

Study of Genotype by Environmental Interaction for weights of Nellore Cattle Using Reaction Norms

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Introduction

Brazil has a large territorial extension and regions with marked climate differences. The Nellore breed is the most numerous beef cattle breed in Brazil and it is distributed throughout the country. There are several beef cattle companies which run their own genetic evaluations including large data sets of animals distributed in various regions of the country. Generally, genotype x environmental interaction is ignored in most of these breeding programs. Selection response in farm animals is often hampered by genotype x environmental interaction. Van Tassel and Berger (1994) reported that even with relatively low levels of interaction effects, the biases in sire variance and heritability estimates were substantial when interaction was not included in the model. Several studies have examined the importance of genotype by environmental interaction on several beef cattle traits (De Mattos D., Bertrand J.K. and Misztal I. (2000), Johnston et al. (2003)). There are different methodologies to study genotype by environmental interaction (Westcott (1986)). Recently, reaction norms models have been applied to verify the effect of genotype x environmental interaction on many economically important traits (Kolmodin et al. (2002), Windig (2006) and Correa, M.B.B., Dionello, N.J.L. and Cardoso, F.F. (2009). Random regression models and covariance functions have been used to study genotype by environment interaction effects in a variety of traits. Usually, the phenotypes are regressed on an environmental gradient and adaptive reaction norms are estimated (Kolmodin et al., (2002), Pégolo et al. (2009)). The objective of this study was to estimate reaction norms for Nellore bull weights adjusted for 450 days of age, using random regression models.

Material and methods

Data. Data from 39,686 animals sired by 61 Nelore bulls, and born from 1984 to 2007 in 30 Brazilian herds belonging to Conexão Delta G Breeding Program were analyzed. The trait analyzed was 450-day adjusted weight (W450). Contemporary groups (CG) were defined as: animals of the same sex, born in the same herd, year and season (summer, winter, spring or autumn), and weighted at the same herd. Weight records out of the range given by the mean of $CG \pm 3$ standard deviations were excluded. Also, CG with less than eight animals were

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excluded. The environmental groups (EG) for random regression analysis were defined as herd and year of birth. Sires with less than 50 offspring or with offspring in less than eight EG were not considered in the analysis. The EG average solutions were standardized to a mean of zero and a standard deviation of one. The EG standardized means were multiplied by ten and only the integer part of these values was considered. Environmental group values below -15 were considered in EG=-15 (bottom limit) and those above +15, in EG=+15 (upper limit).

Analyses. First, an analysis using a univariate animal model was performed to obtain the EG solutions. The model included the additive direct effect as random and fixed effects of EG and the animal age (linear effect) and dam age (linear and quadratic effects) as covariables. For random regression analyses, sire additive direct random effect was modeled through linear or quadratic Legendre polynomials on EG standardized means. Mean trends were taken into account by a linear regression on Legendre polynomials of environmental group means. In addition, CG were included as fixed effects and dam age at calving (linear and quadratic effects) and animal age at recording (linear effects) as covariables. Residual variances were modeled considering 1, 4 (-15 to -11; -10 to -1; 0 to 4; 5 to 15) and 6 (-15 to -11; -10 to -6; -5 to -1; 0 to 4; 5 to 10; 11 to 15) classes. (Co)variance functions were estimated by restricted maximum likelihood (REML) using the Wombat package (Meyer (2006)). Results from different models of analyses were compared by the Akaike Information criterion (AIC) and the Schwarz' Bayesian Information criterion (BIC).

Results and discussion

The distributions of animal weights along the environmental gradient were skewed to the right. The W450 average by EG varied from 245 kg (unfavorable environments) to 355 kg (favorable environments). A summary of random regression analysis is shown in Table 1. The results of both criteria, AIC and BIC, pointed out that a model assuming heterogeneous residual variance fitted the data better than one with homogeneous residual variances. According to BIC results, a step function with 6 classes was the best to model residual variances.

Table 1: Order of fit of sire additive (k_a) effect, number of residual classes (r), number of parameters (np), log likelihood value ($\log L$), Akaike information criterion (AIC), and Schwarz' Bayesian information criterion (BIC)

Model ¹	k_a	r	np	Statistic criteria		
				$\log L$	AIC	BIC
L.r1	2	1	4	-155,813	311,634	311,668
L.r4	2	4	6	-153,836	307,672	307,732
L.r6	2	6	9	-153,817	307,650	307,728
Q.r6	3	6	12	-153,801	307,626	307,729

¹L=linear Legendre polynomials; Q= quadratic Legendre polynomials

Alternative models were compared varying the order of covariance functions for the sire additive genetic effect. Results from AIC indicated a quadratic model as the most adequate to describe the changes in covariance structure of the data with EG. Alternatively, BIC criteria

indicated a linear model as the best to fit the data. BIC criterion attributes a more rigorous penalty to the number of parameters and tends to favor more parsimonious models than AIC. Since the parameter estimates obtained with both models were similar and the linear model tended to be more stable at the extremes, we opted for this last model. The W450 heritability estimates obtained by L.r6 model were from low to moderate (Figure 1). The heritability estimates showed a slightly tendency of increasing at the more favorable EG.

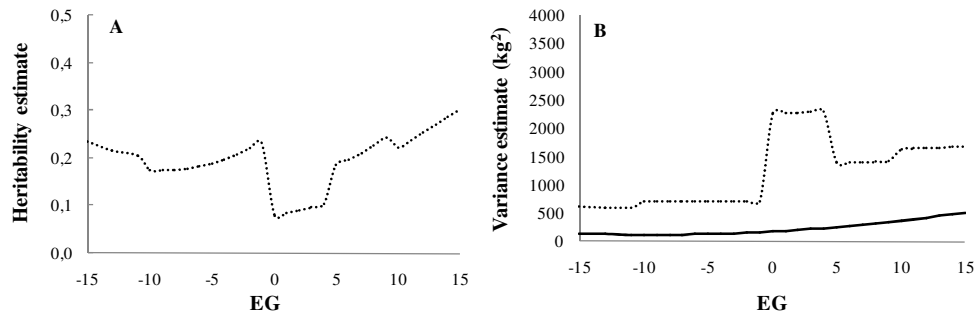


Figure 1: Estimates of heritability (graph A), additive genetic (graph B: solid line) and phenotypic variance (dotted line: graph B) obtained using a linear sire model with 6 classes for residual variances

This tendency is similar from that reported by Pégolo et al. (2009), which applied reaction norms on different environmental gradient for 450-days Nellore weights, and observed the lowest heritability estimates in the intermediate environmental gradient and the highest heritability estimates at extreme environments. Correa et al. (2009) studied the presence of genotype by environment interaction for post weaning gain standardized to 345 days (G345) in Devon cattle via reaction norms, and reported that heritability estimates for G345 increased with the environmental gradient. The sire additive genetic variance estimates increased gradually as the environmental conditions improved. In agreement with Calus M.P.L., Groen A.F. and Jong G. (2002), the heterogeneity of variances has two possible origins, scaling of both genetic and residual variances and genotype by environmental interaction. Phenotypic variance estimates tended to increase along the environmental gradient as a whole. The genetic correlation estimates between W450 in different EG, obtained by L.r6 model varied from 0.12 to 0.99 (Figure 2). For Robertson (1959), genetic correlation estimates below 0.80 are indicative of significant genotype by environment interaction. Genetic correlation estimates were high between similar environments (unfavorable or favorable environments) and low between opposite extremes environments. Our results are similar to those obtained by Pégolo et al. (2009), for Nellore W450. Thus, the results obtained in the present study revealed marked genotype by environment interaction between opposite extreme environments.

Conclusion

Considerable genotype by environment interaction for 450-day weight of Nellore cattle was found using random regression reaction norms models. For genetic evaluation of 450-d

weights it is necessary to consider heterogeneity of residual variances, and a model with linear polynomials for sire additive genetic effects and six classes of residual variances was the most adequate to describe the covariance structure across environmental groups.

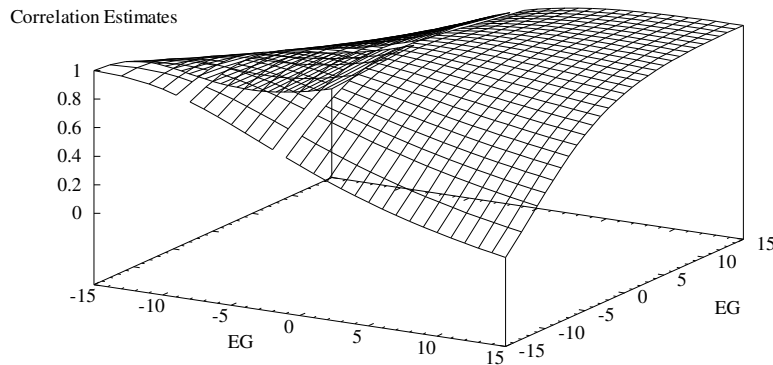


Figure 2: Genetic correlation estimates between 450-days weights in different environmental groups (EG - kg), obtained using a linear sire model with 6 classes for residual variances

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