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Genotype \times environment interaction for long-yearling weight in Canchim cattle quantified by reaction norm analysis¹

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ABSTRACT: The objective of this study was to investigate the presence of genotype \times environment interactions (G \times E) for long-yearling weight in Canchim cattle (5/8 Charolais + 3/8 zebu) in Brazil using reaction norms (RN). The hierarchical RN model included the fixed effect of age of the animal (linear coefficient) and random effects of contemporary groups and additive animal genetic intercept and slope of the RN and contemporary group effects as random effects. Contemporary groups as the most elemental representation of management conditions in beef cattle were chosen to represent the environmental covariate of the RN. The deviance information criteria demonstrated that a homoskedastic residual RN model provided a better data fit compared with a heteroskedastic counterpart and with a traditional animal model, which had the worst fit. The environmental gradient for long-yearling weight

based on contemporary group effects ranged from -105 to 150 kg. The additive direct variance and heritability estimates increased with increasing environmental gradient from 74.33 ± 22.32 to $1,922.59 \pm 258.99$ kg² and from 0.08 ± 0.02 to 0.68 ± 0.03 , respectively. The high genetic correlation (0.90 ± 0.03) between the intercept and the slope of the RN shows that animals with the greatest breeding values best responded to environmental improvement, characterizing scale effect as the source of G \times E for long-yearling weight. The phenotypic plasticity demonstrated by the slope of the RN of the animal indicates the possibility to change genotype expression along the environmental gradient through selection. The results demonstrate the importance of accounting for G \times E in the genetic evaluation of this population.

Key words: beef cattle, genotype \times environment interaction, long-yearling weight, reaction norm

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INTRODUCTION

Genotype \times environment interaction (G \times E) is characterized by different responses of genotypes to environmental variations (Falconer and Mackay, 1996). The G \times E may lead to changes in phenotypes, as well as changes in the absolute and relative magnitude of genetic and environmental variances. This implies that the performance of animals and their progeny can change according to the environmental conditions in which they are raised and selected. Therefore, dif-

ferent selection criteria may be chosen depending on the breeding environment, as suggested by Henderson (1984) and Alencar et al. (2005). In this context, the study of G \times E is important to investigate whether it should be considered in genetic evaluations to increase the response to selection.

The presence of G \times E can be investigated by describing the phenotype of an animal as a continuous function of the environment (Woltereck, 1909; Lynch and Walsh, 1998). This has been recently achieved in animal breeding by using reaction norm (RN) models to describe the gradual and continuous variation of economically important traits over an environmental gradient for dairy cattle (Kolmodin et al., 2002; Calus et al., 2006; Strandberg et al., 2009), beef cattle (Corrêa et al., 2009; Pegolo et al., 2009), sheep (Pollott and Greeff, 2004), and swine (Knap and Su, 2008).

Reaction norms are obtained by means of covariance functions (Kirkpatrick et al., 1990), which are estimated by random regression and allow the performance of

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genotypes at each level of the environmental gradient to be determined, and to evaluate the heterogeneity of genetic and residual variances in each environment. Reaction norms also allow distinguishing between genotypes that are more or less sensitive to environmental changes, called phenotypic plasticity (Bradshaw, 1965). According to Falconer (1990), more sensitive animals are called plastic genotypes and less sensitive animals are called robust genotypes. Therefore, the presence of $G \times E$ may also be characterized as the difference in phenotypic plasticity among individuals (Falconer and Mackay, 1996).

The objective of the present study was to investigate the existence of $G \times E$ using a hierarchical RN model (HRNM) applied to long-yearling weight in Canchim cattle (5/8 Charolais + 3/8 zebu).

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from an existing database (Brazilian Canchim Breeders Association; ABCCAN).

Data Set Edition

The data set of the Brazilian Canchim (5/8 Charolais + 3/8 zebu) beef cattle population, which participates in the Embrapa-Genepplus genetic evaluation program associated with the ABCCAN, was used. Contemporary groups (CG) consisted of a combination of year and season of birth, sex, genetic group of dam, herd at weaning and long-yearling, and feeding regimen from birth to weaning and from weaning to long-yearling. The seasons of birth were 1) September to November, 2) December to February, 3) March to May, and 4) June to August. Feeding regimens at weaning and long-yearling were 1) pasture, 2) pasture plus a supplement, and 3) feedlot.

Genetic connectedness among CG was evaluated using the AMC software (Roso and Schenkel, 2006), with a minimum of 10 genetic connections being required. The final data set used included 14,078 records for long-yearling (about 420 d of age) weight of animals born between 1989 and 2000, 1,398 CG, and 21,788 animals in the pedigree.

Statistical Models

The HRNM were implemented based on the unknown covariate proposition of Su et al. (2006). The covariate was characterized by the CG effects that were jointly estimated with the RN of the animals. In beef cattle, CG combines location, climate, management, and sex and is the most basic environmental entity to which the performance of the animals is the subject and, therefore, a natural candidate RN covariate. This methodology is an alternative to classical modeling of the RN that uses a proxy for the unknown covariate based on

phenotypic means or subclass deviations (Kolmodin et al., 2002; Calus and Veerkamp, 2003) and is employed to minimize possible predicted genetic values bias due to different genetic merit across herds and due to genetic trends (Su et al., 2006).

The HRNM used in the analyses is described as follows:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{E}\mathbf{h} + \mathbf{Z}\mathbf{a} + \mathbf{H}\mathbf{b} + \mathbf{e},$$

where \mathbf{y} = the vector of long-yearling weights; $\boldsymbol{\beta}$ = the vector of fixed effects (overall mean and linear coefficient for long-yearling age); \mathbf{h} = the vector of random CG effects; \mathbf{a} and \mathbf{b} = the vectors of random intercept and slope coefficients of animal additive genetic RN, respectively; \mathbf{e} = the random error vectors; and \mathbf{X} , \mathbf{E} , \mathbf{Z} , and \mathbf{H} = the incidence matrices. Once covariates associated with the RN are treated as unknown, each row of \mathbf{H} has one nonzero element that is equal to the element \mathbf{h} (contemporary group effect) associated with the corresponding record on \mathbf{y} , and all other elements of this row are equal to zero (Su et al., 2006).

Two alternative assumptions on residuals were used: a homogeneous error model (HRNM1), where $\mathbf{e} \sim N(\mathbf{0}, \mathbf{I}\sigma_e^2)$ (i.e., all error terms are associated with a common residual variance σ_e^2 through an identity matrix \mathbf{I}) and a heterogeneous error model (HRNM2), where $\mathbf{e} \sim N\left(\mathbf{0}, \text{diag}\left\{\sigma_e^2 \times \eta^{\hat{h}_j}\right\}\right)$ (i.e., each error term has its specific residual variance as a function of the associated environmental covariate \hat{h}_j). This exponential function on a residual heteroskedasticity parameter, η , was based on the structural model proposed by Cardoso et al. (2005) and posterior means of h_j by the HRNM1 model, \hat{h}_j , were used in the function to facilitate recognizable fully conditional posterior densities.

The priori assumptions for the unknown parameters of the model were uniform density for fixed effects and for the residual heteroskedasticity parameter, whereas normal distributions with a mean of zero were assigned for random effects of CG and for the RN parameters of animals. The covariance matrix was diagonal for the effect of CG (i.e., $\text{Var}[\mathbf{h}] = \mathbf{I}\sigma_h^2$, where σ_h^2 is the CG variance). For genetic effects the covariance matrix was

$$\text{Var}\begin{bmatrix} \mathbf{a} \\ \mathbf{b} \end{bmatrix} = \begin{bmatrix} \sigma_a^2 & \sigma_{ab} \\ \sigma_{ab} & \sigma_b^2 \end{bmatrix} \otimes \mathbf{A},$$

where σ_a^2 and σ_b^2 = the additive genetic variances of the RN intercept and slope, respectively; σ_{ab} = the genetic covariance between the intercept and the slope of RN, and \mathbf{A} = the numerator relationship matrix. An inverse Wishart distribution prior with $v = 2$ df and scale matrix $\mathbf{T} = v \begin{bmatrix} 590 & 2 \\ 2 & 0.02 \end{bmatrix}$ was adopted for the covariance matrix of RN, whereas inverse gamma distributions

were used for residual variance with shape parameter $\alpha_e = 2$ and scale parameter $\beta_e = 3,000$, and for CG variance with respective parameters, $\alpha_e = 2$ and $\beta_e = 3,000$.

Model Comparison

The deviance information criterion (**DIC**) proposed by Spiegelhalter et al. (2002) was used to choose the model that fit the data best. The DIC was calculated by

$$DIC_r = \bar{D}(\boldsymbol{\theta})_r + p_{Dr},$$

where $\bar{D}(\boldsymbol{\theta})_r = \frac{1}{m} \sum_{g=1}^m -2 \log p(\mathbf{y} | \boldsymbol{\theta}^{(g)}, M_r)$ = the posterior mean of the deviance; $\boldsymbol{\theta}$ = the unknown parameters of the model; M_r = model r ; $p(\mathbf{y} | \boldsymbol{\theta}, M_r)$ = the conditional data sampling distribution; $p_{Dr} = \bar{D}(\boldsymbol{\theta})_r - D(\bar{\boldsymbol{\theta}})_r$ = effective number of parameters or complexity of model r ; $D(\bar{\boldsymbol{\theta}})_r = -2 \log p(\mathbf{y} | \bar{\boldsymbol{\theta}}, M_r)$; and $\bar{\boldsymbol{\theta}}$ = the posterior mean of all parameters. Thus, a smaller value of DIC indicates a better fit of the model. An animal model (**AM**) including fixed effects of CG and long-yearling age (linear covariate) and additive direct and residual random effects, which assumed homogeneity of variance, was used for comparison of model fit and CG effects estimated by the HRNM.

Genetic Parameters

Using the environmental gradient information, the breeding value (**BV**) of animal i was estimated for each environmental level using the following formula:

$$BV_i | h = a_i + b_i h,$$

where h = the environmental covariate value, a_i and b_i are, respectively, the RN intercept and slope of animal i . Spearman rank correlations were computed between BV obtained by the AM and calculated for HRNM1 at the 5th, 50th, and 95th environmental percentiles.

Additive genetic variance, heritability, and genetic correlations between a_i and b_i were obtained using the following formulas, respectively:

$$\begin{aligned} \sigma_A^2 | h &= \sigma_a^2 + h^2 \sigma_b^2 \pm 2h\sigma_{ab}, \\ h_A^2 | h &= \frac{\sigma_A^2 | h}{\sigma_A^2 | h + \sigma_e^2 \times \eta^h}, \text{ and} \\ r_{ab} &= \frac{\sigma_{ab}}{(\sigma_a \sigma_b)}. \end{aligned}$$

Note that in the heritability formula above, $\eta = 1$ for the homoskedastic HRNM1.

The phenotypic plasticity of the individuals was classified according to the absolute value of b_i : $|b_i| < \sigma_b =$ robust genotype; $\sigma_b \leq |b_i| < 2\sigma_b =$ plastic genotype; and $|b_i| \geq 2\sigma_b =$ extremely plastic genotype.

Bayesian Inference

A Bayesian approach was used for inference using the Intergen software (Cardoso, 2008). For HRNM1, the fully conditional posterior densities and Gibbs sampling strategy used were those presented by Su et al. (2006). Additionally, a random walk Metropolis-Hastings step was introduced in HRNM2 to sample η from its nonrecognizable posterior density (Cardoso et al., 2005), which can be represented by the following formula when records are ordered by CG:

$$\begin{aligned} p(\eta | \mathbf{y}, \mathbf{a}, \mathbf{b}, \boldsymbol{\beta}, \mathbf{h}, \sigma_e^2, \sigma_h^2, \sigma_a^2, \sigma_b^2, \sigma_{ab}) \\ \propto \eta^{-\left(\sum_{i=1}^{n_h} \frac{n_j \hat{h}_j}{2} + 1\right)} \exp \left[-\frac{1}{2} \sum_{i=1}^{n_h} \left(\frac{\mathbf{e}'_j \mathbf{e}_j}{\sigma_e^2 \eta^{\hat{h}_j}} \right) \right]. \end{aligned}$$

Here, n_h is the number of CG, n_j is the number of records in the j th CG, and \mathbf{e}_j are the residuals of its records.

The chain length was 210,000 iterations, and the initial burn-in period was set to 10,000 iterations, generating posterior samples every 10 cycles. The convergence of the chains was evaluated by trace plot analysis of the values of the samples for all (co)variance components vs. the chain cycle (Figure 1).

RESULTS AND DISCUSSION

The observed means \pm SD (range) of long-yearling weight and long-yearling age were 267 ± 56 kg (100 to 480 kg) and 420 ± 24 d (375 to 465 d), respectively. The DIC indicates that HRNM1 was the model that best fit the data (Table 1) and was chosen for detailed analysis in this study. A similar result was reported by Corr ea et al. (2009) for postweaning BW gain in Devon cattle. The poorer fit of the heteroskedastic model deserves further research to identify structural functions other than the one specified in HRNM2 because other investigators have found heteroskedastic residual variances with RN applications (Calus et al., 2002; Pollett and Greeff, 2004; Knap and Su, 2008) and there is evidence that residual variances show a linear increase with increasing herd production levels (Kolmodin et al., 2002). Moreover, DIC comparison between models is based on model fit, but for genetic evaluation purposes it would be more relevant to compare models based on their prediction ability, which may not be trivial with field data. Provided sufficient information is available, one possible alternative would be to contrast the RN of the sire obtained by different models with their future progeny performance in different environmental

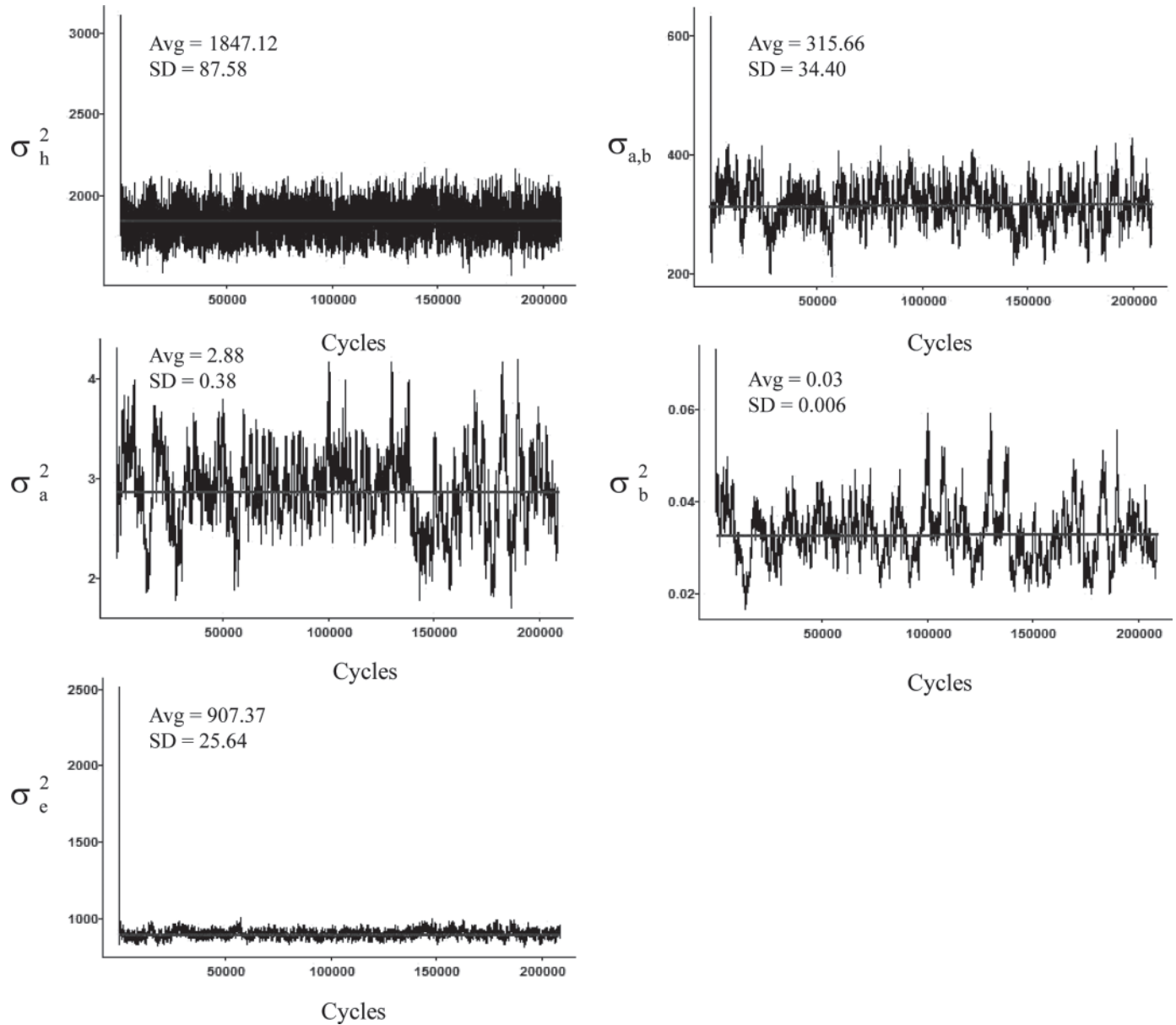


Figure 1. Posterior means and SD and trace plots of (co)variance component vs. Markov chain cycles. σ_h^2 = contemporary group variance; $\sigma_{a,b}$ = covariance between level and slope of reaction norms; σ_a^2 = intercept variance; σ_b^2 = reaction norm slope variance; and σ_e^2 = error variance.

levels, excluding the records of this offspring from the analyses.

Closely similar solutions for CG were obtained with HRNM1, HRNM2, and the AM, with a correlation of 0.99. Similarity between true and estimates of environment values ($r = 0.97$) was observed by Su et al. (2006) in a simulation study. However, the same authors found a correlation between true herd-year effect and herd-year observed mean of only 0.90 and argued that usage of phenotypic means as proxies for environmental values results in poor inferences.

For the HRNM1, the estimated environmental gradient ranged from -105 to 150 kg, with a mean \pm SD of 0.80 ± 41 kg. The additive genetic variance and, consequently, the heritability shown in Figure 2 increased along the environmental gradient. For example, the

Table 1. Summary of the comparison between the hierarchical reaction norm models and the animal model based on the deviance information criterion

Model	Deviance	PD ¹	DIC ²
HRNM1 ³	135,827.03	2,305.83	138,132.86
HRNM2 ⁴	136,139.76	2,050.16	138,189.92
AM ⁵	136,710.82	3,432.29	140,143.11

¹Effective number of parameters.

²Deviance information criterion.

³Homoskedastic reaction norms model.

⁴Heteroskedastic reaction norms model.

⁵Animal model.

Table 2. Spearman rank correlation between breeding values obtained by the animal model (AM) and calculated for homoskedastic reaction norms model (HRNM1) at the 5th, 50th, and 95th environmental gradient percentiles

Model (environmental level)	HRNM1 (low) ¹	HRNM1 (median) ²	HRNM1 (high) ³
AM (overall)	0.933	0.925	0.910
HRNM1 (low) ¹		0.978	0.958
HRNM1 (median) ²			0.996

¹Environmental gradient 5th percentile = -59.9 kg.

²Environmental gradient 5th percentile = -3.1 kg.

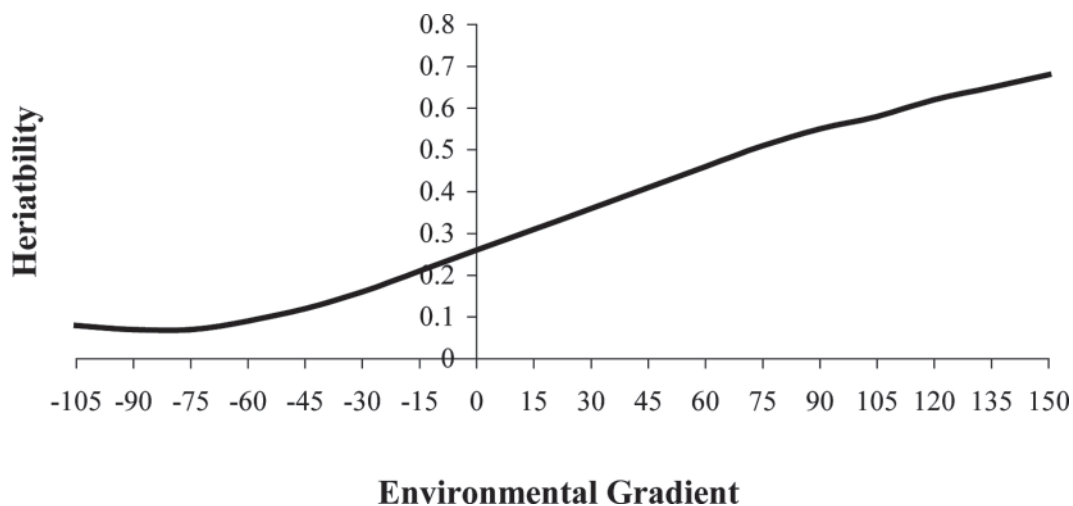
³Environmental gradient 5th percentile = +77.0 kg.

posterior mean heritability ± SD was 0.089 ± 0.015 and 0.511 ± 0.035 , respectively, for the 5th and 95th percentiles. This indicates that a larger phenotypic variation proportion is due to additive genetic factors as the environmental conditions improve, which is in agreement with results of other RN studies for growth and production traits in cattle (Cromie, 1999; Kolmodin et al., 2002; Fikse et al., 2003; Shariati et al., 2007; Corrêa et al., 2009). Therefore, a better response to selection is achieved at greater levels of the environmental gradient (Figure 2). On the other hand, the posterior mean heritability ± SD obtained with the AM was 0.20 ± 0.02 , a value that is less than the estimate with HRNM1 for the average and positive environments.

The posterior mean correlation between a_i and b_i was high (0.90 ± 0.03). This finding indicates that animals with greater BV for long-yearling weight responded better to environmental improvement, characterizing scale effect (Falconer and Mackay, 1996) as the form of G×E for long-yearling weight. This is also supported by the high (>0.90) Spearman rank correlations observed between BV obtained by the AM and calculate for homoskedastic RN model (HRNM1) at the 5th, 50th, and 95th environmental gradient percentiles (Table 2). Figure 3 illustrates predicted RN for a random sample of 7 animals of the studied population, demonstrating G×E by the variation in BV of the animals along the

environmental gradient and some reordering of genotype ranks. Similar results were observed for Brazilian Angus postweaning BW gain (Cardoso et al., 2010). When compared with the traditional AM, genetic evaluations based on the RN model are expected to result in greater response to selection, especially in the best environments (Kolmodin et al., 2003).

The observed frequencies of robust, plastic, and extremely plastic genotypes were 20,288, 1,446, and 54, respectively. This result indicates genetic variability in phenotypic plasticity. Moreover, the minimum estimated animal RN slope of -0.448 indicates that all animals increase their performance with the environmental improvement. This is evident because $h_j + a_i + b_i h_j$ part RN model for a single animal i can be written as $a_i + (1 + b_i) h_j$ (Su et al., 2006), and as long as $b_i > -1$, performance increases with increasing h_j . However, because different individuals have different slopes, reranking can happen under different environments. These adaptive variations might be included in selection indices to select more robust genotypes or to favor more plastic genotypes that respond to environmental improvement of a given trait. Therefore, this breed and other similar populations could benefit from implementing RN predictions to optimize breeding programs that select seedstock for multiple environments (de Jong and Bijma, 2002; Kolmodin and Bijma, 2004).

**Figure 2.** Heritability estimates for long-yearling weight along the environmental gradient in Canchim cattle.

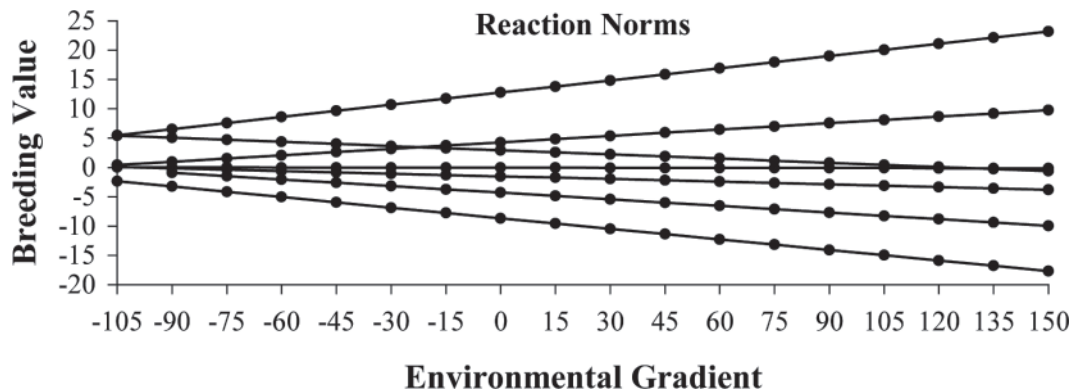


Figure 3. Reaction norms along the environmental gradient for long-yearling weight obtained for some Canchim animals.

High correlations among BV are observed along most of the environmental gradient, with these correlations only decreasing in extremely unfavorable environments (Figure 4). This reordering of BV at decreased levels of the environmental gradient confirmed the existence of $G \times E$. Other studies with beef breeds under grazing conditions in Brazil (Alencar et al., 2005; Corrêa et al., 2009; Cardoso et al., 2010) also demonstrate that genetics suitable for harsh environments is generally quite different from that for average or superior conditions.

Implications

The RN models are a promising tool to jointly take genotype by environment interaction and heterogeneity of genetic variances in different environments into account in genetic evaluation programs. This could increase selection efficiency and genetic progress in each specific environment. Nevertheless, the practical usage of RN in the choice of superior livestock may impose

a change of paradigm and the selection strategies of the breeders, because for each environment a different genetic value will be obtained for the selection candidate. Moreover, required environmental characterization is frequently a challenging task. In this beef cattle study, CG effects were regarded as environmental covariates, because they represented the most elemental set of management conditions in data in the current study. However, small subclass size could be an issue and bias environmental level estimation with this definition. Therefore, further studies on the definition of production and selection environments considering; for example, climate, geographical and herd management and structure variables are warranted before industry application of the RN methodology.

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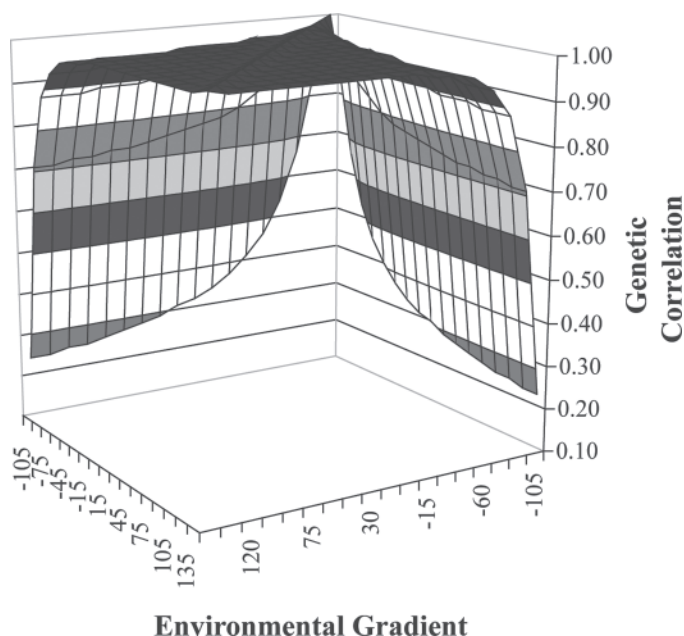


Figure 4. Surface graph of correlations among genotypes along the environmental gradient.

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