



Milk yield persistency in Brazilian Gyr cattle based on a random regression model

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ABSTRACT. With the objective of evaluating measures of milk yield persistency, 27,000 test-day milk yield records from 3362 first lactations of Brazilian Gyr cows that calved between 1990 and 2007 were analyzed with a random regression model. Random, additive genetic and permanent environmental effects were modeled using Legendre polynomials of order 4 and 5, respectively. Residual variance was modeled using five classes. The average lactation curve was modeled using a fourth-order Legendre polynomial. Heritability estimates for measures of persistency ranged from 0.10 to 0.25. Genetic correlations between measures of persistency and 305-day milk yield (Y305) ranged from -0.52 to 0.03. At high selection intensities for persistency measures and Y305, few animals were selected in common. As the selection intensity for the two traits decreased, a higher percentage of animals were selected in common. The average predicted breeding values for

Y305 according to year of birth of the cows had a substantial annual genetic gain. In contrast, no improvement in the average persistency breeding value was observed. We conclude that selection for total milk yield during lactation does not identify bulls or cows that are genetically superior in terms of milk yield persistency. A measure of persistency represented by the sum of deviations of estimated breeding value for days 31 to 280 in relation to estimated breeding value for day 30 should be preferred in genetic evaluations of this trait in the Gyr breed, since this measure showed a medium heritability and a genetic correlation with 305-day milk yield close to zero. In addition, this measure is more adequate at the time of peak lactation, which occurs between days 25 and 30 after calving in this breed.

Key words: Dairy cattle; Covariance function; Genetic parameters; Milk yield persistency

INTRODUCTION

The Gyr (*Bos indicus*) breed is present almost throughout Brazil, accounting for more than 80% of dairy herds as purebreds or as crossbreeds with Holstein cattle. This widespread distribution is mainly due to the fact that these animals can be raised on pasture, in addition to their resistance to endo- and ectoparasites and to high temperature.

One peculiar characteristic of pasture-based milk production systems is the nutritional limitation of peak milk yield of the animals. Peak milk yield is 14 kg milk/day for cows maintained exclusively on tropical grass systems and 30 kg milk/day for cows raised on intensively managed tropical pasture with concentrate supplements (Santos et al., 2007).

Milk yield persistency can be defined as the ability of a cow to maintain milk production after peak lactation. Therefore, one important trait that needs to be improved simultaneously with total milk yield in dairy cattle breeding programs addressing milk production on pasture is milk yield persistency, since this approach permits an increase in production by genetic modification of the shape of the lactation curve. As a consequence, more persistent cows produce higher amounts of milk during lactation without the need to increase peak yield, which is limited in these production systems. In addition, improvement of persistency may contribute to reducing the costs of production systems, since it is associated with reproductive efficiency, resistance to diseases, and feed and health care costs (Sölkner and Fuchs, 1987; Dekkers et al., 1998; Jakobsen et al., 2003).

Several measures of persistency have been proposed (Jamrozik et al., 1997; Jakobsen et al., 2002; Kistmaker, 2003). These measures are calculated using functions of estimated breeding values (EBV) for days in milk obtained with random regression models. Countries such as Canada and the Netherlands have already included the persistency trait in national genetic evaluations.

Milk yield persistency has not yet been studied in the Gyr breed and a better genetic understanding is therefore necessary to include this trait in genetic evaluations of this breed. The objective of the present study was to evaluate measures of milk yield persistency in first lactations of Gyr cows in order to identify the measure that can be applied to genetic evaluations of animals using random regression models.

MATERIAL AND METHODS

A total of 62,758 test-day milk yield (TDMY) records from 7552 first lactations of Brazilian Gyr cows that calved between 1990 and 2007 were used. The age of the cows at calving ranged from 24 to 60 months. The data were obtained from the National Animal Science Archive, managed by the Brazilian National Center for Dairy Cattle Research (Embrapa Gado de Leite). Test-day records obtained between 5 and 305 days of lactation were used. The following criteria were used for inclusion of the cows in the study: first test-day record obtained within 45 days after calving; interval of 15 to 45 days between test days; and more than 3 test-day records. In addition, the availability of a contemporary group, characterized by herd-year-test month (HYM) with at least three cows (daughters of at least two bulls), was established. After data consistency, 27,000 TDMY records from 3362 cows (daughters of 507 bulls), which belonged to 56 herds, were used in the analyses. Most herds were located in the southeast region of Brazil and the remaining ones were from the northeast, midwest, and south regions. After identification of the relationship between animals for five generations, the pedigree file contained 8590 animals.

The TDMY data were modeled using a random regression model considering a fourth-order Legendre polynomial (LP) for the additive genetic effect and fifth-order for the permanent environmental effect. The average lactation curve was modeled using a fourth-order LP.

Heterogeneity of residual variance was considered, which was constant within but heterogeneous between classes of days in milk. The residual variance classes were formed by grouping the days of lactation as follows: 5-30, 31-60, 61-120, 121-270, and 271-305 days in milk.

The random regression model used in the analyses is represented as:

$$y_{ijk} = \text{HYM}_i + \sum_{n=1}^2 b_n x_j^n + \sum_{m=0}^3 \beta_m \varphi_m(t) + \sum_{m=0}^3 \alpha_{jm} \varphi_m(t) + \sum_{m=0}^4 p_{jm} \varphi_m(t) + e_{ijk},$$

where y_{ijk} is the k^{th} observation recorded on lactation day t of animal j in HYM_i ; HYM_i is the effect of the i^{th} contemporary group (2325 classes); b_n is the regression coefficient for linear ($n = 1$) and quadratic ($n = 2$) effects of TDMY as a function of age x_j of the cow at calving, in months; β_m is the set of m fixed regression coefficients to model the average trajectory of the population; $\varphi_m(t)$ is a covariate of the LP according to lactation day (t); α_{jm} , p_{jm} are sets of m additive genetic and permanent environmental random regression coefficients for each cow j , and e_{ijk} is the random error or temporary measurement error associated with observation k of cow j belonging to HYM_i .

The random regression model can be rewritten in matrix form as:

$$y = X\beta + Za + Wp + e,$$

where y is the vector of observations, β is the vector of fixed effects, a is the vector of random regression coefficients of the additive genetic effect of the animal, p is the vector of random regression coefficients of the permanent environmental effect, e is the vector of the residual random effect, and X , Z and W are incidence matrices corresponding to observations for fixed effects, random effects of the animal and permanent environmental effects, respectively. It was assumed that:

$$\begin{bmatrix} \mathbf{a} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} \sim \mathbf{N}(\mathbf{0}, \mathbf{V}), \mathbf{V} = \begin{bmatrix} \Lambda_A \otimes \mathbf{A} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \Lambda_P \otimes \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{R} \end{bmatrix},$$

where: Λ_A and Λ_P are matrices of additive genetic covariance and permanent environmental effect for the random regression coefficients, respectively; \mathbf{A} is the numerator relationship matrix between animals; \mathbf{I} is an identity matrix; \otimes is the direct product between matrices, and $\mathbf{R} = \text{diag}\{\sigma_{es}^2\}$, where s corresponds to the class of days in milk to fit heterogenous residual variances. Thus, $s = 1, 2, 3, 4$, or 5 .

The solutions for the additive genetic random regression coefficients of animal j are represented as $\hat{\mathbf{a}}_j' = [\hat{a}_{0j}, \hat{a}_{1j}, \hat{a}_{2j}, \hat{a}_{3j}]$. The EBV of animal j on day t of lactation was obtained by:

$$\text{EBV}_{jt} = \mathbf{C}_t \hat{\mathbf{a}}_j,$$

where \mathbf{C}_t is the vector of covariates of the LP on day t of lactation.

The estimated breeding value for 305-day milk yield (EBV_{305}) of animal j was obtained by:

$$\text{EBV}_{305} = \sum_{t=5}^{305} \text{EBV}_{jt}$$

Six measures of milk yield persistency (PS_i) based on the EBV for different periods of lactation were evaluated (Table 1). Higher values for PS_i indicate more persistent lactation.

Table 1. Measures of milk yield persistency (PS_i).

PS_i
$\text{PS}_1 = \left(\frac{1}{51} \sum_{t=255}^{305} \text{EBV}_t - \frac{1}{21} \sum_{t=50}^{70} \text{EBV}_t \right)$, (Kistmaker, 2003)
$\text{PS}_2 = \left(\sum_{t=101}^{300} \text{EBV}_t - 200\text{EBV}_{100} \right)$, (Pösö, 2003 <i>apud</i> Kistmaker 2003, personal communication)
$\text{PS}_3 = \left(\sum_{t=61}^{305} \text{EBV}_t - 245\text{EBV}_{60} \right)$, (De Roos et al., 2001)
$\text{PS}_4 = \left(\sum_{t=61}^{280} (\text{EBV}_t - \text{EBV}_{60}) \right)$, (Jamrozik et al., 1997)
$\text{PS}_5 = \left(\frac{1}{51} \sum_{t=230}^{280} \text{EBV}_t - \frac{1}{21} \sum_{t=20}^{40} \text{EBV}_t \right)$, (adapted from Kistmaker, 2003)
$\text{PS}_6 = \left(\sum_{t=31}^{280} (\text{EBV}_t - \text{EBV}_{30}) \right)$, (adapted from Jamrozik et al., 1997)

The covariance components were estimated by the restricted maximum likelihood method using the WOMBAT program (Meyer, 2007).

The genetic variances for PS_i ($\hat{\sigma}_{\text{aPS}_i}^2$) were obtained by:

$$\hat{\sigma}_{\text{aPS}_i}^2 = \mathbf{f}_i' \Lambda_A \mathbf{f}_i,$$

where f_i' is the vector of covariates corresponding to the function of the measure of persistency, and A_A is the matrix of additive genetic covariances between random regression coefficients. Permanent environmental variances for PS_i ($\hat{\sigma}_{pePS_i}^2$) were obtained in a similar manner by replacing Λ_A with Λ_p , the matrix of permanent environmental covariances between random regression coefficients.

The heritabilities of the persistency measures ($h^2_{PS_i}$) were calculated using the equation:

$$h^2_{PS_i} = \hat{\sigma}_{aPS_i}^2 / (\hat{\sigma}_{aPS_i}^2 + \hat{\sigma}_{pePS_i}^2 + \hat{\sigma}_{ePS_i}^2).$$

The residual variances for PS_i ($\hat{\sigma}_{ePS_i}^2$) were obtained as follows:

$$\hat{\sigma}_{ePS_i}^2 = V_e(PS_i) = V_e \left[\left(\frac{1}{51} \sum_{t=255}^{305} MY_t \right) - \left(\frac{1}{21} \sum_{t=50}^{70} MY_t \right) \right];$$

$$V_e(PS_i) = V_e \left(\frac{1}{51} \sum_{t=255}^{305} MY_t \right) + \left(\frac{1}{21} \sum_{t=50}^{70} MY_t \right) - 2COV_e \left[\left(\frac{1}{51} \sum_{t=255}^{305} MY_t \right), \left(\frac{1}{21} \sum_{t=50}^{70} MY_t \right) \right];$$

$$V_e(PS_i) = \frac{[V_e(MY_{255}) + \dots + V_e(MY_{305}) + 2550COV_e(MY_t, MY_{t'})]}{51^2} +$$

$$+ \frac{[V_e(MY_{50}) + \dots + V_e(MY_{70}) + 420COV_e(MY_t, MY_{t'})]}{21^2} - 2COV_e \left[\left(\frac{1}{51} \sum_{t=255}^{305} MY_t \right), \left(\frac{1}{21} \sum_{t=50}^{70} MY_t \right) \right],$$

where t is the day of lactation and MY_t is the milk yield on day t .

Since in the present study the residual variances were considered to be independent and t is always different from t' , the terms containing COV_e are equal to zero. Thus,

$$V_e(PS_i) = [V_e(MY_{255}) + \dots + V_e(MY_{305})]/51^2 + [V_e(MY_{50}) + \dots + V_e(MY_{70})]/21^2.$$

According to the residual variance classes used, $V_e(MY_5)$ to $V_e(MY_{30}) = \hat{\sigma}_{e1}$; $V_e(MY_{31})$ to $V_e(MY_{60}) = \hat{\sigma}_{e2}$; $V_e(MY_{61})$ to $V_e(MY_{120}) = \hat{\sigma}_{e3}$; $V_e(MY_{121})$ to $V_e(MY_{270}) = \hat{\sigma}_{e4}$; and $V_e(MY_{271})$ to $V_e(MY_{305}) = \hat{\sigma}_{e5}$. Therefore, $\hat{\sigma}_{ePS_i}^2 = V_e(PS_i) = [(16\hat{\sigma}_{e4}^2 + 35\hat{\sigma}_{e5}^2)/51^2] + [(11\hat{\sigma}_{e2}^2 + 10\hat{\sigma}_{e3}^2)/21^2]$. $\hat{\sigma}_{ePS_i}^2$ values were obtained in a similar manner for the other measures of PS_i .

RESULTS AND DISCUSSION

TDMY was 9.2 kg, with a standard deviation of 3.6 kg and a coefficient of variation of 38.9%. An increase in milk production (Table 2) was observed during the first three fortnightly intervals. After the third fortnightly interval, production decreased gradually until the end of lactation.

The average lactation curves obtained for cows with milk production and for bulls that had at least one female offspring with milk production are shown in Figure 1. Both curves showed a similar course and peak breeding values occurred between days 25 and 30 of lactation.

Table 3 shows the heritability estimates for the six PS_i and for 305-day milk yield (Y305), as well as the genetic correlations between PS_i and between these measures and Y305. The heritabilities estimated for PS_1 , PS_5 and PS_6 were medium, a finding indicating a substantial genetic component for this trait in the Gyr breed. On the other hand, the heritability estimates for PS_{22} , PS_{33} , and PS_4 were lower. The differences between heritabilities for PS_i measures might be attributed

to the stage of lactation and to the method used for their estimation (Madsen, 1975). Using data from Danish Holstein animals, Jakobsen et al. (2002) estimated a heritability of 0.09 for PS_4 , a value close to that obtained in the present study (0.10). Cobuci et al. (2006) analyzed data from Brazilian Holstein animals using fourth-order LP and assuming homogenous residual variance during lactation. The authors obtained heritability estimates of 0.09, 0.15 and 0.19 for PS_1 , PS_2 and PS_3 , respectively.

Table 2. Milk yield according to days in milk.

Days in milk	N	Mean (kg)	SD (kg)	CV (%)
5-19	1338	10.0	3.7	37.2
20-34	1616	10.7	3.7	35.0
35-49	1596	10.9	3.9	36.1
50-64	1570	10.4	3.6	34.8
65-79	1601	10.3	3.7	36.3
80-94	1539	10.0	3.5	35.4
95-109	1581	9.7	3.6	37.0
110-124	1469	9.6	3.4	36.1
125-139	1481	9.4	3.5	36.9
140-154	1381	9.2	3.4	36.9
155-169	1416	9.0	3.3	36.7
170-184	1345	8.7	3.2	36.8
185-199	1348	8.6	3.2	37.5
200-214	1272	8.3	3.1	37.2
215-229	1284	8.1	3.1	38.2
230-244	1160	7.8	3.1	39.4
245-259	1160	7.8	3.1	40.0
260-274	1032	7.5	3.0	39.6
275-289	973	7.4	3.0	40.8
290-305	838	7.3	2.9	39.8

N = number of observations; SD = standard deviation; CV = coefficient of variation.

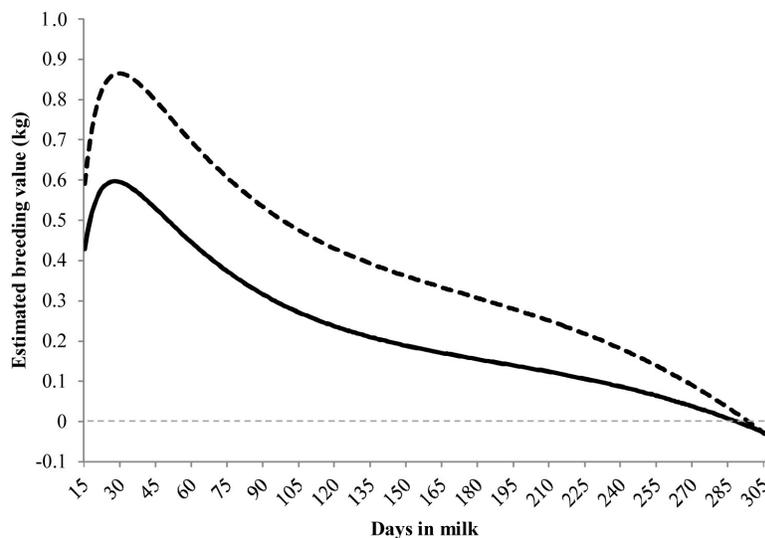


Figure 1. Average lactation curves obtained for cows with milk production (dashed line) and for bulls with at least one female offspring with known milk production (full line).

Table 3. Heritability estimates (diagonal, in bold) and genetic correlations (above the diagonal) between persistency measures (PS_i) and between these measures and 305-day milk yield (Y305).

Trait	Y305	PS ₁	PS ₂	PS ₃	PS ₄	PS ₅	PS ₆
Y305	0.22	-0.46	-0.52	-0.32	-0.28	-0.25	0.03
PS ₁		0.25	0.95	0.95	0.92	0.90	0.59
PS ₂			0.14	0.86	0.82	0.76	0.38
PS ₃				0.12	0.99	0.98	0.80
PS ₄					0.10	0.99	0.83
PS ₅						0.24	0.88
PS ₆							0.16

The genetic correlations between PS_i were generally high, indicating a strong association between these measures. However, PS₆ showed lower genetic correlations with PS₁ and PS₂, indicating that these different measures resulted in re-ranking of animals. The genetic correlations between PS_i and Y305 were negative for PS₁, PS₂, PS₃, PS₄, and PS₅. On the other hand, the genetic correlation between PS₆ and Y305 was close to zero. In studies on Holstein cattle using random regression models, the genetic correlations between different persistency measures and 305-day milk yield ranged from -0.49 to 0.57 (Jakobsen et al., 2002; Kistemaker, 2003; Cobuci et al., 2004, 2006).

PS₆ showed medium heritability and genetic correlations with Y305 close to zero (0.03), desired characteristics of a persistency measure (Dekkers et al., 1998). A persistency measure should show a low correlation with cumulative milk yield during lactation, since otherwise, its inclusion in genetic breeding programs would not be necessary or, if this genetic correlation is negative, the selection for persistency will negatively affect the genetic gain for milk yield.

The percentage of cows or bulls selected in common when different proportions of individuals were selected for persistency (PS₆) and Y305 is shown in Table 4. As expected, a higher percentage of animals were selected in common as the intensity of selection for the two traits decreased.

Table 4. Percentage of cows or bulls selected in common when different proportions of individuals (b) are selected for persistency (PS₆) and 305-day milk yield.

	b (%)					
	1	5	10	20	40	60
Cows in common (%)	3	6	8	14	27	50
Bulls* in common (%)	0	0	10	19	22	49

*Bulls with 8 or more female offspring with known milk production.

Comparison of the five best bulls with at least eight daughters, classified based on EBV₃₀₅ (Figure 2), showed different genetic patterns during lactation for animals with similar breeding values. Bulls B2, B3 and B4 were expected to show higher breeding values for milk yield persistency than bulls B1 and B5.

Similarly, Figure 3 illustrates the genetic curves obtained for the five best bulls with at least 8 daughters classified based on PS₆. In general, the best bulls for milk yield persistency showed negative, although increasing, breeding values almost throughout lactation, except for bull B2. Taken together, these results show that persistency does not depend on the level

of milk production or breeding value for milk yield and is related to the shape of the lactation curve. This supports the auxiliary character of persistency and indicates the need of simultaneous selection for milk yield, since exclusive selection for persistency does not permit genetic improvement of milk production and vice versa. Figure 4 shows two bulls with the same EBV_{305} (483.5 kg) and opposite breeding values for PS_6 . Bull A would be more desired than bull B, since it had a superior genetic lactation pattern, transmitting higher milk yield persistency to its progeny. It is expected that bull A transmitted to its female offspring a small increase in peak yield and a marked increase in production after peak lactation. The opposite should have been observed for daughters of bull B.

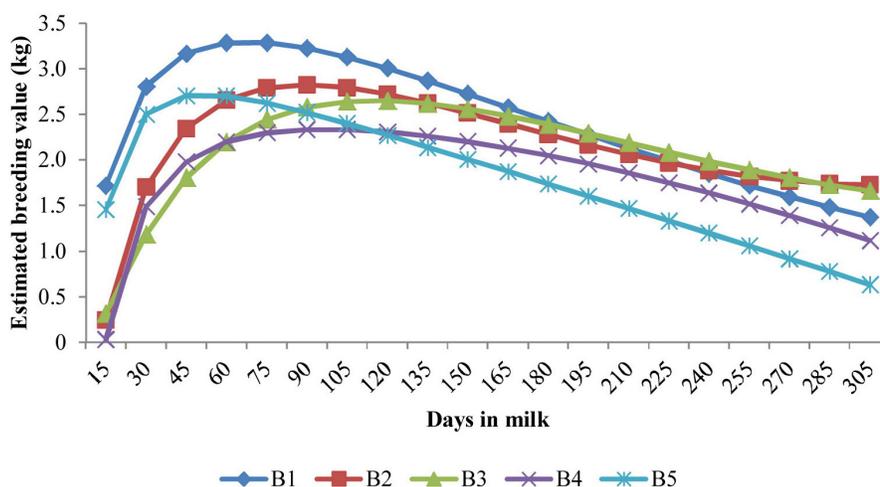


Figure 2. Estimated breeding values along lactation obtained for the five best bulls (B1-B5) classified based on 305-day milk yield with 8 or more daughters.

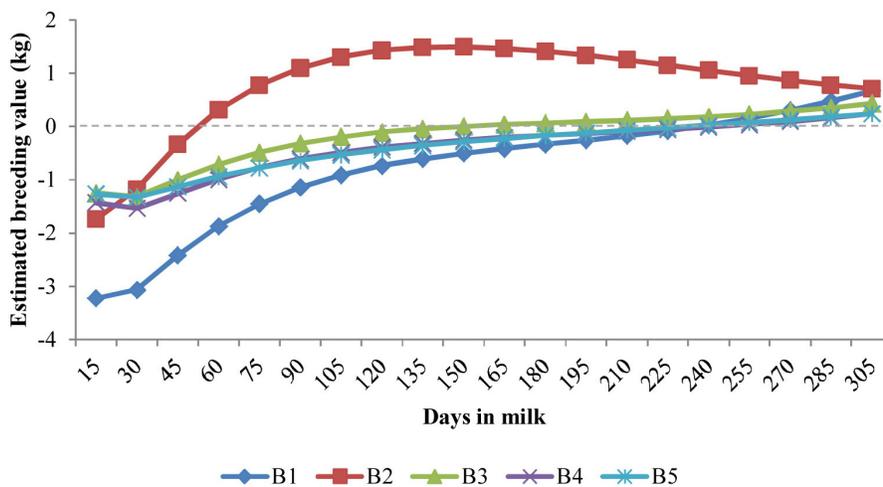


Figure 3. Estimated breeding values along lactation obtained for the five best bulls (B1-B5) classified based on PS_6 with 8 or more daughters.

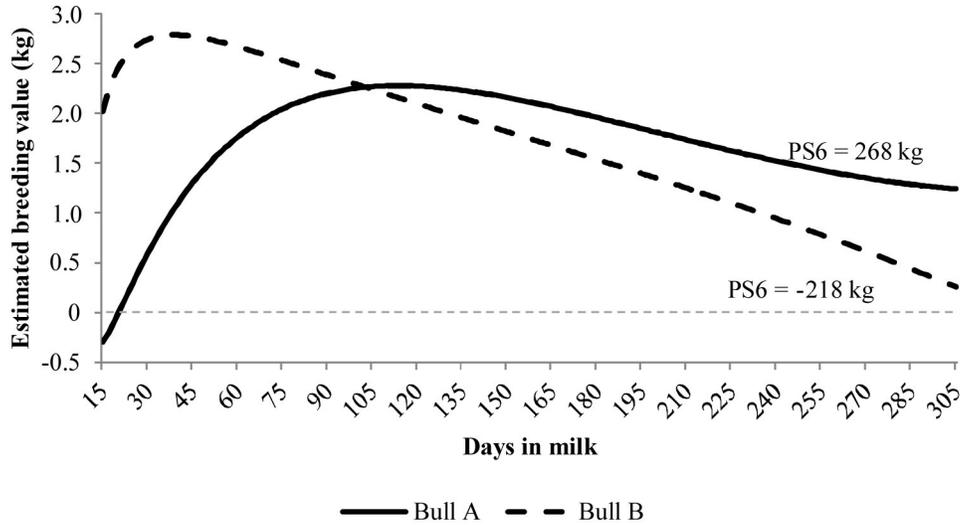


Figure 4. Estimated breeding values along lactation obtained for two bulls (A and B) with the same predicted breeding value for 305-day milk yield (483.5 kg) and opposite breeding values for PS_6 .

The mean EBV_{305} values according to year of birth of the cows (Figure 5) demonstrate a substantial annual genetic gain in Y305, confirming the effectiveness of the national breeding program of this breed. In contrast, there was no genetic gain in persistency (PS_6) (Figure 5).

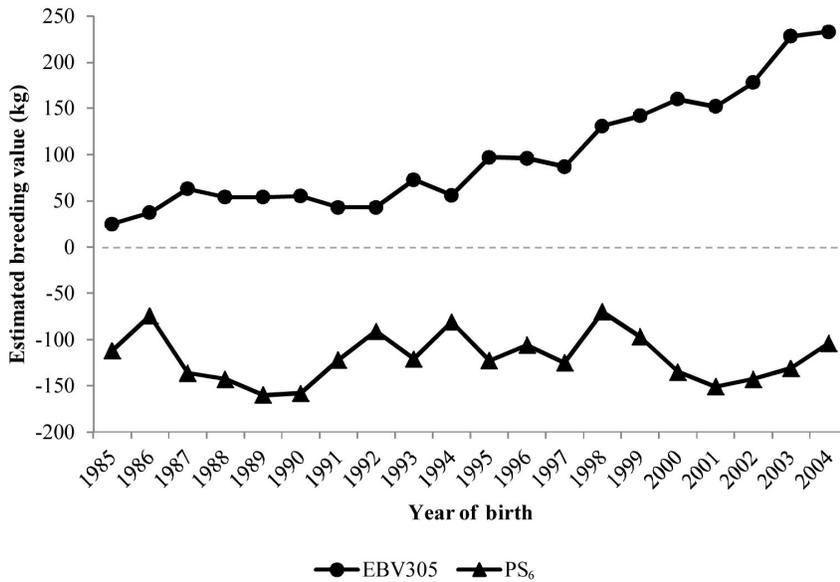


Figure 5. Mean estimated breeding values for 305-day milk yield (EBV_{305}) and milk yield persistency (PS_6) according to year of birth of the cows.

The present results indicate that selection for Y305 did not result in significant improvement of milk yield persistency, a functional trait that is related to a reduction in feed, health care and reproduction costs (Sölkner and Fuchs, 1987; Dekkers et al., 1998; Jakobsen et al., 2003). Strategies of simultaneous selection for milk yield and persistency using selection indices have been investigated by Togashi and Lin (2006, 2007).

Pereira et al. (2011) showed that, for milk yield persistency of Gyr cattle, the lack of adjusting for the effect of pregnancy overestimates breeding values of nonpregnant cows or cows with long days open and underestimates breeding values of cows with short days open. Therefore, this effect should be considered on genetic evaluations for this trait.

The effect of the use of somatotropin, which is generally not included in genetic evaluation models of dairy cattle in Brazil, should be investigated in the Gyr breed to determine its possible influence on genetic evaluations of milk yield and persistency.

CONCLUSIONS

Among the measures of milk yield persistency studied, PS_6 should be preferred in genetic evaluations of this trait in the Gyr breed, since this measure showed a medium heritability and a genetic correlation with 305-day milk yield close to zero. In addition, this measure is more adequate at the time of peak lactation, which occurs between days 25 and 30 after calving in this breed. Simultaneous selection for persistency and milk yield is recommended to obtain genetic gains in milk yield and to change the shape of the lactation curve in a desirable direction.

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