Random regression analysis of test-day milk yields in the first and second lactations of Brazilian Gyr cows

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ABSTRACT. The objective of the present study was to estimate the genetic parameters for test-day milk yields (TDMY) in the first and second lactations using random regression models (RRM) in order to contribute to the application of these models in genetic evaluation of milk yield in Gyr cattle. A total of 53,328 TDMY records from 7118 lactations of 5853 Gyr

cows were analyzed. The model included the direct additive, permanent environmental, and residual random effects. In addition, contemporary group and linear and quadratic effects of the age of cows at calving were included as fixed effects. A random regression model fitting fourth-order Legendre polynomials for additive genetic and permanent environmental effects, with five classes of residual variance, was applied. In the first lactation, the heritabilities increased from early lactation (0.26) until TDMY3 (0.38), followed by a decrease until the end of lactation. In the second lactation, the estimates increased from the first (0.29) to the fifth test day (0.36), with a slight decrease thereafter, and again increased on the last two test days (0.34 and 0.41). There were positive and high genetic correlations estimated between first-lactation TDMY and the remaining TDMY of the two lactations. The moderate heritability estimates, as well as the high genetic correlations between half the first-lactation TDMY and all TDMY of the two lactations, suggest that the selection based only on first lactation TDMY is the best selection strategy to increase milk production across first and second lactations of Gyr cows.

Key words: Covariance functions; Dairy cattle; Genetic evaluation; Legendre polynomial

INTRODUCTION

Random regression models (RRM) have been proposed as the most adequate models to describe changes in the (co)variances of repeated measures obtained throughout the life of an animal, such as milk yield, which is measured monthly (Jamrozik and Schaeffer, 1997). These models assume all production records of the same animal to be the same trait (Kirkpatrick et al., 1994), but consider environmental differences between measures, an approach that permits estimation of the trajectory of the trait over time for each animal as a deviation of the fixed curve estimated for the population. In general, orthogonal Legendre polynomials have been employed in RRM to model the random trajectories for additive and permanent environmental effects, as well as the fixed trajectory, which have shown better convergence properties than models using other functions (Pool et al., 2000; Schaeffer, 2008).

Several studies have demonstrated the existence of a genetic correlation between test-day milk yields of the same lactation and between test-day yields of different lactations (Guo et al., 2002; Yang et al., 2005; Cobuci et al., 2011). However, preliminary studies have shown differences in the lactation curve between the first and second lactation, and between the second and subsequent lactations. In some countries such as Germany, the Netherlands, and the United States, multitrait random regression analysis including the first three lactations has been used for the genetic evaluation of dairy cattle.

The dairy Gyr (*Bos indicus*) breed is present in more than 80% of Brazilian dairy herds as purebreds or as crossbreeds with Holstein cattle (Reis Filho, 2006). It is important that breeding values for milk yield of different lactations are available. However, the breeding program of this breed has focused mainly on first-lactation milk yield. The objective of the present study was to estimate genetic parameters for test-day milk yields in the first and second lactations using RRM in order to contribute to the application of these models in genetic evaluations of milk yield in the Gyr cattle.

MATERIAL AND METHODS

Test-day milk yields (TDMY) of first and second lactations of Gyr (*Bos indicus*) cows were analyzed using bivariate RRM. The data were obtained from the Brazilian Association of Zebu Breeders (Associação Brasileira de Criadores de Zebu - ABCZ).

The test-day records were obtained starting on the fifth day after calving and were truncated at 305 days of lactation, with the first record being obtained up to 45 days after calving. The mean age at first and second calving was 40.4 and 57.42 months, respectively. Test-day milk yields were divided into monthly classes of days in milk, ranging from one to 10 classes. Contemporary groups were formed by herd-year-season of test day (one corresponding to the rainy season (October to March) and the other to the dry season). Only data of animals with at least three animal-observations were kept. Additionally, records exceeding 3.5 standard deviations above or below the overall mean for the contemporary group were eliminated.

A total of 53,328 TDMY records from 7,118 lactations of 5,853 Gyr cows were analyzed. The cows had calved between 1983 and 2009 and belonged to 238 herds in Brazil. The relationship matrix contained 15,209 animals. The structure of the dataset after editing is summarized in Table 1.

Table 1. Number of sires and dams with female offspring with test-day milk yield (TDMY) records, number of contemporary groups, and mean lactation length of the first and second lactation of Gyr cows.

Information	Lactation 1	Lactation 2
Sires with female offspring with production records	731	338
Dams with female offspring with production records	3,725	1,242
Females with production records	5,534	1,584
Number of females in the pedigree	1,827	1,100
Number of sires in the pedigree	7,010	2,939
TDMY	41,338	11,990
Lactation length (days)	292.7	285.6
Contemporary group	1,452	541

Analysis was performed using a bivariate RRM by Bayesian inference on orthogonal Legendre polynomial. The model included the direct additive, permanent environmental and residual random effects. In addition, contemporary group and linear and quadratic effects of the age of cow at calving were included as fixed effects. The average lactation curve of the population was modeled with a fourth-order orthogonal Legendre polynomial. Legendre polynomials were used to fit genetic additive and permanent environmental random effects.

The choice of the order of covariance functions to describe the random effects was based on the results of Pereira et al. (2013) who applied RRM to describe first-lactation TDMY in Gyr cattle employing part of the database used in this study. After comparing the different models based on total residual variance criteria, the percentage of reduction in model complexity (Bozdogan, 2000), and the Akaike and Schwarz Bayesian information criteria (Wolfinger, 1993), the authors indicated a random regression model fitting fourth-order Legendre polynomials for additive genetic and permanent environmental effects, with 5 classes of residual variance.

The matrix presentation of the RRM is given by:

$$y = Xb + Za + Wp + e$$

where y is the vector of observations; b is the vector of systematic effects and fixed regression coefficients; a is the vector of additive genetic random regression coefficients; p is the vector of

permanent environmental random regression coefficients; e is the vector of the random residual effect, and X , Z , and W are incidence matrices corresponding to the observations for systematic effects, random additive genetic effects and permanent environmental effects, respectively. The following assumptions were defined for this model:

$$y | b, a, p, R \sim \text{MVN}(Xb + Za + Wp, R),$$

$$\text{Var} \begin{bmatrix} a \\ p \\ e \end{bmatrix} = \begin{bmatrix} \Lambda_A \otimes A & 0 & 0 \\ 0 & \Lambda_P \otimes I & 0 \\ 0 & 0 & R \end{bmatrix}$$

where Λ_A and Λ_P are additive genetic and permanent environmental covariances, respectively, between the regression coefficients for the two traits. R is the residual covariance matrix between the traits. The same residual variance was assumed within intervals and heterogeneous variances between the intervals. A is the numerator relationship matrix between the animals, I is an identity matrix, and $\otimes$ is the direct product operator between the matrices. The following prior distributions were assumed for the model:

$$\begin{aligned} b &\propto \text{constant}, \\ a | \Lambda_A &\sim \text{MVN}(0, \Lambda_A \otimes A), \\ p | \Lambda_P &\sim \text{MVN}(0, \Lambda_P \otimes I), \\ \Lambda_A | v_a, S_a &\sim IW(v_a, v_a S_a), \\ \Lambda_P | v_p, S_p &\sim IW(v_p, v_p S_p), \\ R | v_e, S_e &\sim IW(v_e, v_e S_e), \end{aligned}$$

where, MNV and IW indicate multivariate normal and inverse Wishart distributions, respectively, and v_a , S_a , v_p , S_p , v_e and S_e correspond to the degree of confidence and prior values for additive genetic, permanent environmental and residual covariance matrices, respectively.

The (co)variance components were estimated by Bayesian inference using the Gibbs sampler of the GIBBS3F90 program (Misztal, 2009). A chain length of 1,500,000 cycles was established, with a burn-in period of 150,000 cycles and a sampling interval of 50 cycles, corresponding to 27,000 samples for subsequent analysis. The variance and heritability estimates for each test day and correlations between test days were obtained based on the covariance functions estimated in each cycle. Convergence was tested using the criteria proposed by Heidelberger and Welch (1983) and Geweke (1992). The R software, with some routines of the Bayesian Output Analysis (BOA) package, was used to calculate Geweke's, and Heidelberger and Welch's statistics (Smith, 2007).

RESULTS AND DISCUSSION

For the two lactations, average TDMY increased until the second test day, i.e., peak

lactation, and decreased, thereafter (Table 2). The occurrence of peak production on, as early as the second test day is common in Gyr cattle. Consequently, the period of lactation is short and lactation persistency is lower when compared to European breeds.

Table 2. Number of observations (N), average milk yield (MY), standard deviation (SD), and number of observations per contemporary group (CG) for monthly test-day milk yields (TDMY) of two lactations in Gyr cows.

	Lactation 1				Lactation 2			
	N	MY (kg)	SD (kg)	CG	N	MY (kg)	SD (kg)	CG
1	4 041	11.3	4.6	1.107	1.251	11.0	5.5	403
2	4 826	12.6	5.5	1.173	1.393	14.1	5.9	437
3	4 870	12.3	5.8	1.235	1.416	13.3	5.9	443
4	4 795	11.9	5.7	1.219	1.369	12.4	5.7	443
5	4 471	11.5	5.7	1.174	1.318	11.6	5.2	432
6	4 228	10.9	5.6	1.135	1.266	10.8	5.0	427
7	3 992	10.4	5.4	1.096	1.208	10.0	4.8	417
8	3 748	9.8	5.2	1.024	1.082	9.2	4.6	398
9	3 374	9.2	5.0	995	939	8.6	4.4	370
10	2 993	8.9	4.8	908	748	8.0	4.1	326

The estimates of phenotypic variances for TDMY indicated similar trajectories for the two lactations, which however, differed in magnitude (Figure 1). Different tendencies of phenotypic variances for first lactation have been reported in the studies of DeGroot et al. (2007) and Biassus et al. (2011), with higher estimates at the beginning and end of lactation. In general, the phenotypic variance estimates for TDMY in this study were higher in the second lactation, a finding also observed in other studies (Jamrozik et al., 1997; Strabel and Jamrozik, 2006).

Figure 1. Posterior means and respective 95% confidence intervals for additive genetic, permanent environmental, and phenotypic variances of test-day milk yields in the first (A) and second lactation (B) of Gyr cows, obtained with bivariate random regression models using Bayesian inference.

The additive genetic variances (Figure 1) increased until TDMY4 and 5, and decreased thereafter until the end of lactation, in the two lactations. These results differ from those reported by Biassus et al. (2011), who found an increase in variances across lactation. A decrease in additive variance at the end of lactation has been observed in other studies (Pool et al., 2000; Lopez-Romero et al., 2003; Costa et al., 2008). This reduction has been attributed to the smaller number of observations during this stage of lactation, a fact that leads to difficulties in adjusting the mathematical functions used for the description of additive and permanent environmental effects. In contrast, DeGroot et al. (2007) observed an increase in additive variances from mid-lactation to the end of lactation in the first three lactations of Holstein cows. The magnitude of the additive variance estimates was higher for TDMY of the second lactation when compared to the first lactation, in agreement with other studies (Strabel and Jamrozik, 2006; DeGroot et al., 2007). However, the differences were of low magnitude.

The permanent environmental variance estimates showed different tendencies in the two lactations, increasing with days in milk in the first lactation and decreasing after the seventh test day in the second lactation. Higher estimates were obtained for most TDMY in the second lactation (Figure 1). Similar results have been reported in different studies (Fujii and Susuki, 2006; Araujo et al., 2006; Cobuci et al., 2011).

The magnitudes of the posterior mean heritabilities showed different tendencies in the two lactations, especially for the first TDMY and the two test days at the end of lactation (Table 3). In the first lactation, the heritabilities increased from early lactation (0.26) until TDMY3 (0.38), followed by a decrease until the end of lactation. In the second lactation, the estimates increased from the first (0.29) to the fifth test day (0.36), with a slight decrease thereafter, and again increased on the last two test days (0.34 and 0.41). In general, the tendency of the heritabilities for TDMY in the first and second lactations was similar to that observed by Bormann et al. (2005), De Roos et al. (2004), and Cobuci et al. (2011), i.e., lower heritabilities at the beginning of lactation, an increase until mid-lactation, and a subsequent decrease until the end of lactation. However, lower estimates were reported in the cited studies, in addition to the observation of higher heritabilities for first-lactation TDMY. For Gyr cattle, Pereira et al. (2013), using first-lactation milk yield records, reported magnitudes of heritabilities similar to that found in the present study for first-lactation yields, with higher estimates in the first-third of lactation and a tendency toward a reduction with advancing lactation.

Table 3. Means and 95% credibility intervals (95CI) of heritability estimates for test-day milk yield (TDMY) in the first two lactations of Gyr cows obtained with bivariate random regression models using Bayesian inference.

	Lactation 1		Lactation 2	
	Mean	95CI	Mean	95CI
1	0.26	0.18-0.35	0.29	0.19-0.43
2	0.34	0.24-0.44	0.31	0.23-0.40
3	0.38	0.29-0.47	0.31	0.23-0.39
4	0.35	0.27-0.45	0.35	0.28-0.45
5	0.35	0.28-0.44	0.36	0.26-0.44
6	0.34	0.26-0.42	0.35	0.25-0.44
7	0.32	0.24-0.40	0.33	0.23-0.44
8	0.28	0.20-0.39	0.33	0.23-0.45
9	0.26	0.18-0.34	0.34	0.20-0.49
10	0.24	0.16-0.31	0.41	0.27-0.57

The genetic correlations of milk yields between two test days within lactation ranged from 0.35 to 0.99 (Figure 2). In general, the genetic correlations were higher between adjacent test days,

and they decreased with increasing distance between test days, in agreement with the results of other studies (Liu et al., 2001; Cobuci et al., 2011). The lowest estimates within the same lactation occurred between the 1st and 10th test day and were 0.46 and 0.48 for the first and second calving, respectively. The highest estimate was observed between the 4th and 5th test day (0.99 for each lactation).

Although the variation in genetic correlations was similar in the two lactations, the magnitude of these correlations tended to decrease with increasing calving order. Furthermore, there was a greater variation in the genetic correlations between second lactation TDMY when compared to the estimates of the first lactation (Figure 2).

Figure 2. Estimates of genetic correlation between milk yields on test days 1, 5 and 10 and the remaining test days for the first (A) and second (B) lactation of dairy Gyr cows, obtained with bivariate random regression models.

The permanent environmental correlations between test days ranged from 0.42 to 0.99 in each lactation (Figure 3). The lowest estimates were obtained between the 1st and 10th test day in the first and second lactation, and the highest estimates between the 7th and 8th test day in the first lactation and between the 2nd and 3rd test day in the second lactation. The permanent environmental correlations were higher between milk yields of adjacent test days and decreased with increasing distance between test days (Liu et al., 2001; Bignardi et al., 2009; Cobuci et al., 2011).

Figure 3. Estimates of permanent environmental correlation between milk yields on test days 1, 5 and 10 and the remaining test days for the first (A) and second (B) lactation of Dairy Gyr cows, obtained with bivariate random regression models.

Figure 4 shows the genetic and permanent environmental correlations, respectively, between milk yields on the 1st, 5th, and 10th test day of the first lactation and TDMY of the second lactation. In general, the genetic correlations showed the same trend as the permanent environmental correlations. However, higher magnitudes were observed for the genetic correlations, ranging from 0.38 to 1.00, whereas the permanent environmental correlations ranged from 0.09 to 0.99.

Figure 4. Estimates of genetic (A, B, C) and permanent environmental (D, E, F) correlations between first-lactation milk yields on test days 1st (A and D), 5th (B and E) and 10th (C and F) and all test-day milk yields of the second lactation of dairy Gyr cows, obtained with bivariate random regression models.

High genetic and permanent environmental correlations were observed between first-lactation TDMY and equivalent and adjacent TDMY of the second lactation, except for 10th TDMY. In general, the results are in agreement with the results reported by Guo et al. (2002), Yang et al. (2005), and Strabel and Jamrozik (2006). The correlations of first-lactation TDMY with those of the second lactation decreased with increasing distance between equivalent test days, except between the 10th TDMY of first lactation and all TDMY of second lactation (Figure 4C), whose genetic correlation estimates were smaller than 0.70.

The positive and medium to high genetic correlations between first-lactation TDMY and the remaining TDMY of the second lactation indicate the existence of a group of genes that affects them in a desirable direction. However, the last part of first and second lactation showed lower genetic correlation with the previous parts and could cause some changes in ranking of sires if only first lactation information would be used. An explanation of this occurrence could be that the breeders record first lactation milk production of cows only if their production is higher than the overall mean of herds.

The analysis of milk yield using bivariate RRM permits to combine the information of correlated traits, in this case, TDMY of different lactations, to predict the genetic merit of animals for traits such as 305-day cumulative milk yield and lactation persistency. Therefore, an RRM including two lactations would consider a larger number of records per cow, which will contribute to more accurate predictions of genetic parameters and breeding values.

CONCLUSIONS

Heritability estimates for the first and second lactation presented moderate values. The genetic correlation estimates ranged from moderate to high, demonstrating genetic association between milk yields across lactation in the same direction, but suggesting differences in this association between periods of lactation. Therefore, the genetic parameters in the first and second lactation obtained in this study indicated the possibility of using test-day records for the prediction of breeding values for milk yield in this population of the Gyr breed.

Conflicts of interest

The authors declare no conflict of interest.

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