Original study

Reaction norms of direct and maternal effects for weight at 205 days in Polled Nellore cattle in north-eastern Brazil

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Abstract

This study investigated the presence of genotype-environment interaction (GEI) for body weight adjusted to 205 days of age (W205) in Polled Nellore cattle raised in north-eastern Brazil using reaction norm (RN) models. The reaction norm hierarchical models (RNHM) included the fixed (linear and quadratic) effect of cow's age, random effect of contemporary group (CG), RN level and slope for additive direct and maternal genetic effects and permanent maternal environmental effect. The one-step reaction norm model with homogeneous residual variance ($RNHM_{1s}Hm$) yielded the best adjustment compared to the others. Based on this model, the estimates of direct additive and maternal variances and increased with environment improvement ($35.34\pm7.92\,kg^2$ to $134.42\pm25.97\,kg^2$ and $12.76\pm5.38\,kg^2$ to $58.22\pm19.74\,kg^2$ for low and high-quality environments, respectively). The estimates of heritability direct additive and maternal too increased with environmental improvement (0.08 ± 0.02 to 0.24 ± 0.04 and 0.03 ± 0.01 to 0.10 ± 0.04). The correlation between the intercept and the slope of RNHM indicates that animals with higher genetic values respond more efficiently to environmental improvements, representing a scale effect for W205. These results allowed us to characterize the GEI for W205 and showed that specific evaluation should be performed with low, intermediary and high production levels.

Abbreviations: AM: Animal model, BF: Bayes Factors, CG: Contemporary group, CPO: Conditional Predictive Ordinate Deviance, DIC: Deviance Information Criterion, GEI: Genotype-environment interaction, MCMC: Markov Chain Monte Carlo, RN: Reaction norm, RNHM: Reaction norm hierarchical models, RNM: Reaction norm models, W205: Weight adjusted to 205 days of age

Introduction

Genotype-environment interaction (GEI) implies that similar genotypes respond differently to environmental changes, which might cause a reclassification or changes in ranking genetic values (Falconer & Mackay 1996). In livestock genetic improvement, this effect can lead to discrepancies in breeding values once the best bloodstock raised in a specific production system might produce an inferior offspring in other environments (Lynch & Walsh 1998)

Brazil has a wide range of environments for animal production since it covers nearly half of South America and encompasses distinct biomes and climate conditions. This is particularly true in north-eastern Brazil, which includes areas with favourable conditions for animal production as well as less favoured ones, near to central region and under the influence of semiarid climate. Therefore, it is important to study genotype-environment interaction (GEI) in this region and necessary to include GEI in estimates of genetic values in order to maximize response to selection.

Usually, reaction norm models (RNM) have been used to assess GEI in several economically important breeds, such as dairy cattle (Bohmanova *et al.* 2008, Streit *et al.* 2012) and beef cattle (Ambrosini *et al.* 2012, Corrêa *et al.* 2009, Fördös *et al.* 2010, Mattar *et al.* 2011, Vostry *et al.* 2009, Szabó *et al.* 2010). The utilization of RNM in identification of high-quality individuals might potentially change the current paradigm of selection strategies, once the predictions of genetic values can differ for the same candidate to selection in distinct environments (Mattar *et al.* 2011).

Reaction norm models (RNM) allow us to describe the gradual and continuous variation of genetic breeding values related to economically important traits throughout an environmental gradient. Although this approach remains overlooked in routine genetic assessments in Brazil, many authors (Ambrosini *et al.* 2012, Alencar *et al.* 2005, Fridrich *et al.* 2008, Espasandin *et al.* 2011) verified the presence of GEI in different populations. Additionally, a model including the maternal effect in GEI studies via RNM has not been performed yet. Therefore, GEI and maternal effects were assessed in the present study for weights adjusted at 205 days in Polled Nellore cattle raised in north-eastern Brazil based on reaction norms using a Bayesian approach.

Material and methods

The work was carried out with records of Polled Nellore animals born from 1975 to 2007 in north-eastern Brazil. The initial database was provided by ABCZ, the Brazilian Association of Zebu Breeders, and comprised 35 221 records. Nonetheless, those individuals without weight data (8 637), disconnected (143), measured outside the interval from 80 kg to 280 kg (164), born from cows below 1.9 years-old and over 25 years-old (171) or with less than 3 progenies (8 390) and from breeders with less than 5 progenies (624), as well as contemporary groups

with less than 5 observations and average weight above +3 standard deviations (6 948) were excluded. Therefore, 10 144 records were used for analysis of weights adjusted at 205 days of age (W205).

The routines created by Cardoso (2008) in SAS v9 (SAS Institute Inc., Cary, NC, USA) were used to prepare the dataset for RN analyses. Afterwards, the connectivity of contemporary groups (CG) was tested based on the total number of genetic links (minimum of 10) using the software AMC (Roso & Schenkel 2006). The connectivity of CG resulted in a main archipelago (CG with the highest number of genetic links and interconnected CG) with 10 144 animals in 1 094 CG and 143 animals in 91 disconnected CG. Only the main archipelago was used for the analysis.

The CG was formed so that all animals shared a common production environment, including herd, year, birth period and sex. The birth periods were grouped into four classes (period 1: May, June and July; period 2: August, September and October; period 3: November, December and January; and period 4: February, March and April).

The software INTERGEN (Embrapa Pecuária Sul, Bagé, RS, Brazil) was used with a standard animal model (AM) to obtain the estimates of mean environmental effects according to CG and to provide a comparative analysis in relation to RNM. This software adjusts Bayesian hierarchical models with parameters defined in structured levels or stages comprising the diversity of animal performance data. In the case of RNM, the individual genetic value is obtained by a function of the mean environmental level corresponding to the solution of CG to which the record belongs, i.e., there is a specific genetic value for each animal in each environmental level (Cardoso & Tempelman 2012).

Initially, a standard animal model (AM) that disregards GEI was adopted to estimate individual genetic values and to obtain the estimates of mean environmental effects based on CG:

$$y_{ij} = x_i'\beta + X_j + a_i + m_i + ep_i + e_{ij} \tag{1}$$

where y_{ij} is the record of animal i in environment j, β is the vector of fixed effects (linear and quadratic for cow's age), x_i' is the incidence vector, X_j is the random CG environmental effect, a_i is the additive genetic value of animal $\dot{i}$, m_i is the maternal genetic value of animal $\dot{i}$, ep_i is the maternal permanent environmental effect; and e_{ij} is the residual error.

In addition, two methodologies were implemented to describe the reaction norm hierarchical models (RNHM). Firstly, we used the model proposed by Kolmodin et $al.$ (2002) assuming the environment solutions of AM as co-variables in two-step RNHM (RNHM$_{2s}$), as follows:

$$y_{ij} = x_i'\beta + \phi\hat{X}_j + a_i + m_i + ep_i + b_{1i}\hat{X}_{j1} + b_{2i}\hat{X}_{j2} + e_{ij} \tag{2}$$

where ϕ is the fixed regression coefficient, a_i is the additive genetic value for the RN intercept or level in animal i, m is the maternal genetic value for the RN intercept or level in animal i, ep_i is the permanent maternal environmental effect, b_{1i} is the random regression coefficient or direct RN slope of animal i in the environment represented by $\hat{X}_j$, b_{2i} is the random regression coefficient or maternal RN slope of animal i in the environment represented by $\hat{X}_j$; X_j is the predictor obtained in (1) and e_{ij} is the residual error.

Secondly, the one-step RNHM (RNHM$_{1S}$) proposed by Su *et al.* (2006) was used. Albeit similar to the previous model (2), RNHM$_{1S}$ is distinguished by the simultaneous estimation of CG solutions and intercepts and slopes of RN. In this model, the CG effects are regarded as unknown co-variables in RNM, in which the estimates for environmental effects were used as a covariant to obtain the slope of the animal RN, that is X_j and b_i are jointly estimated as follows:

$$y_{ij} = x_i'\beta + X_j + a_i + m_i + ep_i + b_{1i}X_j + e_{ij} \tag{3}$$

Two different assumptions were adopted for the residual variance in tested models: (a) homoscedasticity for AM, RNHM$_{2S}$ (RNHM$_{2S}$Hm) and RNHM$_{1S}$ (RNHM$_{1S}$Hm) where $e_i \sim N(0,\sigma_e^2)$ is the residual variance; and (b) heteroscedasticity for RNHM$_{2S}$ (RNHM$_{2S}$He) and RNHM$_{1S}$ (RNHM$_{1S}$He), with $e_i \sim N(0,\sigma_{ej}^2)$ and $\sigma_{ej}^2 = \sigma_e^2 \eta^{x_j}$, where η is the heterogeneity parameter of residual variance at X_j environmental level, following the structural model proposed by Cardoso *et al.* (2005).

The direct additive and maternal genetic variances in environment X, $\sigma_A^2|X$ and $\sigma_m^2|X$, were obtained by:

$$\sigma_A^2|X = var\,(a_i + b_{1i}X_j) = \sigma_a^2 + \sigma_b^2 x^2 + 2\sigma_{a,b}X$$

$$\sigma_m^2|X = var\,(a_i + b_{2i}X_j) = \sigma_m^2 + \sigma_b^2 x^2 + 2\sigma_{a,b}X \tag{4}$$

where σ_a^2 are the additive genetic variance components estimated for the RN intercept, σ_m^2 are the maternal genetic variance components estimated for the RN intercept, σ_b^2 are the variance components estimated for the RN slope, and σ_{ab}^2 are the estimate of covariance components between RN intercept and slope.

The heritabilities were estimated by the ratio between genetic variance and phenotypical (genetic+environmental) variance, as follows:

$$h_a^2|X = \frac{\sigma_a^2|X}{\sigma_a^2|X + \sigma_m^2|X + \sigma_{pe}^2 + \sigma_e^2|X}$$

$$h_m^2|X = \frac{\sigma_a^2|X}{\sigma_a^2|X + \sigma_m^2|X + \sigma_{pe}^2 + \sigma_e^2|X} \tag{5}$$

where $\sigma_e^2|X$ is the residual variance in environment *X*, obtained by $\sigma_e^2|X = \sigma_e^2 \hat{\eta}^X$ in the heteroscedastic model and by σ_e^2 in the homoscedastic model.

A Bayesian approach (Gianola & Fernando 1986) via Markov Chain Monte Carlo (MCMC) method (Blasco 2001) was implemented to obtain the parameter estimates according to the following procedure (Figure 1): a) a pilot sample was analysed with 55 000 cycles, 5 500 burn-in and thinning of 5; b) using the variance component obtained in (a) and R package (R Development Core Team 2008) - Bayesian Output Analysis - BOA (Smith 2007), the test by Raftery & Lewis (1992) was applied to determine the new chain size and thinning; moreover, and c) the burn-in was evaluated according to Heidelberger & Welch (1983).

The final analyses comprised runs with chains from 330 000 to 660 000 cycles. A *posteriori* means, standard deviations and percentiles (0.025 and 0.975) of parameter values were obtained from their marginal posterior densities obtained through KDE procedure available in SAS (SAS Institute Inc., Cary, NC, USA)
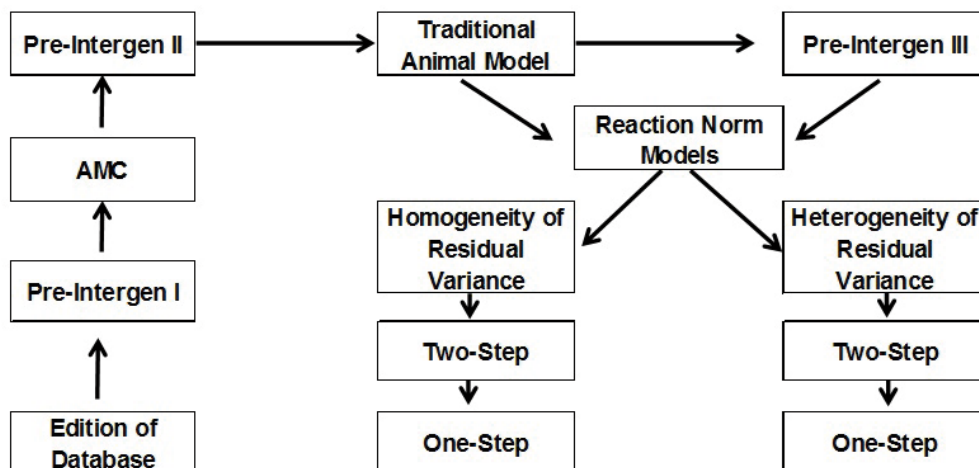
Figure 1
Flowchart showing the stages required to analyses in the INTERGEN software

The Geweke's convergence diagnostic for Markov chains (Geweke, 1992) was performed. This is a standard Z-test for equality of the means of the conditional data distribution logarithm, denoted by $l_i^{(j)} = \log p\,(y|\theta^{(j)}, M_j)$ in the first 10 % and the last 50 % of the Markov chain, similarly to the statistics proposed by Brooks and Roberts (1998):

$$Z_i = \frac{(\bar{l}_i^A - \bar{l}_i^B)}{\sqrt{\frac{1}{n_A}|\hat{S}_i^A(0) + \frac{1}{n_B}|\hat{S}_i^B(0)}}$$

where $l_i^A = \frac{1}{n_A}\sum_{j=1}^{n_A} l_i^{(j)}$, $l_i^B = \frac{1}{n_B}\sum_{j=n^*}^{m} l_i^{(j)}$, $n_A = 66{,}000$, $n_B = 330{,}000$, $n^* = 330{,}001$, and with $\hat{S}_i^A(0)$ and, $\hat{S}_i^B(0)$ where the respective estimates of spectral density at frequency zero was obtained by the procedure SPECTRA in SAS (SAS Institute Inc., Cary, NC, USA), for the first n_A and the last n_B cycles in the MCMC of length m. Extreme absolute values of the Z_i score in a two-tailed test reject the convergence test.

The following criteria were used to verify the best adjusted model: Deviance Information Criterion (DIC) (Spiegelhalter et al. 2002); Conditional Predictive Ordinate Deviance (CPO) (Gelfand 1996) and Bayes Factors (BF), described as the deviance based on the Monte Carlo estimator (Newton & Raftery 1994). These deviations represent the degree of separation of the evaluated model in relation to a hypothetically perfectly adjusted model, in which the lowest values indicate the best adjustment.

Results and discussion

The two-step RNHM assuming homogeneity or heterogeneity of residual variance (RNHM$_{2S}$Hm and RNHM$_{2S}$He, respectively) presented convergence flaws and resulted in overestimated parameters. Once the data could not be adjusted to both models, the present results are based on animal model (AM), one-step homoscedastic (RNHM$_{1S}$Hm) and heteroscedastic (RNHM$_{1S}$He) norm reaction models.

Convergences at 5 % ($P>0.05$) were obtained in all AM parameters while the parameters in RNHM$_{1S}$Hm converged at 1 % ($P>0.01$) using Geweke's test. Using the same test, Cardoso *et al.* (2011) mean converges of Z=1.08 ($P=0.2788$) for the standard animal model; Z=2.15 ($P=0.0310$) for RNHM$_{2S}$Hm; Z=−1.68 ($P=0.0913$) for RNHM$_{1S}$Hm; Z=−2.25 ($P=0.0238$) for RNHM$_{2S}$He; and Z=−0.92 ($P=0.3545$) for RNHM$_{1S}$He.

Amongst the tested MNR, RNHM$_{1S}$Hm yielded improved data adjustment, being the best model in two out of the three analysed criteria (DIC and CPO). The RNHM$_{1S}$Hm was inferior only by BF and had the second best adjustment under this criterion (Table 1).

Table 1

Deviance values based on Bayes Factors (BF), deviance information criterion (DIC) and condition predictive ordinate (CPO) obtained in standard animal model (AM) and one-step homoscedastic (RNHM$_{1S}$Hm) and heteroscedastic (RNHM$_{1S}$He) hierarchical reaction norms models

Model	DIC	CPO	BF
AM	89 388.50 (2nd)	91 269.01 (2nd)	85 673.88 (1st)
RNHM$_{1S}$Hm	88 351.23 (1st)	90 549.61 (1st)	87 947.24 (2nd)
RNHM$_{1S}$He	89 995.46 (3rd)	92 046.88 (3rd)	88 882.07 (3rd)

1st, 2nd, and 3rd indicate the adjustment ranking

Reaction norm models based on homogeneous and heterogeneous residual variance were previously used to assess standardized post-weaning weight gain in Angus (Cardoso & Tempelman 2012), Devon (Corrêa *et al.* 2009), Hereford (Cardoso *et al.* 2011) and Canchim (Mattar *et al.* 2011) cattle. These authors compared homoscedastic RNHM to heteroscedastic RNHM and AM and concluded that the former yielded the best adjustments.

Markov chains with 660 000 iterations and burn-in of 60 000 (10 % discarded) were obtained in homoscedastic RNHM (chosen model), generating posterior samples at every 113 cycles. Besides the Geweke's test (Geweke 1992), the chain convergence was also evaluated by line graphs of the sample values in all co-variance components against the chain cycle (data not shown).

In RNHM$_{1S}$Hm, the environmental gradient solutions ranged from −54 to 60 kg, characterizing low and high-quality environments (management levels). The direct and maternal heritability estimates in AM were 0.35±0.03 and 0.10±0.02, respectively (Figure 2). These values were higher than the estimated ones by RNHM$_{1S}$Hm in all RN levels, and also superior to the values reported by Cardoso & Tempelman (2004) (0.19±0.02) and Corrêa *et al.* (2009) (0.13±0.017) for direct heritability of standardized post-weaning weight gain (PWG365) in AM. However, it should be pointed out that both reports were based on Bos taurus breeds raised in southern Brazil, where the production system is completely different from that performed in the north-eastern region.

On the other hand, the direct heritability estimated by AM in the present study was inferior while maternal heritability was higher to those reported by Malhado *et al.* (2005) based on restricted likelihood for W205 in Polled Nellore from Bahia state, north-eastern Brazil (0.24±0.04 and 0.20±0.06, respectively).
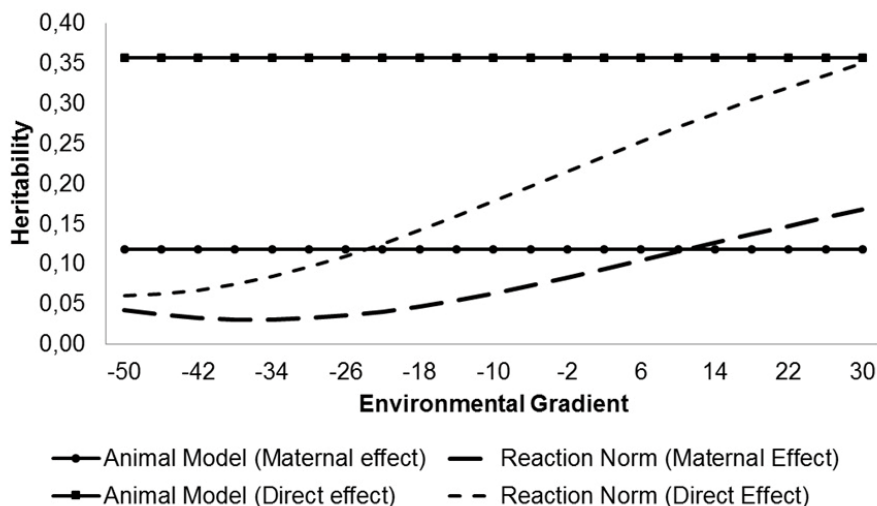
Figure 2
Direct and maternal heritability values of weight at 205 days of age (W205) in animal model (AM) and one-step homoscedastic hierarchical reaction norms models (RNHM$_{1S}$Hm) according to environmental gradient

The mean a *posteriori* correlation between RN slope and intercept was 0.81±0.10 and 0.70±0.15, for direct and maternal effect, respectively. This result indicates that animals with higher direct and maternal genetic values responded more efficiently to environmental improvements, i.e. they comprise more responsive genotypes of high plasticity, characterizing a scale effect of GEI (Falconer & Mackay 1996). Scale effects have also been reported by Mattar *et al.* (2011) in Canchim cattle and by Kolmodin *et al.* (2002) in protein production of Nordic dairy cattle. Such effect can be observed at all environmental levels, with a special increase in the genetic values of breeders in high-quality production systems (Figure 3).

The scores of some breeders have also changed along the environmental gradient, both for direct and maternal genetic values (Figures 3A and 3B). This kind of interaction is a major handicap for selection, once it results in inadequate choice of breeders to certain environments, thus jeopardizing the effectiveness of genetic improvement.

The slope of RN ranged from −0.36 to 0.23 degrees for the direct effect with a higher incidence of robust and intermediary genotypes (−0.20 and 0.20 degrees), observed in 99.35 % (10 100) of animals. Plastic genotypes (−0.36 to −0.21 and 0.21 to 0.23 degrees) were identified in only 0.65 % (44) of animals.

In the case of maternal effect, the slope values were less variable (−0.15 to 0.14 degrees) thus indicating less variation of the genotypic values across different environments. Nonetheless, the RN for both direct and maternal effects in the 10 breeders with the largest offspring revealed changes in genetic values according to environmental gradient even in less plastic genotypes (Figure 3A and 3B).

These results demonstrate the importance of including GEI in genetic assessments to reach the best performance in distinct environments by selecting highly productive robust genotypes or giving preference to plastic genotypes that respond positively to environment improvements.
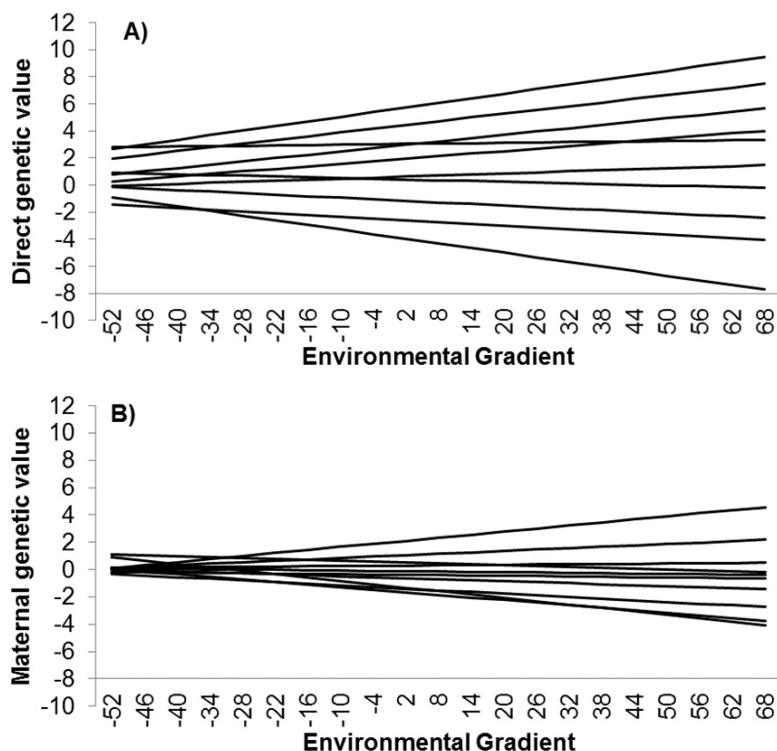
Figure 3
Reaction norm for direct (A) and maternal (B) effect in W205 along the environmental gradient in the ten most used breeders

Spearman's ranking correlations of breeders with highest genetic values ranged from 0.48 to 0.93 in each environment and model when 5 % of top-ranked breeders were chosen (above the diagonal) and from 0.51 to 0.97 when 10 % of top-ranked breeders (below the diagonal) were used (Table 2). The lowest correlation values were observed when the animal model was compared to RN models, thus confirming the interaction between genotype and environment (GEI). No considerable changes in ranking were observed when comparing low, medium and high levels of RNHM$_{1S}$Hm. Slight differences were detected between the results based on 5 % and 10 % top-ranked breeders (Table 2).

Table 2
Spearman's correlations among classifications of Polled Nellore breeders with the highest genetic values raised in north-eastern Brazil (5 % above the diagonal and 10 % below the diagonal) according to animal model (AM) and one-step hierarchical reaction norms model (RNHM$_{1S}$Hm) at different environmental levels.

Models	AM		RNHM$_{1S}$Hm (Low)		RNHM$_{1S}$Hm (Medium)		RNHM$_{1S}$Hm (High)	
AM			0.6	0.067	0.81	0.001	0.72	0.001
RNHM$_{1S}$Hm (Low)	0.52	0.005			0.67	0.005	0.48	0.078
RNHM$_{1S}$Hm (Medium)	0.77	0.000	0.67	0.000			0.93	0.000
RNHM$_{1S}$Hm (High)	0.76	0.000	0.61	0.000	0.97	0.000		

When only 5 % of the top-ranked breeders were taken into account, the greatest difference in classification was observed between low-level RNHM and high-level RNHM (0.48), followed by correlation between AM and low-level RNHM (0.60) and medium-level RNHM and high-level RNHM (0.67). The correlation values considering 10 % of the best breeders behaved similarly, ranged from 0.52 to 0.97. The highest difference in this case was obtained between AM and low-level RNHM (0.52) and between low-level RNHM and high-level RNHM (0.61). Both results, based on 5 % or 10 % top-ranked breeders, indicate changes in ranking.

In Devon cattle, Corrêa *et al.* (2010) obtained Spearman's correlation values for standard post-weaning weight at 365 days varying from 0.12 to 0.98 and from 0.75 to 0.99 for the best 5 % and 10 % breeders, respectively. According to these authors, these values implied moderate to high ranking changes. Different scores were also reported in dairy cattle by Kolmodin *et al.* (2002), indicating that classification of low-performance ranks would be beneficial only if performed in a specific environment.

Genetic correlations between genetic values at distinct environments were narrower for direct effect in $RNHM_{1S}Hm$ (0.33 to 1.00) and higher for maternal effect (-0.24 to 1.00) (Figure 4), which characterizes GEI. The present results differ from those reported by Corrêa *et al.* (2009), who described negative genetic correlations among environmental gradient levels in standard post-weaning weight gain at 365 days. On contrary, Mattar *et al.* (2011) observed values between 0.24 and 1.00, suggesting that animals were more responsive to improvement of environmental conditions. Both studies show that the genetic pool required for productivity in each environmental level should be different.
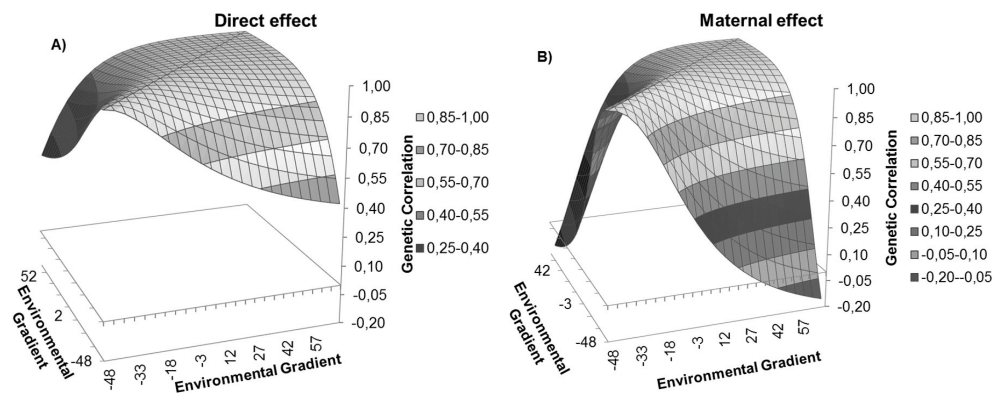

Figure 4
Response surface graph of correlations between direct (A) and maternal (B) genetic values and environmental gradient

The application of reaction norm models in GEI studies of Polled Nellore cattle from northeastern Brazil is new and allowed us to identify GEI in this population. A scale effect was observed, with differentiated responses of genotypes in relation to the environmental gradient that determined changes in animal ranking. These changes were more accentuated in high-quality production systems; as the environmental conditions improve, the differences

between genetic values increase once animals are able to express their full genetic potential. Genotype-environment interaction (GEI) is present for both direct and maternal effects in Polled Nellore cattle from north-eastern Brazil, both for direct and maternal effect. The assumption of one-step homogeneous residual variance in the reaction norm hierarchical model (RNHM$_{1S}$Hm) yielded the best adjustment to data. Scale effects in GEI and ranking changes along the environmental gradient were observed, as confirmed by the correlation variation among breeders of high genetic values. The inclusion of this methodology in improvement programs might increase selection effectiveness, leading to faster genetic progress in this economically important breed.

Acknowledgements

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