

Genetic parameter estimates for live weight and daily live weight gain obtained for Nellore bulls in a test station using different models

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ABSTRACT

The objective of this study was to estimate (co)variance components and genetic parameters for live weight (LW) and daily live weight gain (LWG) of Nellore bulls in a test station using multi-trait and random regression models. In addition, breeding values for these traits were predicted by multi-trait and random regression analyses, and the rank of animals based on breeding values was compared with the current selection criterion of the test station (own performance). A total of 4758 Nellore bulls tested in a central station of the Beef Cattle Research Center (CPPC) between 1978 and 2007, including 2211 bulls from the CPPC herd and 2547 from commercial herds, were used. During the test, four LWs were recorded at intervals of 56 days (LW_{1d} , LW_{56d} , LW_{112d} and LW_{168d}). LWG was calculated as the difference between two consecutive weights for three periods: 1 to 55 (LWG_1), 56 to 111 (LWG_2), and 112 to 168 (LWG_3) days on test. For LW and LWG, the multi-trait model included the fixed effects of contemporary group (year-month of birth), dam age class, and animal age at recording as covariate. For random regression analysis, direct additive genetic and animal permanent environmental effects were modeled using linear, quadratic and cubic polynomial functions. Residual variances for LW and LWG were modeled using a step function with 1 or 3 classes, respectively. Contemporary group (year-month of birth and month of recording) and dam age class were included as fixed effects. The (co)variance components were estimated by the Restricted Maximum Likelihood method using the WOMBAT software. According to model comparison criterion, the model including cubic and quadratic Legendre polynomials to fit genetic and animal permanent environmental effects, respectively, was the most appropriate to describe the covariance structure of LW. For LWG, the BIC value indicated that the model including quadratic and linear Legendre polynomials was the most appropriate to fit genetic and animal permanent environmental effects, respectively. The variance component and genetic parameter estimates for LW and LWG obtained by random regression and multi-trait analyses were similar. Random regression on Legendre polynomials of days on test was more appropriate than multi-trait models to describe the genetic variation of growth traits in station-tested Nellore bulls. Selection based on breeding values for LWG during the test would result in the selection of bulls different from those chosen if final weight is applied as a selection criterion.

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1. Introduction

Weights and weight gains at specific ages or during specific periods are commonly applied as selection criteria in

most beef cattle breeding programs in the world, since these traits show moderate to high genetic correlations with carcass weight, are easy to measure, and respond to selection (Razook et al., 2001). Brazil possesses the largest commercial Nellore herd in the world and many beef cattle breeding programs have been implemented for this breed over the last two decades (Albuquerque et al., 2006). These breeding programs publish an annual summary of Expected Progeny Differences (EPD) predicted by the BLUP procedure for many economically important traits, such as growth and reproductive traits and visual scores.

The evaluation of weight gain of beef bulls in test stations permits to compare young bulls from different herds under standard environmental conditions and, thus, the identification of genetically superior bulls for growth traits among test station bulls (Liu and Makarechian, 1993). In addition, the use of station-tested bulls is an attractive alternative for the genetic evaluation of populations that show poor connectedness among herds (Razook et al., 1997). In many countries such as South Africa (Nephawe et al., 2006), Canada (Schenkel et al., 2002), United States (<http://www.ansi.okstate.edu/>), France (Fouilloux et al., 2000) and the Czech Republic (Krejčová et al., 2010; Přebyl et al., 2006), young bulls continue to be evaluated in test stations. In Brazil, there are several beef bull weight-gain test stations recognized by the Brazilian Association of Zebu Breeders (www.abcz.org.br) and distributed over different regions of the country, where about 1500 bulls are evaluated every year. In these test stations, the best animals for final live weight or average live weight gain are selected based on individual performance, without considering information from relatives. In this case, the individual performance of each bull is evaluated in relation to the contemporary group (CG) and the best bulls in terms of growth traits are sold to a semen producing company or to farmers for natural breeding. However, this testing is relatively expensive and the annual number of bulls that can be tested at the station is limited, a fact compromising the connectedness between CGs. Furthermore, genetic evaluation of bulls in test stations using an animal model (BLUP) has not yet been implemented. Beef cattle farmers and researchers are still looking for alternative methods to improve the results of bull weight-gain test stations.

Few studies have so far reported genetic parameters for growth traits obtained in central bull test stations. Most of these studies were conducted in temperate countries and involved *Bos taurus* breeds (Gengler et al., 1995; Krejčová et al., 2010; Liu and Makarechian, 1993; Schenkel et al., 2002). Available records from previous years might be connected through the relationship matrix and could be used for analysis to increase the accuracy of selection. Moreover, multi-trait analysis and random regression models can be applied to improve the modeling of genetic and environmental effects of repeated weight records (Nephawe et al., 2006; Schenkel et al., 2002), and thus increase the accuracy of selection. In this respect, Schenkel et al. (2002) compared random regression models and two-step analysis for the evaluation of live weight gain in station-tested bulls and concluded that random regression models are more appropriate since they accounted for changes over time in genetic and environmental effects.

Since 1976, an experimental selection program based on postweaning growth performance of *Bos indicus* and

tropically adapted *B. taurus* breeds has been conducted by the Instituto de Zootecnia at the Beef Cattle Research Center (CPPC) in Sertãozinho, São Paulo, Brazil, to estimate the response to selection for higher body weight in breeds of interest for the tropics (Razook et al., 2002). In this experimental program, bulls have been selected for yearling weight adjusted to 378 days of age, expressed as a deviation from the average of the CG, which was obtained at the end of a 168-day feeding performance test conducted under feedlot conditions. Although application of this criterion has improved (genetic progress) the growth performance of the herds (Mercadante et al., 2003; Packer et al., 1986; Razook et al., 1998, 2002), there is consensus that the BLUP animal model needs to be implemented and that the evaluation procedure needs to be modified. Thus, alternative methods are needed for data analysis of repeated live weight (LW) and daily live weight gain (LWG) records of station-tested bulls in order to increase the response to selection. The objective of this study was to estimate (co)variance components and genetic parameters for LW and LWG of Nellore bulls in a test station using multi-trait and random regression models. In addition, breeding values for these traits were predicted by multi-trait and random regression analyses, and the rank of animals based on breeding values was compared with the current selection criterion of the test station (own performance).

2. Material and methods

2.1. Data set and management

The data belong to the CPPC, a research unit of the Instituto de Zootecnia (www.iz.sp.gov.br), located in the north of the State of São Paulo, Brazil (latitude 21°10' south and longitude 48°5' west). This region is characterized by a wet tropical climate, with average annual temperature and rainfall of 24 °C and 1312 mm, respectively. Beef bull testing in this central station has been performed annually since 1955. During the test, animals are allowed ad libitum access to a diet consisting of 45% hay (*Hyparrhenia rufa* or *Brachiaria decumbens*), 33% ground corn, 22% cotton bran or another protein source, and mineral salt. The chemical and nutritional composition of the supplement is 11% crude protein, 67% TDN, and 88% total dry matter.

A total of 4758 Nellore bulls tested between 1978 and 2007, including 2211 bulls from the CPPC herd and 2547 from commercial herds, were used. A total of 18,949 LW records and 13,980 LWG records were utilized. The animals were the progeny of 824 sires and 3136 dams. The relationship matrix contained 26,479 animals, 4016 sires and 12,780 dams and all generations back were used. In order to meet the standards of the central bull test station, the maximum age difference of animals at the beginning of the test should be 90 days. The animals should be non-castrated males and born between August and October of the previous year. The central bull test station standards of the CPPC have been described by Razook et al. (1997) and are applied in most central test stations in Brazil.

During the test, four LWs were recorded at intervals of 56 days (LW_{1d} , LW_{56d} , LW_{112d} and LW_{168d}) after a fasting period of 12 h. LWG was calculated as the difference between

two consecutive weights for three periods: 1 to 55 (LWG₁), 56 to 111 (LWG₂), and 112 to 168 (LWG₃) days on test. At the beginning of the test, the animals were weighed after a 12-hour fast and weights were adjusted to 210 days of age using the following formula: $LW_{210} = \{[(LW_{1d} - BW)/\text{initial age}] \times 210\} + BW$, where LW_{1d} is the initial weight and BW is the birth weight. Animals with fewer than three weight records were excluded from the analyses. At the end of the test, animals were ranked according to final weight adjusted to 378 days of age (LW₃₇₈) using the following formula: $LW_{378} = LW_{210} + (LWG_{112} \times 168)$, where LW_{210} is the standard weight at 210 days of age and LWG_{112} is the LWG during the last 112 days of the test (Razook et al., 1997). The final weight adjusted to 378 days of age, expressed as a deviation from the average of the CG (DW₃₇₈), is the selection criterion currently applied in the CPPC bull test station (Razook et al., 1997).

2.2. Multi-trait analyses

Four LWs were considered for multi-trait analyses: LW at the beginning of the test (LW_{1d}) and at 56 (LW_{56d}), 112 (LW_{112d}) and 168 days of the test (LW_{168d}). The model included the fixed effects of CG, age class of dam (2 to 12 years), and animal age at recording as covariate (linear and quadratic effect). CGs were defined by animals born in the same year and month. Additive genetic effects were included as random effects. The same model (fixed and random effects) was applied to analyze LWG₁, LWG₂ and LWG₃ records. Records of LW and LWG exceeding 3 standard deviations above or below the mean of the CG were excluded. The descriptive statistics and data structure of the LW and LWG records are shown in Table 1. For LW and LWG, the matrix representation of the general model is:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e},$$

where \mathbf{y} = vector of observations; \mathbf{b} = vector of fixed effects; \mathbf{a} = vector of direct additive genetic effects, and \mathbf{e} = vector of random residual effects associated with the observations. \mathbf{X}

Table 1

Number of records and descriptive statistic for live weight and live weight gain at different days on test of Nellore bulls.

| Live weight (kg) | | | | | |
|---------------------------|-------------------|-------|-------|--------|-------|
| Trait ^a | Number of records | Mean | SD | Min | Max |
| LW _{1d} | 4742 | 202.4 | 35.1 | 67.0 | 348.0 |
| LW _{56d} | 4743 | 244.9 | 37.8 | 90.0 | 387.0 |
| LW _{112d} | 4739 | 290.5 | 40.0 | 133.0 | 443.0 |
| LW _{168d} | 4725 | 326.8 | 37.5 | 192.0 | 471.0 |
| Live weight gain (kg/day) | | | | | |
| Trait ^b | Number of records | Mean | SD | Min | Max |
| LWG ₁ | 4660 | 0.754 | 0.217 | -0.036 | 1.536 |
| LWG ₂ | 4660 | 0.816 | 0.158 | 0.107 | 1.411 |
| LWG ₃ | 4660 | 0.749 | 0.174 | 0.161 | 1.393 |

^a LW_{1d}; LW_{56d}; LW_{112d}; LW_{168d}: live weight at the beginning of the test, 56, 112 and at 168 days of the test, respectively.

^b LWG₁; LWG₂ and LWG₃: live weight gain from 1 to 55; from 56 to 111 and from 112 to 168 days on test, respectively.

and \mathbf{Z} are incidence matrices relating \mathbf{b} and \mathbf{a} to \mathbf{y} . It is assumed that:

$$\begin{bmatrix} a \\ e \end{bmatrix} \sim N(0, \mathbf{V}); \mathbf{V} = \begin{bmatrix} \mathbf{G} \otimes \mathbf{A} & 0 \\ 0 & \mathbf{R} \otimes \mathbf{I}_{NR} \end{bmatrix},$$

where \mathbf{G} = direct genetic (co)variance effects; \mathbf{A} = relationship matrix; \mathbf{I} = identity matrix; NR = number of animals with records; \mathbf{R} = residual (co)variance matrix, and \otimes = direct product of matrices.

2.3. Random regression models

Four weights (LW_{1d}, LW_{56d}, LW_{112d} and LW_{168d}) and three LWG periods (LWG₁, LWG₂ and LWG₃) were considered for random regression analysis. For the two traits, the CGs were defined by animals born in the same year and month and weighed in the same month. Records of LW and LWG exceeding 3 standard deviations above and below the mean of the CG were excluded. Only records of animals with at least three records and belonging to the CG of at least five animals were kept. A total of 348 and 261 CGs were formed for LW and LWG, respectively. There was an average of 3.9 and 3.0 records per animal for LW and LWG, respectively.

The population mean trend was taken into account using cubic and linear regression on orthogonal polynomials (Legendre polynomials) of days on test for LW and LWG, respectively. Additive genetic and animal permanent environmental effects modeled by polynomials of different orders (k) were included as random effects. The additive genetic effects (a) were modeled using linear, quadratic and cubic polynomial functions to describe the LW trajectory, with $k_a = 2, 3$ and 4 random regression coefficients, respectively, and linear and quadratic polynomial functions to describe LWG during the different test periods, with $k_a = 2$ and 3 random regression coefficients, respectively. The animal permanent environmental effects (c) were modeled using linear, quadratic and cubic polynomial functions to describe the LW trajectory, with $k_c = 2, 3$ and 4 random regression coefficients, respectively, and linear and quadratic polynomial functions to describe LWG during the different test periods, with $k_c = 2$ and 3 random regression coefficients, respectively.

Residual variances were modeled using a step function with 1 or 4 classes (1, 56, 112, and 168 days on test) for LW, and 1 or 3 classes (56, 112, and 168 days on test) for LWG. For the two traits, the CG, age class of dam (2 to 12 years) and population mean trend were included as fixed effects. For LW and LWG, the matrix representation of the models is:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wc} + \mathbf{e},$$

where \mathbf{y} is the vector of observations; \mathbf{b} is the vector of systematic effects and fixed regression coefficients; \mathbf{a} is the vector of random coefficients for direct additive effects; \mathbf{c} is the vector of random coefficients for animal permanent environmental effects; \mathbf{e} is the vector of residual effects, and \mathbf{X} , \mathbf{Z} , and \mathbf{W} are the corresponding incidence matrices. The model is based on the following assumptions:

$$E \begin{bmatrix} y \\ a \\ c \end{bmatrix} = \begin{bmatrix} \mathbf{Xb} \\ 0 \\ 0 \end{bmatrix}; \mathbf{V} \begin{bmatrix} a \\ c \\ e \end{bmatrix} = \begin{bmatrix} K_a \otimes \mathbf{A} & 0 & 0 \\ 0 & K_c \otimes \mathbf{I} & 0 \\ 0 & 0 & \mathbf{R} \end{bmatrix},$$

where \mathbf{K}_a and \mathbf{K}_c are (co)variance matrices between random regression coefficients for additive genetic and animal permanent environmental effects, respectively; \mathbf{A} is the relationship matrix; \mathbf{I} is an identity matrix, and \mathbf{R} is a diagonal matrix of temporary environmental variances which could vary depending on days on test allowing homogeneous or heterogeneous residual variances. For the two traits, the correlations between random regression coefficients for different effects were set to zero.

The (co)variance components were estimated by the restricted maximum likelihood method using the WOMBAT software (Meyer, 2006). The models were compared using the Bayesian, or Schwarz, information criterion (BIC) (Schwarz, 1978), and by inspecting the variance component and genetic parameter estimates. For BIC, p denotes the number of parameters estimated, Sz is the sample size, $r(X)$ is the rank of the coefficient matrix of fixed effects in the analysis model, and $\log L$ is the log of the restricted maximum likelihood estimation. The information criterion is then given as:

$$\text{BIC} = -2\log L + p\log(Sz - r(X)).$$

The breeding values for LW_{168d} were predicted using multi-trait analysis and random regression models. The random regression models used to predict the breeding values were chosen based on model comparison criterion. To predict the breeding value for total LWG during the test, LWG during the first period, i.e., 1 to 55 days on test (LWG_1), was not included in the calculations since this period was considered to be an adaptation period. Thus, the breeding value for total LWG during the test (LWG_{112}), i.e., 56 to 168 days on test, was obtained by the sum of LWG_2 and LWG_3 breeding values predicted by multi-trait analysis or by the most adequate, based on model comparison criterion, random regression model. The breeding values predicted for LW_{168d} and LWG_{112} were compared with individual performance, i.e., the final weight adjusted to 378 days of age, expressed as a deviation from the average of the CG (DW378). The DW378 is the selection criterion currently used in the CPPC bull test station. The rank of animals (Spearman correlations) based on the breeding values predicted for LW_{168d} and LWG_{112} by multi-trait or random regression analysis was compared with the rank of animals based on DW378 considering different selection intensities, i.e., 2%, 5% and 20% of the best bulls selected for DW378.

3. Results and discussion

The number of records and descriptive statistics for LW at 1, 56, 112, and 168 days on test and for LWG during the different test periods is shown in Table 1. The corresponding animal age (mean \pm SD) at 1, 56, 112, and 168 days on test was 219 ± 23 , 275 ± 24 , 332 ± 24 , and 387 ± 24 days, respectively. The LWG during the three periods was moderate, indicating that the growth rate was not very intensive during the test. The highest coefficient of variation was observed for LWG_1 (28.7%), probably due to pretest environmental carry-over effects on LWG.

3.1. Model comparison

A summary of the results of fitting multi-trait and random regression models for LW and LWG is shown in Table 2. The number of parameters in the models ranged from 7 to 21 for LW and from 7 to 15 for LWG. The order of fit for additive genetic and permanent environmental effects was kept constant in order to define the best variance structure to model the residual variances for LW and LWG. For LW, the model considering heterogeneous residual variances showed a poorer fit than the model including homogenous residual variances. In contrast, for LWG the log L and BIC values showed a significant improvement in the goodness of fit when residual variances were considered to be heterogeneous. These results indicate a different behavior of the residual variances for LWG along the test period, requiring a heterogeneous variance structure for residual effects. Thus, residual variances for LW and LWG were modeled using a step function with 1 and 3 classes, respectively.

First, a model considering the same number of regressions for all effects was fitted and then the polynomial order for additive genetic and animal permanent environmental effects was increased. For LW and LWG, the log L values increased with the number of parameters in the model (Table 2). The BIC values indicated the Leg32res3 model, with 12 parameters, to be the most adequate model to fit the LWG data. An increase in the order of fit to three and two for additive genetic and animal permanent environmental effects, respectively, did not improve the criterion (BIC). In addition, convergence problems occurred and the last eigenvalues of the random coefficient matrix were practically zero, indicating a possible overparameterized model. For LW, the log L values indicated the Leg44res1 model to be the most adequate to fit the data. Alternatively, the BIC criterion suggested the Leg43res1 model, with 17 parameters, to be the best to fit the data. Since BIC criteria tend to choose more parsimonious

Table 2

Order of fit for additive genetic (k_a) and animal (k_p) permanent environment effects, number of residual classes (r), number of parameters (np), log likelihood value ($\log L$) and Bayesian information criterion (BIC) expressed relative to the best model.

| Model | k_a | k_p | r | np | Statistic criteria | |
|-------------------------|-------|-------|-----|------|--------------------|------|
| | | | | | $\log L$ | BIC |
| <i>Live weight</i> | | | | | | |
| Leg22res1 | 2 | 2 | 1 | 7 | -433 | 766 |
| Leg22res4 | 2 | 2 | 4 | 10 | -817 | 1503 |
| Leg23res1 | 2 | 3 | 1 | 10 | -154 | 207 |
| Leg32res1 | 3 | 2 | 1 | 10 | -202 | 303 |
| Leg33res1 | 3 | 3 | 1 | 13 | -135 | 98 |
| Leg34res1 | 3 | 4 | 1 | 17 | -48 | 64 |
| Leg43res1 | 4 | 3 | 1 | 17 | -16 | 0 |
| Leg44res1 | 4 | 4 | 1 | 21 | 0 | 9 |
| Multiple-trait | | | | 20 | -3018 | 6034 |
| <i>Live weight gain</i> | | | | | | |
| Leg22res1 | 2 | 2 | 1 | 7 | -155 | 263 |
| Leg22res3 | 2 | 2 | 3 | 9 | -41 | 53 |
| Leg22res2 | 2 | 2 | 2 | 8 | -51 | 65 |
| Leg23res3 | 2 | 3 | 3 | 12 | -41 | 82 |
| Leg32res3 | 3 | 2 | 3 | 12 | 0 | 0 |
| Leg33res3 | 3 | 3 | 3 | 15 | -3 | 29 |
| Multiple-trait | | | | 12 | -40 | 80 |

models, the Leg43res1 model is the most adequate to describe variations in LW along the test period. Furthermore, genetic parameter estimates for LW remained practically unchanged. For the two traits (LW and LWG), the multi-trait model resulted in a poorer fit than the most adequate random regression model according to the log L and BIC criteria.

Several studies have demonstrated that higher order polynomials are necessary to model permanent environmental effects of weight traits (Albuquerque and Meyer, 2001; Arango et al., 2004; Meyer, 2001; Schenkel et al., 2002). In this respect, Schenkel et al. (2002), modeling consecutive weight records taken at intervals of 28 days from bulls tested in central evaluation stations in Canada, reported that third- and fourth-order polynomials are sufficient to adequately fit additive genetic and permanent environmental effects, respectively. Albuquerque and Meyer (2001), adjusting random regressions for weight records from birth to 630 days of age in Nellore cattle, reported that third-order and fourth-order polynomials were sufficient to model direct additive genetic and animal permanent environment effects, respectively. In general, agreement exists regarding the models used to estimate covariance functions for weights in central test stations between previous studies on *B. taurus* breeds and the present study fitting Zebu breed data.

3.2. Covariance components and parameter estimates

The variance estimates for LW obtained with the Leg43res1 and multi-trait models are shown in Fig. 1. The additive genetic variance estimates for LW obtained with Leg43res1 slightly increased with age. These results agree with those reported by Schenkel et al. (2002) who applied random regression models to adjust weight records of bulls tested in central evaluation stations. For LW_{1d}, LW_{56d} and LW_{112d}, the additive genetic variances estimated with finite dimensional models were slightly higher than those obtained with the infinite dimensional model (Leg43res1). However, the additive genetic variance for LW_{168d} estimated with the multi-trait model was slightly lower than that obtained with Leg43res1. The animal permanent environmental and phenotypic variances for LW increased with days on test. Higher phenotypic variance estimates for LW were obtained with the multi-trait model throughout the test period. The variance estimates for LWG during the different test periods obtained with the Leg32res3 model are shown in Table 3. The additive genetic and phenotypic variances for LWG₁, LWG₂ and LWG₃ obtained with the multi-trait model were similar (data not shown). The additive genetic variance estimates obtained with the Leg32res3 model were similar for LWG₁ and LWG₂ and lower for LWG₃ (Table 3).

The heritability estimates for LW obtained with the Leg43res1 model were moderate and decreased over time (Fig. 2). The heritabilities estimated with the finite dimensional model were similar along the trajectory, ranging from 0.53 at younger ages to 0.38 at older ages, and followed the same trend as that seen with the Leg43res1 model (Fig. 3). Riley et al. (2007) analyzed feedlot weight records applying random regression models and reported heritability estimates ranging from 0.31 during the early feeding period to 0.53 at the end of the feeding period. Furthermore, Schenkel

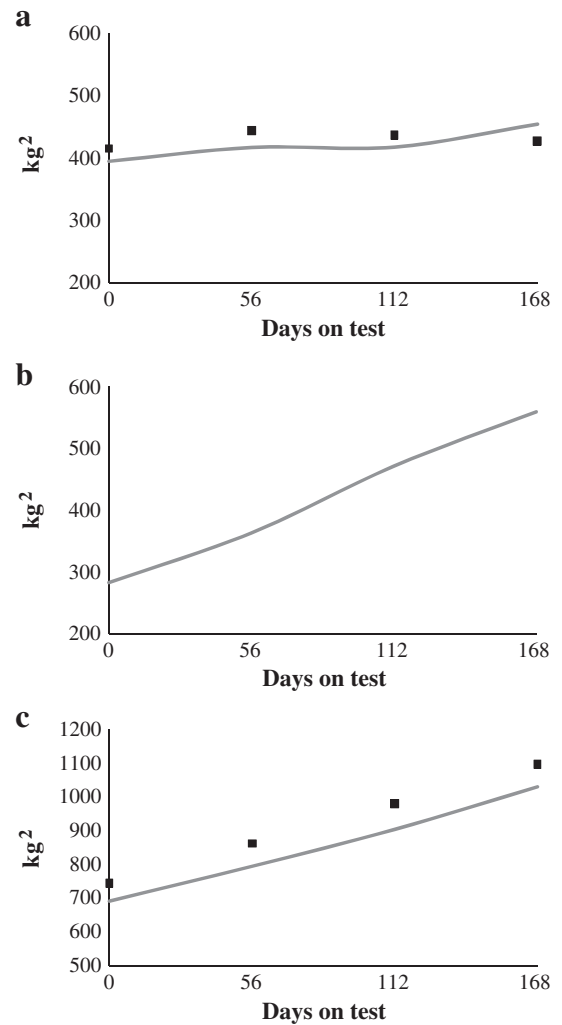


Fig. 1. Estimates of additive genetic (a), animal permanent environment (b) and phenotypic (c) variances for live weight obtained with Leg43res1 (solid line) and multi-trait model models (■).

et al. (2002) reported a similar trend for heritability estimates of weights in station-tested bulls, ranging from 0.32 to 0.40 over 140 days on feed. The heritabilities for LW observed in the present study seem to be consistent with estimates obtained by conventional (non-random regression) analysis. In this respect, Koots et al. (1994) and Mercadante et al. (1995) reported mean heritability estimates for yearling

Table 3

Estimates of additive genetic (σ_a^2), animal permanent environment (σ_e^2) and phenotypic (σ_{ph}^2) variances, and heritability (h^2), animal variance estimates as proportions of phenotypic (c^2) and temporary environmental variances (e^2) for LWG obtained with Leg32res3 model.

| Trait ^a | σ_a^2 | σ_e^2 | σ_{ph}^2 | h^2 | c^2 | e^2 |
|--------------------|--------------|--------------|-----------------|-------------|-------------|-------|
| LWG ₁ | 0.0063 | 0.0067 | 0.035 | 0.18 ± 0.04 | 0.18 ± 0.04 | 0.64 |
| LWG ₂ | 0.0063 | 0.0031 | 0.021 | 0.30 ± 0.04 | 0.15 ± 0.02 | 0.55 |
| LWG ₃ | 0.0042 | 0.0049 | 0.019 | 0.21 ± 0.03 | 0.25 ± 0.05 | 0.54 |

^a LWG₁; LWG₂ and LWG₃: live weight gain from 1 to 55; from 56 to 111 and from 112 to 168 days on test, respectively.

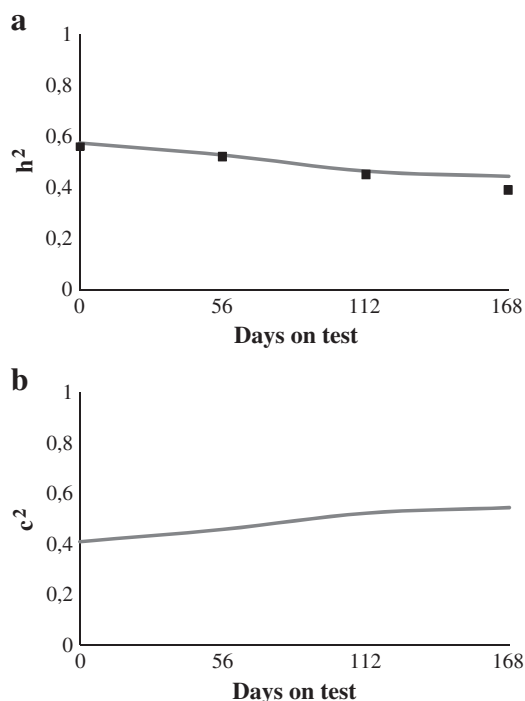


Fig. 2. Heritability (a) and animal (b) variance estimates as proportions of phenotypic variances for live weight obtained with models Leg43res1 (solid line) and with multi-trait model (■).

weight of 0.33 and 0.38, respectively, when compiling *B. taurus* and *B. indicus* studies.

The heritability estimates for LWG obtained with the Leg32res3 model were moderate (Table 3) and lower than those estimated for LW. The heritability for LWG₂ was higher than the estimates for LWG₁ and LWG₃. Přibyl et al. (2008), studying dual-purpose Czech Fleckvieh bulls in performance test stations, also observed the highest heritability estimates for LWG in the middle of the experimental period (at about 250 days of age). Similar heritability estimates for LWG were obtained with the multi-trait model (0.18 ± 0.04 , 0.30 ± 0.04 and 0.22 ± 0.03 for LWG₁, LWG₂ and LWG₃, respectively). Applying multi-trait animal models, Miglior et al. (1994), for station-tested Limousin cattle, and Gengler et al. (1995), for station-tested Belgian Blue cattle, reported higher heritability estimates for LWG (0.55) than those obtained in this study. Schenkel et al. (2002), using random regression models, estimated heritabilities for weight gain up to different standard days on test that increased with length of test, ranging from 0.14 to 0.38. Recently, Krejčová et al. (2010) applied random regression and multi-trait models to estimate genetic parameters for average daily gains of Czech Pied bulls in central test stations. The authors reported that, for younger ages, the heritability estimates obtained with third- and fourth-degree random regression models did not agree with those of multi-trait analysis. In contrast, for intermediate and older ages for which a significantly larger number of records were available, closely similar estimates were obtained by random regression and multi-trait analyses.

The animal permanent environmental variance estimates as a proportion of phenotypic variances (c^2) for LW obtained with the Leg43res1 model increased along the trajectory (Fig. 2), ranging from 0.41 to 0.54. These results agree with those reported by Schenkel et al. (2002) who studied station-tested bulls in Canada. However, Riley et al. (2007) reported a different trend for c^2 estimates, with the observation of higher values at the beginning of the test (0.58). For LWG, c^2 estimated with the Leg32res3 model was higher in the first and last test periods (Table 3). The c^2 estimates for LW increased over time and were slightly lower than h^2 at the beginning of the test. For LWG, the c^2 estimates for LWG₁ and LWG₂ remained almost constant, whereas higher estimates were observed for LWG₃. For LWG₁ and LWG₃, the c^2 estimates were similar to the h^2 estimates. Schenkel et al. (2002) reported higher variances due to permanent environmental effects for weight gain than for weight at different days on test.

The estimates of temporary environmental effects (e^2) for LWG were much higher than those estimated for LW. The results of random regression analysis showed that e^2 had a larger impact on LW and LWG at the beginning of the test (0.018 and 0.64, respectively), whereas this impact decreased at the end of the test (0.012 and 0.54). Similar results have been reported by Schenkel et al. (2002). The present findings suggest that environmental effects on LW and LWG decrease along the test period, suggesting that an adaptation period is necessary in performance bull test stations.

3.3. Correlation estimates

The genetic correlations between LW_{1d}, LW_{56d}, LW_{112d} and LW_{168d} obtained with the Leg43res1 and multi-trait models were high and similar, ranging from 0.82 to 0.98, and decreased as the difference in days on test increased. These results suggest that selection for higher LW at any day on test would also increase final LW (LW_{168d}). Schenkel et al. (2002), modeling weight records obtained during a 140-day testing period of bulls in central stations by random regression, reported genetic correlations ranging from 0.86 to 0.99. The animal permanent environmental and phenotypic estimated correlations between LW_{1d}, LW_{56d}, LW_{112d} and LW_{168d} were similar to the genetic correlations, ranging from 0.78 to 0.98, and from 0.78 to 0.92, respectively. According to Přibyl et al. (2007), the LW is a cumulative trait which repeats the whole previous history of the animal, therefore high genetic, animal permanent environmental and phenotypic correlation estimates are expected between live weight records measured at different ages.

The estimated genetic correlations between LWG₁, LWG₂ and LWG₃ obtained with the Leg32res3 and multi-trait models were similar and moderate, ranging from 0.48 to 0.68. In agreement with Schenkel et al. (2002), the genetic correlations for LWG were lower than those obtained for LW. The lowest genetic correlation was observed for the first 55 days on test when compared to the other periods (0.49 and 0.51 with LWG₂ and LWG₃, respectively). The genetic correlations between LWG during the different periods indicate differences in the genetics of daily gain along the growth curve and different environmental relationships. The last two periods of the test (56 to 111 and 112 to

168 days on test) were highly genetically correlated (0.66), indicating that LWG during the last 112 days on test is in part controlled by the same set of genes compared with the LWG during the first 55 days. Schenkel et al. (2002) reported high genetic correlations (>0.95) between LWG during the last three periods of test (28-day interval). According to these authors, performance during the first 56 days on test (especially the first 28 days) is partially controlled by different genes when compared with performance during the last 84 days on test.

The animal permanent environmental correlation estimates varied from 0.061 to 0.78. The lowest estimate was between LWG_1 and LWG_3 . Krejčová et al. (2008) reported that the animal permanent environmental correlation estimates for cumulative gain decrease to negative values with increasing the distance. The phenotypic correlations between LWG_1 , LWG_2 and LWG_3 were much lower than the genetic correlations, ranging from 0.11 to 0.30. Compensatory growth has been suggested to be the main cause of the lower phenotypic correlation between performance at the beginning of the test and the remaining test period (Kemp, 1990). The correlation estimated between LWG during the first 55 days with the LWG during the last 112 days, suggest that animals that did not perform well during the first period compensate by gaining more during the last two periods of the test.

3.4. Breeding values

For bulls with own LW_{168d} records, the mean and standard deviation of breeding values for LW_{168d} , as well as the percentage of animals with the highest DW378, are shown in Table 4. At all selection intensities, the breeding values for LW_{168d} obtained by multi-trait analysis were lower than those estimated with the Leg43res1 model. However, the breeding values for LWG_{112} obtained with the multi-trait and Leg32res3 models were similar at all selection intensities. These results might be explained by the slightly higher additive genetic variances for LW_{168d} obtained with the Leg43res1 model. Similar results have been reported by Boligon et al. (2011a) for weight records from weaning to mature age, who estimated higher breeding values when random regression models applying Legendre polynomials or B-splines as basis functions rather than a multi-trait

model were used. On the other hand, Albuquerque and El Faro (2008), using weight records from birth to yearling from Nelore cattle, obtained higher breeding values with finite dimensional models (standard two-trait analysis) compared to random regression models.

Considering all bulls with own LW_{168d} records (4725), the rank correlations between breeding values for final weight (LW_{168d}) predicted with the multi-trait and Leg43res1 models and based on DW378 were moderate (Table 5). When selected groups of animals were analyzed such as the best 20%, 5%, and 2% for DW378, rank correlations were lower, particularly those obtained with the Leg43res1 model. At all selection intensities, the rank correlations between breeding values for LWG_{112} and DW378 were much lower than the rank correlations between LW_{168d} and DW378. In general, the percentage of bulls selected for higher DW378 that would also be selected based on LW_{168d} or LWG_{112} breeding values obtained by multi-trait and random regression analyses decreased as the selection intensity increased. At high selection intensity, changes in the bulls selected would mainly occur when LW_{168d} breeding values are estimated with the Leg43res1 model or when LWG_{112} is used as a selection criterion.

The rank correlations between LW_{168d} breeding values predicted with the multi-trait and Leg43res1 models were high at all selection intensities, ranging from 0.77 to 0.98. Příbyl et al. (2008) reported a similar rank correlation (0.94) between breeding values for LW at 400 days of age obtained by single-trait and random regression analyses for dual-purpose Czech Fleckvieh bulls. The rank correlations between LWG_{112} breeding values predicted with the multi-trait and Leg43res1 models were high (0.99) at all selection intensities. These results agree with those reported by Krejčová et al. (2010), who predicted breeding values for LWG of bulls during a performance test using random regression or multi-trait models and concluded that the same bulls will be selected, irrespective of the model. Considering all bulls, the rank correlations of bulls selected for LW_{168d} or LWG_{112} were low, ranging from 0.25 to 0.29. However, when the best 20%, 5% and 2% bulls were considered for LW_{168d} , rank correlations between LW_{168d} and LWG_{112} breeding values were much lower (data not shown), indicating a possible re-ranking especially among top bulls. Higher rank correlations

Table 4

Means and standard deviations (std) of breeding values (in kg) for live weight at 168 days of the test (LW_{168d}) and live weight gain from 56 to 168 days on test (LWG_{112}) estimated by multi-trait analyses or random regression models, for the top animals selected for DW378^a.

| Models | All sires | | 20% best | | 5% best | | 2% best | |
|--------------------------|-----------|------|----------|------|---------|------|---------|------|
| | Mean | Std | Mean | Std | Mean | Std | Mean | STD |
| <i>LW_{168d}</i> | | | | | | | | |
| DW378 | 0 | 32.2 | 44.4 | 15.4 | 66.1 | 12.3 | 77.3 | 11.9 |
| Multi-trait | 8.69 | 16.3 | 31.3 | 7.5 | 42.1 | 5.9 | 47.9 | 5.0 |
| Leg43res1 | 9.81 | 17.1 | 33.6 | 7.8 | 44.9 | 5.6 | 50.4 | 4.6 |
| <i>LWG₁₁₂</i> | | | | | | | | |
| multi-trait | 0.02 | 0.09 | 0.16 | 0.04 | 0.23 | 0.04 | 0.26 | 0.03 |
| Leg32res3 | 0.02 | 0.09 | 0.16 | 0.04 | 0.23 | 0.04 | 0.26 | 0.03 |

^a DW378: final weight standardized to 378 days of age, as deviance from the average of contemporary group.

Table 5

Rank correlations and percentage of bulls (between parenthesis) selected for LWG_{112} or LW_{168d} breeding value predicted by multi-trait analyses or random regression models, applying different selection intensity based on DW378^a.

| Models | All sires | 20% best | 5% best | 2% best |
|---------------------------------------|-----------|-----------|------------|------------|
| ^b <i>LW_{168d}</i> | | | | |
| multi-trait | 0.71 | 0.42 (62) | 0.41 (45) | 0.15 (43) |
| Leg43res1 | 0.70 | 0.35 (58) | 0.30 (42) | −0.12 (29) |
| ^c <i>LWG₁₁₂</i> | | | | |
| multi-trait | 0.38 | 0.11 (40) | −0.07 (18) | 0.19 (11) |
| Leg32res3 | 0.39 | 0.11 (39) | −0.07 (18) | 0.19 (11) |

^a DW378: final weight standardized to 378 days of age, as deviance from the average of contemporary group.

^b LW_{168d} : weight at 168 days of the test.

^c LWG_{112} : live weight gain from 56 to 168 days on test.

(0.89) between breeding values for LW at 400 days of age and LWG from 100 to 400 days of age have been reported by Přebyl et al. (2008).

3.5. General discussion

The statistical criteria indicated that random regression models are the most adequate to fit LW and LWG data. According to Přebyl et al. (2007), random regression models allow a better evaluation of bulls' growth rate in performance test stations. In addition, random regression models are more parsimonious, have less computational requirements, and required less time to attain the convergence. These aspects are important to define an appropriate model for large-scale genetic evaluations. Random regression and multi-trait models handle environmental factors and dependences between growths in different phases differently (Přebyl et al., 2007). Moreover, random regression models permit a better fit of environmental and genetic effects for LW and LWG since all records available are included in the analysis. In this respect, several studies using simulated and real data (Boligon et al., 2011a; Strabel et al., 2001; Tier and Meyer, 2004) have confirmed that random regression models permit to obtain (co) variance components with a lower prediction error variance and more reliable breeding values than finite dimensional models (multi-trait models).

Most studies investigating genetic parameters for growth traits of bulls in test stations have reported heritability estimates for LWG instead of LW (Albera et al., 2001; Eriksson et al., 2002; Krejčová et al., 2007, 2008; Zumbach et al., 2010). Nevertheless, both traits are common growth measures in cattle, the LWG has been preferred since it reflects the growth rate of the animal over a time interval and is less influenced by factors that may have previously affected the growth of animals (Krejčová et al., 2008; Přebyl et al., 2008). In the CPPC bull test station, the final weight adjusted to 378 days of age, expressed as a deviation from the average of the CG (DW378), is applied as a selection criterion, which has promoted genetic progress of growth traits in the experimental herd (Mercadante et al., 2003; Packer et al., 1986; Razook et al., 1998, 2002). The present results show that genetic evaluation based on LWG would lead to the selection of bulls different from those chosen if LW_{168d} or DW378 is applied as a selection criterion. The LW_{168d} and DW378 reflect cumulative growth, which is influenced by genetic potential (direct and maternal) and environmental effects. According to Přebyl et al. (2008), LW is a cumulative trait and is therefore difficult to model correctly in a moment of evaluation the differences in accumulation of all internal and external factors previously influencing the growth of animals. Probably, a strategy combining LWG during the test and final LW in a selection index, with different weighting of each trait, would be a suitable strategy to select bulls.

On the basis of the results of this study, it is expected that the response to selection would be higher for LW_{168d} than for LWG₁₁₂. The potential for genetic improvement not only depends on the heritability of the trait, but also on its relationship with other economically important traits. In this respect, studies involving Nellore cattle have demonstrated that the genetic correlations of postweaning LW or postweaning LWG until yearling with other economically important traits,

such as scrotal circumference and age at first calving, were of similar magnitude (Boligon et al., 2010a, 2010b, 2011b; Yokoo et al., 2007). Therefore, the application of either LW or LWG as a selection criterion should promote a similar correlated response in other economically important traits.

4. Conclusions

The variance component and genetic parameter estimates for LW and LWG obtained by random regression and multi-trait analysis were similar. Random regression models on Legendre polynomials of days on test were more appropriate than multi-trait models to describe the genetic variation of growth traits in station-tested Nellore bulls. Selection based on breeding values for LWG during the test would result in the selection of bulls different from those chosen if final weight is applied as a selection criterion.

Conflict of interest statement

We wish to confirm that there are no known conflicts of interest associated with this publication (Genetic parameter estimates for live weight and daily live weight gain obtain for Nellore bulls in a test station using different models) and there has been no significant financial support for this work that could have influenced its outcome.

We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us.

We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institution concerning intellectual property.

We understand that the Corresponding Author is the sole contact for the *Livestock Science* Editorial process (including Editorial Manager and direct communications with the office). She is responsible for communicating with the other authors about progress, submissions of revisions and final approval of proofs.

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