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Influence of genotype-environment interaction on the classification of Nellore bulls in Southern Brazil

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ABSTRACT. The aim of this study was to assess the occurrence of genotype-environment interaction, as well as its effects on the magnitude of genetic parameters and the classification of Nellore breeding bulls for the trait adjusted weight at 205 days (W205) on Southern Brazil. The components of (co)variance were estimated by Bayesian inference, using a linear-linear animal model in a bi-trait analysis. The proposed model for the analyses considers as random the direct additive genetic and maternal effects and residual effects, and as fixed effects the contemporary groups, sex, season of birth and weighing, and calving age as covariable (linear and quadratic effects). The *a posteriori* mean estimates of the direct heritabilities for W205 in the three States varied from 0.24 in Paraná (PR) to 0.34 in Santa Catarina (SC). The estimates of maternal heritability varied from 0.23 in SC and Rio Grande do Sul (RS) to 0.28 in PR. The *a posteriori* mean distributions of the genetic correlation varied from 0.52 between SC and RS, to 0.84 between PR and RS, suggesting that the best breeding bulls in SC are not the same as in RS.

Keywords: beef cattle, variance components, genetic correlation, bayesian inference, genetic parameters.

Interação genótipo-ambiente na classificação de touros da raça Nellore na região Sul do Brasil

RESUMO. O objetivo deste trabalho foi verificar a ocorrência de interação genótipo-ambiente, bem como seu efeito sobre a magnitude dos parâmetros genéticos e na ordem de classificação dos reprodutores para a característica peso ajustado aos 205 dias (P205) para a raça Nellore no sul do Brasil. Os componentes de (co)variância foram estimados por meio da inferência Bayesiana, adotando um modelo animal linear-linear, em análise bi-característica. O modelo proposto para todas as análises considera como aleatórios os efeitos genéticos aditivos diretos e maternos e o residual e como fixos os efeitos de grupos de contemporâneos, sexo, estação de nascimento e de pesagem e a idade da vaca ao parto como co-variável (efeitos lineares e quadráticos). As estimativas médias *a posteriori* das herdabilidades diretas para P205 nos diferentes Estados variaram de 0,24 no Paraná (PR) a 0,34 em Santa Catarina (SC). As estimativas de herdabilidade materna variaram de 0,23 em SC e Rio Grande do Sul (RS) a 0,28 no PR. As médias das distribuições *a posteriori* das correlações genéticas variaram de 0,52, entre SC e RS, a 0,84, entre PR e RS, sugerindo que os melhores reprodutores em SC não são os mesmos no RS.

Palavras-chave: bovinos de corte, componentes de variância, correlação genética, inferência Bayesiana, parâmetros genéticos.

Introduction

Beef cattle in Brazil, due to the country's large territorial extension, is practiced in different environmental conditions, submitting animals to variations in handling conditions during their productive live (Ferraz & Felício, 2010). Thus, animals tested in different environments may present different performances, generating financial gains or losses, since different genotypes are produced according to the genotype's response to

the environment (Prado et al., 2009). Hence, it is necessary to consider the interaction genotype-environment in programs of genetic improvement, since this effect may present biased estimates of genetic variance, leading to changes in selection criteria (Alencar et al., 2005).

The genetic improvement programs in progress commonly disregard the presence of the genotypeenvironment interaction and assume constant additive and residual genetic variation for all the 196 Bresolin et al.

herds. However, evidence has been found of the presence of heterogeneous variation and of genotype-environment interaction, when data are obtained from different regions of the country, as well as from different management systems (Espasandin et al., 2011; Faria et al., 2011; Lopes et al., 2008; Zapata et al., 2010).

There are different methods to assess the presence of genotype-environment interaction. They consist in considering the same trait expressed in different environments as distinct, hence being determined by different groups of genes (Falconer, 1952). Usually, these traits are combined in bi- or multi-traits analyses, in which the weight of the genotype-environment interaction is given by the genetic correlation between the traits (Robertson, 1959). Some studies use the reaction norm models (Calus et al., 2004; Corrêa et al., 2009; Pégolo et al., 2009) to check for the presence of the genotype-environment interaction, because it allows the measurement of the genotypes' responses to environmental changes.

Considering the impact of this interaction on the genetic progress of beef cattle and its financial consequences over this activity, the aim of this study was to verify the existence of genotype-environment interaction, as well as its effects on the magnitude of variances, on genetic parameters and on the classification of bulls, considering the trait adjusted weight at 205 days of age, for the Nellore breed in Southern Brazil.

Material and methods

For the present study, 96,075 weaning weight records of **Nellore** beef cattle from States of Paraná (PR), Rio Grande do Sul (RS) and Santa Catarina (SC) were used, from 1975 to 2009, preserved by the Brazilian Association of Zebu Breeders (ABCZ). Only those animals raised in Cfa climate, according to Köppen and Geiger (1928), were considered for the analysis. This climate type is defined as temperate or warm temperate, characterized by well-defined winter and summer seasons, high humidity and rainfall throughout the year, presenting mean temperature between -3 and 18°C, and over 10°C in the hottest months of the year.

The data file has been edited, keeping records of the breeding bulls' sons in the three aforementioned States. Four season of birth and weighing were considered (autumn, winter, spring and summer) and three raising conditions (semi-stabled, stabled and grazing regime). For the establishment of the contemporary groups (CG) animals from the same city, state, year of birth and weighing, and raised in the same conditions were gathered. Sex and season of birth and weighing were not considered for the CG's, but as separated effects, since they considerably decreased the amount of information, rendering the study. Weighing records outside the interval of more or less three standard deviations compared to CG's means were excluded. The observed weaning weights were adjusted for 205 days (W205) through the following equation: W205 = (OW – BW/ WA) * 205 + BW, in which: OW = observed weight; BW = birth weight; WA = weaning age.

For the evaluation of the genotype-environment interaction, it was assumed that the same trait expressed in different environments is a distinct trait, determined by different groups of genes, according to Falconer (1952).

The connectivity between the regions was evaluated by the connection test of the CGs, using the software AMC (Roso et al., 2004), based on the total number of genetic links (minimum of 10). After each connection test, the non-connected animals were removed, as well as the CGs with less than three animals.

Three bi-trait analyses were applied: Paraná x Santa Catarina, Paraná x Rio Grande do Sul and Santa Catarina x Rio Grande do Sul, to establish the heritabilities and the genetic correlations between the W205 traits in these States. The *pedigree* file counted with 14.454 connected animals. Table 1 presents the descriptive statistics according to the States.

Table 1. Descriptive statistics of the trait adjusted weight for 205 days old animals of the Nellore breed from Southern Brazil.

	Paraná	Santa Catarina	Rio Grande do Sul
NN	6,239	4,253	3,962
Mean (kg)	186.063	160.272	164.745
SD (kg)	36.288	37.606	35.792
CV (%)	19.503	23.463	21.726
CG (N)	356	183	242
Bull (N)	661	267	336
Cow (N)	3,727	2,011	2,136

N= number of information; SD= standard deviation; CV= coefficient of variation; CG= number of contemporary groups.

The (co)variance components were estimated by Bayesian inference, adopting linear-linear animal model in a bi-trait analysis. The proposed model for all the analyses considers as random the direct additive genetic and maternal effects and residual effects, and as fixed effects of the CG, sex, birth season (BS) and weighing season (WS) and the calving age (CA) as covariable (linear and quadratic effects). The general model of analysis may be described as:

$$y = X\beta + Z_1 a + Z_2 m + e,$$

in which:

 γ = vector of the observations for the trait (W205); X = matrix of incidence of the fixed effects(CG, sex, BS, WS e CA); Z_1 = matrix of incidence associated with direct additive genetic effects; Z_2 = matrix of incidence associated with maternal additive genetic effects; β , a and m = vector of solutions for the fixed effects, vector of direct additive genetic effects and vector of maternal additive genetic effects, respectively and ε = vector of residues. It was assumed that $E[y] = X\beta$; Var (a) = $A \otimes \Sigma_a$, $Var(m) = A \otimes \Sigma_m$ and $Var(e) = I_n \otimes \Sigma_{e_n}$ in which Σ_{a} is the matrix of direct additive genetic covariances between the traits; Σ_{m} is the matrix of maternal genetic covariances; Σ_e is the matrix of residual covariances; A is the parentage matrix; I is the identity matrix and \otimes is the direct product between the matrix.

To estimate the (co)variance components and the genetic parameters using Bayesian inference, the softwares GIBBSF90 and POSTGIBBSF90 (Misztal et al., 2014) were used. In the Bayesian inference context, the *a priori* information about the parameters are used in association with sampling data through the similarity function, thus generating a joint *a posteriori* (Guedes et al., 2005; Mello et al., 2006). The complete conditional distribution of the parameters were obtained from the joint *a posteriori* densities, in other words from the density of the parameters, considering the initial observations and information.

Through the software GIBBSF90 (Misztal et al., 2014) a chain of 1 million iterations was implemented, without sampling and initial discard. Then, the software POSTGIBBSF90 (Misztal et al., 2014) was used to discard the 50 thousand initial iterations, considered the chains heating period. To ensure the independence of the samples, an interval of removal at every 200 iterations was considered, generating a total of 4.750 samples of the (co)variance components.

The initial discard and sampling interval were defined according to the Raftery and Lewis (1992) test, from the Bayesian Output Analysis package (BOA) of the R software, version 2.10.1 (Smith, 2007). The convergence was verified using the Heidelberger and Welch test (Heidelberger & Welch, 1983) and the Geweke criterion (Geweke, 1991) from the same package. The initial discard was performed also considering the visual inspection of the chains.

Heritabilities, genetic correlations and Monte Carlo error were calculated using the (co)variance samples. Monte Carlo error is the error in the estimation of the parameter due to the number of samples used in the Gibbs chain, which is obtained for each (co)variance component, dividing this variance by the number of samples. Thus, the square root of this value approximates the standard deviation of the errors associated with the size of the Gibbs chain.

Marginal distribution of the parameters, calculated from the integration of *a posteriori* joint distributions, which provides the estimators of interest (mean, mode and median), were obtained using the software GIBANAL (Van Kaam, 1998).

The effect of the interaction genotype-environment was evaluated by comparison of the heritability estimates obtained for the trait W205 in the different States, by genetic correlation between the direct expressions of this traits in the offspring of the same breeding bull in different States and by the correlation between the classification of predicted genetic values for the breeding bulls in the three States. The correlation between the classification orders of the genetic values predicted for the 623 bulls, considered as an indicator of the genotype-environment interaction, was obtained by the procedure PROC CORR, Spearman (SAS, 2004). According to Robertson (1959), genetic correlation values below 0.80 indicate an important effect of the genotype-environment interaction.

Results and discussion

The means, modes and medians of the genetic parameters estimates were similar in all analyses, which indicate symmetry of the *a posteriori* distributions (Tables 2, 3 and 4). Another indicative of the Gibbs chains convergence is associated to the Monte Carlo error (MCE) for the genetic parameters. MCE was low for all the traits, indicating that the size of the chain was enough for obtaining precise estimates of the *a posteriori* parameters. Besides, all the chains passed through the Heidelberger and Welch (1983) and by the Geweke (1991) criterion.

The mean a posteriori estimates of the heritabilities for the trait adjusted weight at 205 days (W205), considered distinct in the different States, were not similar, indicating a genotype-environment interaction (GEI). An absence of overlapping in the credibility region was also observed for this trait in the three States (Table 2). These results may indicate variance heterogeneity for W205, comparing the States. However, Diaz et al. (2011) reported that the presence of variance heterogeneity is not necessarily associated to GEI and, from the practical point of view of the selection, it is not the most important interaction. The authors also report that the absence of variance heterogeneity may be a result of the phase of life, since the animals are less exposed to environmental effects from birth to weaning, due to maternal care, especially breast-feeding.

The *a posteriori* estimates of direct heritability for W205, considered as different traits in the combination of pairs of States, varied from 0.24 to

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0.34, the higher value observed in the State of Santa Catarina and the lower in the State of Paraná (Table 2). Studies concerning the effect of GEI presented discrepancy between the values of direct heritability for W205. Souza et al. (2003) and Fridrich et al. (2008) reported similar values, that varied between 0.16 to 0.38 for Nellore bulls in different regions of Brazil; Fridrich et al. (2005) found values between 0.02 e 0.20 for Tabapuã bulls in four regions of Brazil; Toral et al. (2004) estimated values between 0.36 and 0.59 for Nellore bulls in three microregions (Alto Taquari, Campo Grande and Pantanal). However, due to the low number of information used and the heterogeneous raising conditions, the estimates of the (co)variance components may be biased in the present study.

A posteriori estimates of maternal heritability for the trait W205, considered distinct in the different pairs of States, varied from 0.23 to 0.28 (Table 3). Fridrich et al. (2008) estimated values between 0.09 and 0.29 in the different regions of the country (South, Southeast, West-central, North and Northeast) and Lopes et al. (2008) recorded values between 0.16 and 0.48 between the three Southern States, both for the Nellore breed. Still considering the Nellore breed, Faria et al. (2011) found values of 0.25 for animals belonging to ten Brazilian herds. However, Souza et al. (2011) estimated, for the same breed, values of 0.05 and 0.08 for the West-central and Southeast regions, respectively.

The means of the *a posteriori* distributions for the genetic correlations for W205 varied from 0.52 to 0.84 in the different pairs of States (Table 4), pointing the effect of the GEI between SC and RS, which agrees with studies performed with different beef cattle breeds by Espasandin et al. (2011); Fridrich et al. (2005); Lopes et al. (2008); Mascioli et al. (2006); Souza et al. (2003); Zapata et al. (2010). However, between PR and SC, the genetic correlation for the traits were near 0.8, considered the reference value for the importance of the GEI, according to Robertson (1959). On the other hand, the genetic correlation for the traits between the States of PR and RS were higher than 0.8, pointing to the absence of GEI.

The evidence of GEI between SC and RS indicates that the group of genes responsible for the expression of the trait W205 is distinctly expressed in these environments. Therefore, the response obtained for the selected trait in one of the environments will not be similar to that observed in the other. Hence, the lack of consideration of this effect may lead to errors in the identification of genetically superior animals. According to Lopes et al. (2008), the inclusion of the region of birth in the analysis model may enhance the accuracy of the prediction of genetic values, and the genetic evaluation by state may be more efficient in the identification of genetically superior animals.

Table 2. A posteriori estimates of direct heritability (h²) and genetic correlations (rg) for the trait adjusted weight at 205 days (W205), considered distinct in the States of Paraná, Santa Catarina and Rio Grande do Sul for the Nellore breed.

	PR and SC		PR a	nd RS	SC and RS		
	h ² _{PR}	h ² _{SC}	h_{PR}^2	h_{RS}^2	h_{SC}^2	h_{RS}^2	
Mean	0.26 ± 0.03	0.34 ± 0.05	0.24 ± 0.02	0.27 ± 0.04	0.32 ± 0.05	0.31 ± 0.5	
Mode	0.25	0.32	0.25	0.28	0.34	0.30	
Median	0.26	0.34	0.24	0.27	0.32	0.30	
MCE	0.0004	0.0008	0.0005	0.0007	0.0008	0.0008	
CR	0.21 - 0.33	0.24 - 0.45	0.18 - 0.31	0.20 - 0.28	0.22 - 0.43	0.20 - 0.41	

MCE = Monte Carlo's error; CR = credibility region (95%).

Table 3. A posteriori estimates of maternal heritabilities (h²) for the trait adjusted weight at 205 days (W205), considered distinct in the States of Paraná, Santa Catarina and Rio Grande do Sul for the Nellore breed.

	PR and SC		PR and RS		SC and RS	
	h ² _{PR}	h ² _{SC}	h_{PR}^2	h_{RS}^2	h ² _{SC}	h ² _{RS}
Mean	0.27 ± 0.03	0.23 ± 0.02	0.28 ± 0.03	0.23 ± 0.03	0.23 ± 0.04	0.24 ± 0.03
Mode	0.25	0.22	0.27	0.22	0.24	0.24
Median	0.27	0.23	0.27	0.22	0.23	0.24
MCE	0.0006	0.0005	0.0007	0.0006	0.0007	0.0006
CR	0.19 - 0.34	0.18 - 0.28	0.19 - 0.34	0.13 - 0.38	0.09 - 0.28	0.16 - 0.30

MCE = Monte Carlo's error; CR = credibility region (95%).

Table 4. A posteriori estimates of genetic correlations (r_p) for the trait adjusted weight at 205 days (W205), for the Nellore breed from Southern Brazil.

	PR and SC	PR and RS	SC and RS		
	$r_{_{g}}$	$r_{_{g}}$	r_g		
Mean	0.78 ± 0.06	0.84 ± 0.05	0.52 ± 0.07		
Mode	0.78	0.84	0.54		
Median	0.78	0.84	0.52		
MCE	0.0009	0.0010	0.0012		
CR	0.64 - 0.89	0.68 - 0.94	0.23 - 0.88		

PR = Paraná; SC = Santa Catarina; RS = Rio Grande Sul; MCE = Monte Carlo's error; CR = credibility region (95%)

Considering the classification of the bulls according to the genetic value (Table 5), it is noticed that, for example, the bull classified in second place in SC is in the 372° and 351° positions in PR and RS, respectively. Similarly, the sensitivity to a different environment may also be observed for the bull classified in third place in RS, but in 24° in PR e 445° in SC. Nevertheless, the offspring of some bulls presented similar performances in the three environments, obtaining similar classifications in the three States. The bull in the first position in the States of PR and SC is the second one in RS, evidencing the robustness that some animals present for the trait W205 in different environments.

A higher correlation between the classifications of the bulls in the three States is verified for PR and RS (Figure 1). Higher data dispersion is observed between SC and the other two States, indicating lower correlation between these environments, since the genetic values estimated for them are different. This dispersion seems to be more pronounced between the States of SC and RS. Thus, bulls with high performance in SC may not present the same performance in RS.

The success of an animal genetic improvement program depends on the proportion of genetic gain obtained from one generation to another. Thus, special attention must be given to breeding bulls and/or semen used in the farms, descendant of herds or regions that may present different environmental origins. Therefore, when this difference in classification is neglected, even if it a small difference, it may result in an inadequate choice of breeding bulls. The result may be a decrease in the genetic progress of the selected population.

Table 5. Classification of breeding bulls according to the genetic values for the trait adjusted weight at 205 days (W205) in the States of Paraná, Santa Catarina and Rio Grande do Sul, for 693 Nellore bulls.

Classification in PR		Classification in SC			Classification in RS			
PR	SC	RS	SC	PR	RS	RS	PR	SC
1º	1º	2°	1º	1°	2°	1º	3°	34°
2°	3°	4°	2°	372°	351°	2°	1°	1°
3°	34°	1°	3°	2°	4°	3°	24°	445°
4°	4°	5°	40	4°	5°	40	2°	3°
5°	5°	6°	5°	5°	6°	5°	4°	40
6°	8°	9°	6°	90	11°	6°	5°	5°
7°	12°	7°	7°	8°	10°	7°	7°	12°
8°	7°	10°	8°	6°	90	8°	17°	161°
9°	6°	11°	90	10°	12°	90	6°	8°
10°	90	12°	10°	97°	107°	10°	8°	7°

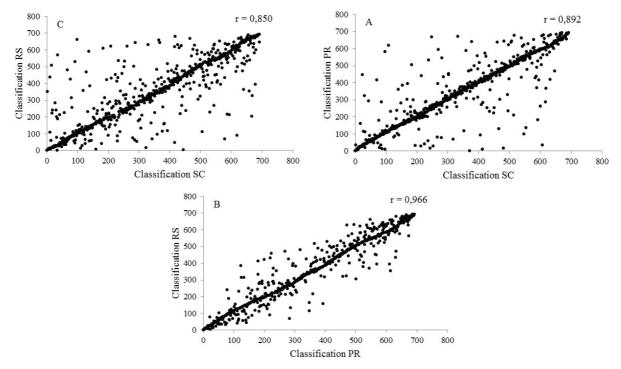


Figure 1. Correlation (r) and dispersion diagram of the classification of Nellore breeding bulls (693) for the trait adjusted weight at 205 days old between: A = Paraná (PR) and Santa Catarina (SC); B = Paraná (PR) and Rio Grande do Sul (RS); C = Santa Catarina (SC) and Rio Grande do Sul (RS).

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Conclusion

A genotype-environment interaction was found for the **Nellore** cattle breed, considering the trait adjusted weight at 205 days old, between the States of Santa Catarina and Rio Grande do Sul.

The magnitude of the genetic parameters was not the same and the genotype-environment interaction demonstrated influence on the classification of most of the breeding bulls in all the three States from Southern Brazil, considering the surveyed trait.

The genotype-environment interaction deserves attention, especially when the same breeding bulls are used in the States of Santa Catarina and Rio Grande do Sul, since it is expected that performance of their offspring in these States will be different.

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