2005 for yearling weight obtained by single-trait and multiple-trait analyses.

	BVuni	BVGO	BVMT	BVSP	BVMS	BVMG
BVuni	-	0.97	0.97	0.98	0.98	0.93
BVGO	-	-	0.94	0.97	0.98	0.87
BVMT	-	-	-	0.96	0.95	0.96
BVSP	-	-	-	-	0.96	0.90
BVMS	-	-	-	-	-	0.88
BVMG	-	-	-	-	-	-

BVuni - predicted breeding value in single trait analyses; BVGO, BVMT, BVSP, BVMS and BVMG - predicted breeding value for the states of Goiás, Mato Grosso, São Paulo, Mato Grosso do Sul and Minas Gerais, respectively, in multiple-trait analyses.

Table 6 - Mean predicted genetic values for multiple-trait analysis when selection was done with 1%, 5% and 10% of the best males born in 2005, and the percentage reduction (in parentheses) when selection was done by single-trait analysis.

P (%)	BVGO	BVMT	BVSP	BVMS	BVMG
1	30.25 (-3.67%)	27.33 (-4.11%)	33.03 (-1.91%)	27.75 (-3.17%)	30.33 (-10.30%)
5	21.84 (-3.53%)	20.56 (-3.43%)	23.90 (-2.87%)	20.48 (-2.79%)	22.89 (-9.44%)
10	18.06 (-3.63%)	17.20 (-3.06%)	18.78 (-2.48%)	17.05 (-2.98%)	19.08 (-8.12%)

P (%) - percentage of selected animals. BVGO, BVMT, BVSP, BVMS, BVMG - mean predicted genetic values for the states of Goiás, Mato Grosso, São Paulo, Mato Grosso do Sul and Minas Gerais, respectively.

This result may reflect either changes in the classification of animals from different states, as demonstrated by the genetic correlation in multiple-trait analysis, or differences in the variance (scaling) between states. However, since the change was more pronounced in the state of Minas Gerais, which had a genetic variance similar to the average of the other states, the first option seems more plausible.

Greater differences between predicted breeding values were found in three situations when the intensity of selection was higher. This finding may be related to heterogeneity in the variance observed for the states of Minas Gerais, Mato Grosso and Mato Grosso do Sul. Similar results were reported by Carvalho *et al.* (2002) who evaluated the effect of residual heterogeneity on selection. These authors concluded that ignoring the heterogeneity of variance led to a reduction in the response to selection when the intensity of selection was increased.

Despite evidence of a GEI between various pairs of states, the state of Minas Gerais was most influenced by the presence of this interaction. However, based on these results and the fact that the use of single-trait analysis (which ignores the effect of GEI) led to substantial losses, we conclude that the analysis chosen should consider the presence of GEI when this is evident, *i.e.*, when genetic correlations of less than 0.80 are found. The multiple-trait model provides more reliable estimates of breeding values because it considers both genetic and environmental differences among states, thereby reducing the bias of estimates. However, the application of multiple-trait analysis results in higher costs than single-trait analysis.

The results of this study support the current concern regarding the presence of GEI and the best approach to deal with this event. Thus, it is not only important to evaluate the effect of this interaction on the classification of animals in different environments, but also to assess the effect of this change on the genetic gain of the population.

In conclusion, a GEI was observed for yearling weight between pairs of the states studied. Subsequent analysis identified two groups of states for genetic evaluation: the first included the states of Minas Gerais and Mato

Grosso, and the second included the states of Goiás, São Paulo and Mato Grosso do Sul. The effect of GEI on selection was highest for the state of Minas Gerais. In genetic evaluations of yearling weight, analyses that consider the presence of GEI are preferable to those that do not include this interaction.

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