



Associations among growth, scrotal circumference, and visual score of beef cattle in performance tests on pasture or in feedlots

Fernanda Santos Silva Raidan¹, Juan Salvador Andrade Tineo¹, Mariana Mamedes de Moraes¹, Thiago Campos Escarce¹, Andresa Eva Melo de Araújo¹, Muller Marques de Carvalho Gomes¹, Henrique Torres Ventura², Fabio Luiz Buranelo Toral^{1*}

¹ Universidade Federal de Minas Gerais, Escola de Veterinária, Departamento de Zootecnia, Belo Horizonte, MG, Brazil.

² Associação Brasileira dos Criadores de Zebu, Uberaba, MG, Brazil.

ABSTRACT - This study aimed to evaluate associations among final weight (FW), average daily gain (ADG), scrotal circumference (SC), and visual score (VS) of beef cattle in performance tests on pasture or in feedlots. Genetic parameters for FW, ADG, SC, and VS of young Nellore bulls performance-tested on pasture or in feedlots were evaluated by mixed model. The performance test and final age were considered as fixed effects and additive genetic and residual effects were considered as random effects. Additive genetic and residual variances for final weight and average daily gain were smaller on pasture than in feedlots. There was no difference between genetic and residual variances and heritability for scrotal circumference on pasture or in feedlots. Genetic variance and heritability for visual score on pasture were smaller than those in feedlots. The posterior means (and highest posterior density intervals with 90% of samples (HPD90) in parentheses) for heritability were 0.46 (0.42; 0.50) and 0.49 (0.41; 0.55) for FW, 0.25 (0.22; 0.29) and 0.25 (0.19; 0.30) for ADG, 0.56 (0.51; 0.61) and 0.60 (0.51; 0.68) for SC, and 0.31 (0.27; 0.34) and 0.42 (0.36; 0.48) for VS on pasture or in feedlots, respectively. The genetic correlations (posterior means with HPD90 in parentheses) were 0.74 (0.69; 0.79) and 0.67 (0.58; 0.77) between FW and ADG; 0.49 (0.43; 0.55) and 0.60 (0.53; 0.68) for FW and SC; 0.79 (0.75; 0.83) and 0.85 (0.80; 0.90) for FW and VS; 0.37 (0.29; 0.46) and 0.34 (0.19; 0.50) for ADG and SC; 0.65 (0.59; 0.71) and 0.74 (0.64; 0.84) for ADG and VS; and 0.46 (0.39; 0.52) and 0.53 (0.44; 0.62) for SC and VS, obtained on pasture or in feedlots, respectively. The genetic and residual (co)variances of growth, scrotal circumference, and visual score of beef cattle vary across environments; however, genetic and residual correlation and efficiency of correlated response among these traits remain constant on pasture or in feedlots.

Key Words: *Bos indicus*, genetic correlation, heritability, phenotypic selection

Introduction

Performance test is an important tool in beef cattle breeding programs worldwide. The evaluations can be conducted on pasture (Lopes et al., 2013) or in feedlots (Cernicchiaro et al., 2014). The occurrence of genotype × environment interactions in beef cattle has been well documented in the literature (Burrow, 2012; Guidolin et al., 2012; Raidan et al., 2015; Santana Junior et al., 2015). Differences in response to selection of the same trait in different environments may occur, especially for traits with

low heritability (Raidan et al., 2015). Nevertheless, there is a lack of knowledge regarding the genetic and residual associations between different traits according to the environment.

Genetic correlation indicates the magnitude and direction of correlated responses to selection. Gene linkage and pleiotropy partially explain the joint variation of two traits (Wisser et al., 2011). In turn, residual correlation includes associations arising from environmental effects that are not considered in the statistical model and non-additive genetic effects (Kruuk et al., 2000). The knowledge of the associations between growth, scrotal circumference, and visual score are important in beef cattle breeding programs because they help choose the most efficient methods of selection and selection criteria for each environment. Still, it is possible to reduce the measurement costs and increase profitability in breeding programs by means of the correct choice of selection methods and criteria.

Variances and heritability of the same trait are not constant in different environments (Guidolin et al., 2012; Santana Junior et al., 2015) and covariance may also change because it is variance-dependent. Correlations

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*Corresponding author: flbtoral@ufmg.br

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reflect relationships between covariance and variances and if the last two parameters change, the first one may also change. Therefore, associations between traits might change according to the environment. This study aimed to evaluate the associations and efficiency of the indirect selection for growth, scrotal circumference, and visual score of beef cattle in performance tests on pasture or in feedlots.

Material and Methods

The present study was based on data corresponding to 33,013 young Nelore bulls that were subjected to 751 official performance tests by the Associação Brasileira dos Criadores de Zebu (Table 1). These performance tests were conducted between 2003 and 2012 in the northern states (Acre, Rondônia, Pará, and Tocantins), northeastern states (Bahia and Maranhão), midwestern states (Goiás, Mato Grosso, and Mato Grosso do Sul), southeastern states (Espírito Santo, Minas Gerais, and São Paulo), and southern states (Paraná and Rio Grande do Sul) of Brazil. A total of 24,910 animals participated in 538 tests conducted on pasture in the aforementioned states, except Rio Grande do Sul, and 8,103 animals were evaluated in 213 tests conducted in feedlots in the aforementioned states, except Acre, Roraima, Tocantins, Maranhão, and Bahia.

The tests conducted on pasture lasted 294 days (70 days for adaptation and 224 days for testing). The tests conducted with the animals in feedlots lasted 168 days (56 days for adaptation and 112 days for testing). The animals were weighed at the beginning and end of the adaptation period and at the end of the testing period. The assessed

traits included final weight (FW), average daily gain (ADG), scrotal circumference (SC), and visual score (VS). The VS value for each animal was obtained by adding the scores of body structure (E), precocity (P), muscling (M), navel (U), breed (R), posture (A), and sexual characteristics (S). The visual scores of E, P, M, and U were evaluated by visual appraisal on a scale from 1 to 6, and the R, A, and S traits were evaluated on a scale from 1 to 4. To obtain the VS, the animals that received scores of 5 or 6 for U had their scores converted to 2 and 1, respectively, to reflect the fact that values of 3 and 4 are more desirable. The FW was adjusted to 550 days of age in the performance tests on pasture and to 426 days of age in feedlot tests according to the duration of each type of test. Individual records of each trait that exceeded the intervals given by the performance test means \pm 3.5 standard deviations were excluded and all animals from performance tests on pasture or in feedlots with less than 20 and 8 animals, respectively, were also excluded.

The numerator relationship matrix was constructed from pedigree data that consisted of the pedigree of an animal and pedigree of some of its ancestors. The ancestors retained in the pedigree were those that were parents of the animals with data or that were connected to other animals in the pedigree (Toral and Alencar, 2010). The relationship matrix included records of 140,498 animals. The 33,013 animals assessed were offspring of 2,356 sires and 24,118 dams. A total of 2,356 sires with progeny records of FW and ADG were identified, corresponding to 2,047 sires with progeny on pasture, 688 sires with progeny in feedlots, and 379 sires with progenies in both types of performance tests. The correspondent numbers of sires were 1,816; 1,347; 469; and 249 for SC and 2,281; 1,962; 688; and 369 for VS.

Table 1 - Descriptive statistics for final weight, average daily gain, scrotal circumference, and visual score of young Nelore bulls tested in performance tests on pasture or in feedlots

Trait	Environment	n	Mean	SD	CV
Final age (days) ¹	Pasture	24,910	553.05	24.39	4.41
	Feedlot	8,103	423.59	26.41	6.23
Final age (days) ²	Pasture	14,888	552.72	25.24	4.57
	Feedlot	4,676	420.73	28.01	6.66
Final age (days) ³	Pasture	23,509	574.73	24.41	4.25
	Feedlot	8,046	423.66	26.43	6.24
Final weight (kg)	Pasture	24,910	350.35	53.09	15.15
	Feedlot	8,103	371.65	57.13	15.37
Average daily gain (kg/day)	Pasture	24,910	0.54	0.16	29.63
	Feedlot	8,103	0.83	0.27	32.53
Scrotal circumference (cm)	Pasture	14,888	26.61	3.38	12.70
	Feedlot	4,676	25.41	3.31	13.03
Visual score (units)	Pasture	23,509	24.62	4.00	16.25
	Feedlot	8,046	25.17	4.09	16.92

¹ Only for animals with final weight and average daily gain data.

² Only for animals with scrotal circumference data.

³ Only for animals with visual score data.

SD - standard deviation; CV - coefficient of variation.

Samples of the posterior distributions of the genetic parameters were obtained by Bayesian inference in a Markov chain Monte Carlo simulation using the Gibbs sampler in an eight-trait analysis. The statistical model employed was:

$$y_{hijk} = u_h + T_{hj} + b_{h(j)}(Age_k - \overline{Age_j}) + a_{hi} + e_{hijk},$$

in which y_{hijk} represents the observed value of trait h of animal i in test j with final age of k ; u_h is the overall constant present in all observations of trait h ; T_{hj} is the effect of test j (j had 538 and 213 levels for pasture and feedlot, respectively) on trait h ; $b_{h(j)}$ is the coefficient of the linear regression of the final age k , nested in test j , for trait h ; Age_k is the final age k ; $\overline{Age_j}$ is the mean final age of the animals in test j ; a_{hi} is the direct additive genetic effect of animal i , for trait h ; and e_{hijk} is the error associated with each observation.

The eight-trait model can be written in the matrix form as:

$$\begin{bmatrix} Y_1 \\ Y_2 \\ \vdots \\ Y_8 \end{bmatrix} = \begin{bmatrix} X_1 & \Phi & \dots & \Phi \\ \Phi & X_2 & \dots & \Phi \\ \vdots & \vdots & \ddots & \vdots \\ \Phi & \Phi & \dots & X_8 \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \\ \vdots \\ \beta_8 \end{bmatrix} + \begin{bmatrix} Z_1 & \Phi & \dots & \Phi \\ \Phi & Z_2 & \dots & \Phi \\ \vdots & \vdots & \ddots & \vdots \\ \Phi & \Phi & \dots & Z_8 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \\ \vdots \\ a_8 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ \vdots \\ e_8 \end{bmatrix},$$

in which Y_h is the vector of the observations for trait h ; X_h is the incidence matrix for the fixed effects for trait h ; β_h is the vector of solutions for the fixed effects for trait h ; Z_h is the incidence matrix for the random effects for trait h ; a_h is the vector of solutions for the additive genetic value of each animal for trait h ; and e_h is the vector of residuals associated with each observation of trait h .

The uniform prior distribution was assumed for fixed effects ($\beta_1, \beta_2, \dots, \beta_8$); normal distributions were assumed for the random effects (a_1, a_2, \dots, a_8); inverted Wishart distributions were assumed for the covariance matrices ($G_0 | S_a, \nu_a$, and $R_0 | S_e, \nu_e$), in which $G = G_0 \otimes A$ is the genetic covariance matrix; G_0 is the matrix of genetic covariance between the eight traits; $R = R_0 \otimes I$ is the residual covariance matrix; R_0 is the residual covariance matrix between the eight traits, with residual covariance between traits h and h' equal to zero ($\sigma_{e_h e_{h'}} = 0$) every time the traits are not measured in the same environment; ν_a and ν_e are the degrees of freedom of the inverted Wishart distribution of the genetic covariances; and S_a and S_e are the hyperparameters of the inverted Wishart distribution. The full conditional posterior distributions are given in Sorensen and Gianola (2002).

Gibbs chains of 410,000 iterations were generated for each parameter with a burn-in period of 10,000 iterations and a sampling interval of 200 iterations. Analysis was

performed using GIBBS1F90 software (Misztal et al., 2014). The convergence diagnostics of the chains were conducted using Heidelberger and Welch (1983) and Geweke (1992) tests and the visual analysis of the trace plots was performed using the Bayesian Output Analysis Program - BOA package (Smith, 2005) in the computer program R 2.15.0 (R Development Core Team 2015).

Samples of the posterior distributions of the direct and indirect responses to selection were obtained with the samples of the covariance components, initially considering the selection of 5% of the males with phenotypic data (selection intensity = 2.06). Only the selection of males was considered; therefore, the mean selection intensity used for the calculation of the responses was 1.03. The responses to direct selection were obtained by solving the equation:

$$\Delta G_h = i_h h_h^2 \sigma_{P_h},$$

in which ΔG_h is the expected genetic gain per generation for trait h ; i_h is the selection intensity for trait h ; h_h^2 is the heritability for trait h ; and σ_{P_h} is the phenotypic standard deviation for trait h .

The efficiency of the correlated response (ECR), considering the same selection intensity for all traits, was obtained by:

$$ECR_{h,h'} = \frac{\Delta G_{hh'}}{\Delta G_h} = r_{a_{hh'}} \frac{h_{h'}}{h_h},$$

in which $\Delta G_{hh'}$ is the expected genetic gain per generation for trait h upon selection for trait h' ; h' is the trait under selection; h is the indirectly selected trait; and $r_{a_{hh'}}$ is the genetic correlation between traits h and h' . The other terms have been previously described.

Results

The posterior means for additive genetic and residual variances for FW and ADG were higher for animals raised in feedlots (Table 2). However, heritability for FW and ADG were similar in both environments. The posterior means for additive and residual genetic variance and heritability for SC on pasture or in feedlots were similar (Table 2). For VS, the posterior means for additive genetic variance and heritability were higher in animals raised in feedlots, while the residual variances were similar in both environments (Table 2).

The genetic covariances were higher for animals evaluated in feedlots, but the highest posterior density interval with 90% of the samples (HPD90) for covariances between ADG and SC and between SC and VS, on pasture or in feedlots, overlapped (Table 3). The genetic correlations between traits (FW, ADG, SC, and VS) on pasture were equal to those corresponding correlations in animals evaluated in

feedlots (Figure 1). The change in environment, i.e., pasture or feedlot, did not result in changes of posterior means for covariances or residual correlations between the traits, except for the residual covariances and correlations of FW with ADG and of ADG with VS (Table 3 and Figure 1).

The genetic correlations between FW, ADG, SC, and VS on pasture with the same traits in feedlots were positive (Table 4). The genetic correlations between FW, ADG, and SC measured on pasture and FW, ADG, and SC, measured in feedlots, were previously presented and explained by Raidan et al. (2015). The posterior means (and HPD90) for genetic correlation between FW and ADG were 0.74 (0.69; 0.79) on pasture and 0.67 (0.58; 0.77) in feedlots (Figure 1). These values were higher than the genetic correlation between FW measured on pasture and ADG measured in feedlots (mean of 0.42, with HPD90 from 0.26 to 0.54) and higher than the genetic correlation between FW in feedlots and ADG on pasture (mean of 0.46, with HPD90 from 0.34 to 0.60) (Table 4).

The posterior means (HPD90) for direct response to selection were 14.54 (13.18; 15.90) kg/generation

and 18.96 (15.87; 21.83) kg/generation for FW; 0.0022 (0.0019; 0.0025) kg.day⁻¹/generation and 0.0039 (0.0030; 0.0049) kg.day⁻¹/generation for ADG; 1.47 (1.32; 1.61) cm/generation and 1.59 (1.35; 1.83) cm/generation for SC; and 1.04 (0.92; 1.15) points/generation and 1.55 (1.32; 1.80) points/generation for VS in animals raised on pasture and in feedlots, respectively. Considering the same selection intensity, direct responses for FW, ADG, and VS were greater in animals raised in feedlots.

The HPD90 values of the efficiency of correlated responses on pasture and in feedlots overlapped (Figure 2). Therefore, the correlated responses obtained for different traits on pasture and in feedlots were similar. The efficiencies of correlated response for each pair of trait were less than one (Figure 2). These results indicate the superiority of direct selection over indirect selection, except for the indirect response for ADG and VS through selection for FW (Figure 2). In these cases, the HPD90 included the value one, indicating that the correlated responses for ADG or VS through selection for FW were similar to direct responses.

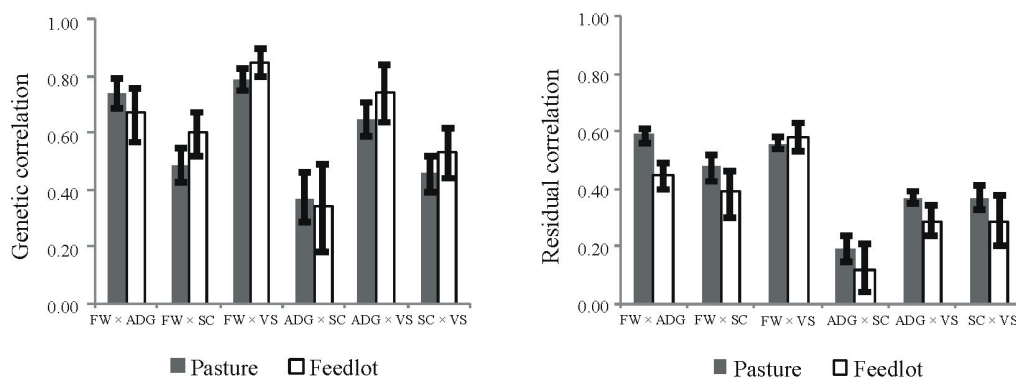


Figure 1 - Posterior means and highest posterior density intervals (with 90% of samples - error bars) for genetic and residual correlations among final weight (FW), average daily gain (ADG), scrotal circumference (SC), and visual score (VS) of young Nellore bulls tested in performance tests on pasture or in feedlots.

Table 2 - Posterior means (with highest posterior density intervals with 90% of samples in parentheses) of the genetic parameters for final weight, average daily gain, scrotal circumference, and visual score of young Nellore bulls tested in performance tests on pasture or in feedlots

Trait	σ_a^2	σ_e^2	h^2
	Pasture		
Final weight	432.18 (387.80; 475.00)	504.23 (470.80; 533.40)	0.46 (0.42; 0.50)
Average daily gain	0.0018 (0.0015; 0.0020)	0.0053 (0.0051; 0.0056)	0.25 (0.22; 0.29)
Scrotal circumference	3.60 (3.24; 4.02)	2.87 (2.59; 3.16)	0.56 (0.51; 0.61)
Visual score	3.32 (2.95; 3.73)	7.53 (7.23; 7.85)	0.31 (0.27; 0.34)
	Feedlot		
Final weight	694.64 (568.00; 804.20)	727.16 (643.70; 810.20)	0.49 (0.41; 0.55)
Average daily gain	0.0061 (0.0044; 0.0074)	0.0018 (0.0017; 0.0020)	0.25 (0.19; 0.30)
Scrotal circumference	4.00 (3.32; 4.68)	2.66 (2.21; 3.18)	0.60 (0.51; 0.68)
Visual score	5.38 (4.54; 6.33)	7.36 (6.73; 8.04)	0.42 (0.36; 0.48)

σ_a^2 - additive genetic variance; σ_e^2 - residual variance; h^2 - heritability.

Table 3 - Posterior means (with highest posterior density intervals with 90% of samples in parentheses) for genetic and residual covariances among final weight (FW), average daily gain (ADG), scrotal circumference (SC), and visual score (VS) of young Nellore bulls tested in performance tests on pasture or in feedlots

Trait	Genetic covariance		Residual covariance	
	Pasture	Feedlot	Pasture	Feedlot
FW × ADG	65.46 (56.79; 74.24)	137.74 (104.40; 170.70)	96.82 (89.70; 103.40)	164.63 (140.30; 188.70)
FW × SC	19.28 (16.10; 22.84)	31.90 (23.94; 38.62)	18.17 (15.81; 20.81)	17.40 (12.53; 22.88)
FW × VS	29.93 (26.19; 33.36)	51.97 (42.33; 61.50)	34.31 (31.69; 37.03)	42.45 (35.53; 49.16)
ADG × SC	3.00 (2.24; 3.71)	5.21 (2.60; 7.79)	2.39 (1.78; 2.92)	2.63 (0.71; 4.48)
ADG × VS	5.09 (4.33; 5.86)	13.31 (10.16; 16.30)	7.48 (6.82; 8.03)	10.61 (8.25; 12.88)
SC × VS	1.59 (1.28; 1.90)	2.45 (1.82; 3.08)	1.72 (1.49; 1.97)	1.31 (0.84; 1.80)

Table 4 - Posterior means (with highest posterior density intervals with 90% of samples in parentheses) for genetic correlations between final weight, average daily gain, scrotal circumference, and visual score of young Nellore bulls tested in performance tests on pasture with the same traits of animals tested in feedlots

Feedlot	Pasture			
	Final weight	Average daily gain	Scrotal circumference	Visual score
Final weight	0.74 (0.63; 0.85)	0.46 (0.34; 0.60)	0.33 (0.22; 0.46)	0.57 (0.43; 0.72)
Average daily gain	0.42 (0.26; 0.54)	0.44 (0.29; 0.60)	0.19 (0.04; 0.36)	0.42 (0.26; 0.59)
Scrotal circumference	0.44 (0.33; 0.57)	0.33 (0.21; 0.46)	0.84 (0.74; 0.93)	0.35 (0.23; 0.48)
Visual score	0.56 (0.44; 0.68)	0.41 (0.25; 0.55)	0.28 (0.16; 0.39)	0.71 (0.59; 0.83)

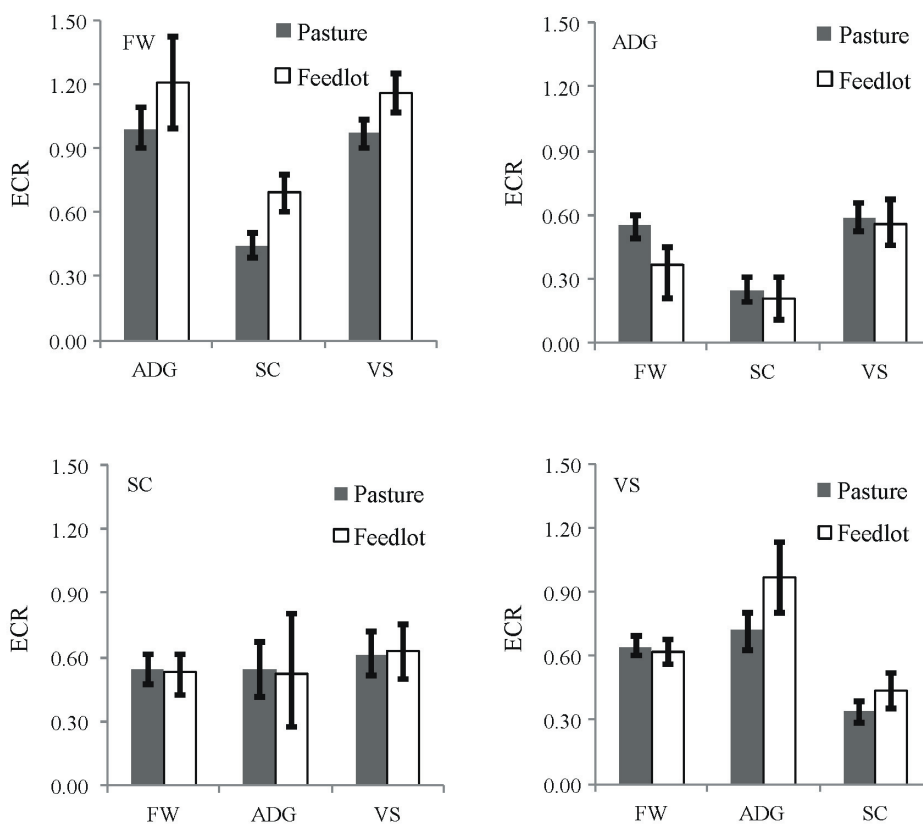


Figure 2 - Posterior means and highest posterior density intervals (with 90% of samples - error bars) for efficiency of the correlated response (ECR) for final weight (FW), average daily gain (ADG), scrotal circumference (SC), and visual score (VS) of young Nellore bulls tested in performance tests on pasture or in feedlots, when selection is applied for FW, ADG, SC, and VS.

Discussion

The nutritional plan on pasture may limit the expression of genetic differences for the traits evaluated in this work (Hammond, 1947). The posterior means of heritability for FW (0.46) and ADG (0.25) were lower than the values of 0.73 and 0.31 estimated by Fragomeni et al. (2013) for young Nellore bulls on pasture performance tests and lower than the values of 0.69 and 0.32 estimated by Neves et al. (2014) for young Nellore bulls in feedlot tests. The posterior means of heritability for SC were higher than the values of 0.42, 0.43, and 0.37 estimated by Boligon et al. (2010), Yokoo et al. (2010), and Neves et al. (2014), respectively. Estimates of heritability for visual scores of E (0.26), P (0.34), M (0.28), U (0.43), R (0.18), A (0.06), and S (0.18) were low to high (Lima et al., 2013).

Genetic differences across populations (from differences in genetic bases and/or differences in selection objectives) and differences in the means and standard deviations of each trait explain part of the differences in the genetic parameters across studies. Nevertheless, heritability for FW, ADG, SC, and VS were moderate to high and indicate that those traits may be used as selection criteria and that phenotypic selection in individual performance tests may result in genetic progress over generations.

The magnitude of the variances affects covariance between traits. Thus, differences in covariances between traits on pasture or in feedlots represent differences in their variances on these environments, suggesting that correlation might be more useful than covariance for evaluation of associations between traits. Genetic (FW, ADG, and VS) and residual variances (FW and ADG) and heritabilities (FW, ADG, and VS) for some traits vary according to the environment, but genetic and residual correlations between traits remained constant. The Nellore population used in this study is under constant evolution and there are no specific lines for pasture or feedlot systems. Thus, we expected gene frequencies in animals on pasture or in feedlots to be very similar. Moreover, the segregation of genes with pleiotropic effects at the same frequencies might explain the constant genetic correlations among FW, ADG, SC, and VS across pasture and feedlots (Sheridan and Barker, 1974; Roach, 1986).

The genetic correlation between FW and ADG obtained in this study (Figure 1) was similar to that of 0.74 reported by Fragomeni et al. (2013) and greater than 0.25 estimated by Lima et al. (2013) for Nellore young bulls on pasture performance tests. The FW is dependent on initial body weight, ADG, and days on test. Days on test were constant

either on each pasture or in each feedlots tests and the adaptation period reduced the differences in weight at the beginning of the test. Thus, it is expected that FW and ADG become highly correlated traits.

The genetic correlations between growth traits (FW and ADG) and SC (Figure 1) were higher than the values of 0.19 (Santana Junior et al., 2012) and 0.38 (Boligon et al., 2011) obtained using field records. Data recording in performance tests is more precise than data recording in field conditions and this difference in precision might explain the higher correlations obtained in our study. The genetic correlation between growth traits and SC indicates that the selection for FW or ADG can be an alternative for improving fertility and sexual precocity in Nellore cattle.

The genetic correlations between growth (FW and ADG) and VS obtained in this study (Figure 1) were high. Lima et al. (2013) reported genetic correlations of 0.41 (0.61), 0.83 (0.90), 0.91 (0.66), 0.32 (0.44), 0.17 (0.70), 0.54 (0.18), and 0.87 (0.97) between FW (ADG) and visual scores of E, P, M, U, R, A, and S, respectively, which are components of the VS. Thus, the direct selection for VS implies genetic progress for growth and the selection for growth also implies genetic gain for VS.

The genetic correlations between SC and VS were moderate (Figure 1). The genetic correlations between body condition score (BCS) and SC have been reported as positive (Boligon and Albuquerque, 2010). Moreover, VS values of E, P, M, U, R, A, and S are highly correlated (Lima et al., 2013). Thus, a positive and moderate genetic correlation between VS and SC is expected and changes in VS and SC can be achieved by direct and indirect selection.

Differences in the genetic bases, means and standard deviations, pleiotropy, and gene linkage can explain differences between the estimates of genetic correlation between traits across populations. The genetic correlation between traits across herds or generations remain constant when pleiotropy is the primary cause (Sheridan and Barker, 1974; Carey, 1988). However, genetic correlations between traits across herds or generations tend towards change when gene linkage is the most important cause of genetic correlation (Sheridan and Barker, 1974; Carey, 1988). Gene linkage depends on selection intensity, gene effects, gene frequency, and strength of linkage (Sheridan and Barker, 1974), factors that might vary across herds or generations.

In general, the genetic correlations, from moderate to high magnitude, indicate that there are favorable associations between the evaluated traits and that the selection for any of the traits provides genetic gains in the same direction for the other traits despite the environment.

The residual correlations were also positive, indicating that the environment acts in a similar way on the various evaluated traits. The posterior means for the residual correlations between FW and ADG and between ADG and VS were higher in animals raised on pasture (Figure 1), probably because the pasture tests are longer than the feedlot tests.

Genetic variance and heritability for VS were higher for animals raised in feedlots than for animals raised on pastures (Table 2) and the posterior mean (and HPD90) for the genetic correlation between VS on pastures and VS in feedlots was lower than the thresholds of 1.0 and 0.8 presented by Falconer (1952) and Robertson (1959), respectively. This result indicates the presence of a genotype \times environment interaction for VS and the breeding values and correlated response for this trait measured on pasture or in feedlot could be different. In fact, the posterior mean (and HPD90) for efficiency for a correlated response for VS on pasture through selection for VS in feedlots was 0.60 (0.50; 0.74), and that for a correlated response for VS in feedlots through selection for VS on pasture was 0.83 (0.68; 0.99). These results confirm that, for the same selection intensity in two environments, the specific environment selection promotes greater genetic gain for this trait.

The positive and favorable trend in genetic correlation between one trait on pasture and another trait in feedlots was observed for all pairs of traits. Thus, the selection to improve one trait on pasture could increase the means of other traits in feedlots (Table 4). We did not find studies in the literature that assessed genetic correlations between FW, ADG, SC, and VS in different environments. These associations indicate that it is possible to achieve direct and indirect genetic progress on pasture and in feedlots through selection.

The selection is more efficient in an environment that allows the maximum expression of genetic differences (Hammond, 1947 and Kearney et al., 2004). However, it is important to highlight that selection intensity also plays an important role in indirect response to selection because the assumption of constant selection intensity across environments is conservative (Raidan et al., 2015). At times, the selection intensity on pasture may be higher than the selection intensity in feedlots and indirect selection (on pasture) might be as efficient as direct selection (in feedlots).

The results obtained in this study indicate that the same strategy applied for ranking young bulls on pasture might be used for ranking young bulls in feedlots. The moderate to high correlations between FW, ADG, SC, and VS on

pasture with FW, ADG, SC, and VS in feedlots (Table 4) contribute to explain these results.

The genetic correlation between FW and initial test weight was greater than the genetic correlation between initial test weight and ADG (0.67 vs 0.33, according to Lima et al., (2013)). Thus, the indirect response for initial test weight might be higher than the indirect response for ADG, as stated by Fragomeni et al. (2013). The increase in initial test weight reflects the efficiency of cow-calf operation and the increase of ADG in performance tests reflects the efficiency of the backgrounding operation. The increase of cow-calf and backgrounding efficiencies will increase the beef chain efficiency. However, the performance test is designed to evaluate the performance of animals after weaning and young bulls should be ranked by selection indices with higher relative emphasis for post-weaning traits.

The genetic correlations between average daily gain from birth to yearling (550 days of age) with age at first calving, weight at first calving, and mature body weight were better (-0.38, 0.52 and 0.53) than the genetic correlations between body weight at yearling with age at first calving (-0.24), weight at first calving (0.66), and mature body weight (0.62) (Castro-Pereira et al., 2007a,b). Moreover, the genetic correlations between scrotal circumference with age at first calving (-0.47 to -0.37), weight at first calving (0.04 to 0.09), and mature body weight (-0.24 to -0.17) (Silva et al., 2000; Castro-Pereira et al., 2007b) are also favorable and indicate that increasing SC by genetic selection will reduce age at first calving, keep weight at first calving unaltered, and reduce mature body weight. Thus, the relative weights of ADG and SC in selection indexes for the ranking of young bulls in performance tests should be higher than the relative weight of FW.

Conclusions

The genetic and residual covariances vary according to the environment, but genetic and residual correlations and the efficiency of the correlated responses for growth, scrotal circumference, and visual scores of beef cattle remain constant on pasture and in feedlots.

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References

- Boligon, A. A. and Albuquerque, L. G. 2010. Correlações genéticas entre escores visuais e características reprodutivas em bovinos Nelore usando inferência bayesiana. *Pesquisa Agropecuária Brasileira* 45:1412-1418.
- Boligon, A. A.; Silva, J. A. V.; Sesana, R. C.; Sesana, J. C.; Junqueira, J. B. and Albuquerque, L. G. 2010. Estimation of genetic parameters for body weights, scrotal circumference, and testicular volume measured at different ages in Nelore cattle. *Journal of Animal Science* 88:1215-1219.
- Boligon, A. A.; Baldi, F. and Albuquerque, L. G. 2011. Genetic parameters and relationships between growth traits and scrotal circumference measured at different ages in Nelore cattle. *Genetic and Molecular Biology* 34:225-230.
- Burrow, H. M. 2012. Importance of adaptation and genotype-environment interaction in tropical beef breeding systems. *Animal* 6:729-740.
- Carey, G. 1988. Inference about genetic correlations. *Behavior Genetics* 18:329-338.
- Castro-Pereira, V. M.; Alencar, M. M. and Barbosa, P. F. 2007a. Estimativas de parâmetros genéticos e de ganhos direto e indireto à seleção para características de crescimento de machos e fêmeas da raça Canchim. *Revista Brasileira de Zootecnia* 36:1037-1044.
- Castro-Pereira, V. M.; Alencar, M. M. and Barbosa, R. T. 2007b. Estimativas de parâmetros genéticos e de ganhos direto e indireto à seleção para características reprodutivas e de crescimento em um rebanho da raça Canchim. *Revista Brasileira de Zootecnia* 36:1029-1036.
- Cernicchiaro, D. G. R.; Xiang, S.; White, B. J. and Bello, N. M. 2014. Hierarchical Bayesian modeling of heterogeneous variances in average daily weight gain of commercial feedlot cattle. *Journal of Animal Science* 91:2910-2919.
- Falconer, D. S. 1952. The problem of environment and selection. *The American Naturalist* 86:293-298.
- Fragomeni, B. O.; Scaletz, D. C. B.; Toral, F. L. B.; Bergmann, J. A. G.; Pereira, I. G. and Costa, P. S. T. 2013. Genetic parameters and alternatives for evaluation and ranking of Nelore young bulls in pasture performance tests. *Revista Brasileira de Zootecnia* 42:559-564.
- Geweke, J. 1992. Evaluating the accuracy of sampling-based approaches to calculating posterior moments. p.169-193. In: *Bayesian statistics*. 4th ed. Bernardo, J. M.; Berger, J. O.; Dawid, A. P. and Smith, A. F. M. Oxford University Press, Oxford.
- Guidolin, D. G. F.; Buzanskas, M. E.; Ramos, S. B.; Venturini, G. C.; Lôbo, R. B.; Paz, C. C. P.; Munari, D. P. and Oliveira, J. A. 2012. Genotype-environment interaction for post-weaning traits in Nelore beef cattle. *Animal Production Science* 52:975-980.
- Hammond, J. 1947. Animal breeding in relation nutrition and environmental conditions. *Biology Reviews* 22:195-213.
- Heidelberger, P. and Welch, P. D. 1983. Simulation run length control in the presence of an initial transient. *Operations Research* 31:1109-1144.
- Kearney, J. F.; Schutz, M. M.; Boettcher, P. J. and Weigel, K. A. 2004. Genotype x environment interaction for grazing versus confinement. I. Production traits. *Journal of Dairy Science* 87:501-509.
- Kruuk, L. E. B.; Clutton-Brock, T. H.; Slate, J.; Pemberton, J. M.; Brotherstone, S. and Guinness, F. E. 2000. Heritability of fitness in a wild mammal population. *Proceedings of the National Academy of Science* 97:698-703.
- Lima, P. R. M.; Paiva, S. R.; Cobuci, J. A.; Braccini Neto, J.; Machado, C. H. C. and McManus, C. 2013. Genetic parameters for type classification of Nelore cattle on central performance tests at pasture in Brazil. *Tropical Animal Health and Production* 45:1627-2634.
- Lopes, F. B.; Magnabosco, C. U.; Paulini, F.; Silva, M. C.; Miyagi, E. S. and Lôbo, R. B. 2013. Genetic analysis of growth traits in Polled Nelore cattle raised on pasture in tropical region using Bayesian approaches. *PLoS One* 8:e75423.
- Misztal, I.; Tsuruta, S.; Lourenço, D.; Aguilar, I.; Legara, A. and Vitezica, Z. 2014. Manual for BLUPF90 family of programs. Georgia, Athens.
- Neves, H. H. R.; Reis, F. P.; Paterno, F. M.; Guarini, A. R.; Carvalheiro, R.; Silva, L. R.; Oliveira, J. A. and Queiroz, S. A. 2014. Herd-of-origin effect on the post-weaning performance of centrally tested Nelore beef cattle. *Tropical Animal Health and Production* 46:1235-1241.
- R Development Core Team 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.
- Raidan, F. S. S.; Passafaro, T. L.; Fragomeni, B. O.; Josahkian, L. A.; Pereira, I. G. and Toral, F. L. B. 2015. Genotype x environment interaction in individual performance and progeny tests in beef cattle. *Journal of Animal Science* 93:920-933.
- Roach, D. A. 1986. Life history variation in *Geranium carolinianum*. I. Covariation between characters at different stages of the life cycle. *The American Naturalist* 128:47-57.
- Robertson, A. 1959. The sampling variance of the genetic correlation coefficient. *Biometrics* 15:469-485.
- Santana Junior, M. L.; Eler, J. P.; Ferraz, J. B. S. and Mattos, E. C. 2012. Genetic relationship between growth and reproductive traits in Nelore cattle. *Animal* 6:565-570.
- Santana Junior, M. L.; Eler, J. P.; Bignardi, A. B.; Menéndez-Buxadera, A.; Cardoso, F. F. and Ferraz, J. B. S. 2015. Multi-trait linear reaction norm model to describe the pattern of phenotypic expression of some economic traits in beef cattle across a range of environments. *Journal of Applied and Genetics* 56:219-229.
- Sheridan, A. K. and Barker, J. S. F. 1974. Two-trait selection and genetic correlation II. Changes in the genetic correlation during two-trait selection. *Australian Journal of Biology and Science* 27:89-101.
- Silva, A. M.; Alencar, M. M.; Freitas, A. R.; Barbosa, R. T.; Barbosa, P. F.; Oliveira, M. C. S.; Corrêa, L. A.; Novaes, A. P. and Tullio, R. R. 2000. Herdabilidades e correlações genéticas para peso e perímetro escrotal de machos e características reprodutivas e de crescimento de fêmeas na raça Canchim. *Revista Brasileira de Zootecnia* 29:2223-2230.
- Smith, B. J. 2005. Bayesian Output Analysis program (BOA) version 1.1 user's manual. Available at: <<http://www.public-health.uiowa.edu/boa/BOA.pdf>>. Accessed on: Sept. 29, 2014.
- Sorensen, D. and Gianola, D. 2002. Likelihood, Bayesian and MCMC methods in quantitative genetics. New York, New York.
- Toral, F. L. B. and Alencar, M. M. 2010. Alternatives for analysis of performance data and ranking of Charolais x Nelore crossbred bulls in performance tests. *Revista Brasileira de Zootecnia* 39:1483-1490.
- Wisser, R. J.; Kolkman, J. M.; Patzoldt, M. E.; Holland, J. B.; Yud, J.; Krakowsky, M.; Nelson, R. J. and Balint-Kurti, P. J. 2011. Multivariate analysis of maize disease resistances suggests a pleiotropic genetic basis and implicates a GST gene. *Proceeding of the National Academy of Science USA* 108:7339-7344.
- Yokoo, M. J. I.; Lôbo, R. B.; Araujo, F. R.; Bezerra, L. A. F.; Sainz, R. D. and Albuquerque, L. G. 2010. Genetic associations between carcass traits measured by real-time ultrasound and scrotal circumference and growth traits in Nelore cattle. *Journal of Animal Science* 88:52-58.