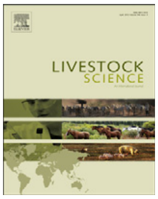
Livestock Science 152 (2013) 114–119

Contents lists available at SciVerse ScienceDirect

Livestock Science

journal homepage: www.elsevier.com/locate/livsci



Genetic parameters for test-day milk yield, 305-day milk yield, and lactation length in Guzerat cows

D.J.A. Santos [a],*, M.G.C.D. Peixoto [b], R.R.A. Borquis [a], R.S. Verneque [b], J.C.C. Panetto [b], H. Tonhati [a]

[a] *Departamento de Zootecnia, Faculdade de Ciências Agrárias e Veterinárias, Universidade Estadual Paulista, Acesso Prof. Paulo Donato Castelani, km 5, 14884-900 Jaboticabal, SP, Brazil*
[b] *Embrapa Gado de Leite, Rua Eugênio do Nascimento, 610, 36.038-330, Juiz de Fora, MG, Brazil*

ARTICLE INFO

Article history:
Received 29 November 2011
Received in revised form
6 November 2012
Accepted 19 December 2012

Keywords:
Zebu
Variance components
Genetic gain
Milk yield

ABSTRACT

Milk production in tropical environments requires the use of crossbreeding systems including breeds well adapted to harsh conditions, but with lower productivities when compared to specialized breeds. Besides the genetic improvement for milk production, lactation lengths also need to be studied for most of these breeds. Accordingly, genetic parameters were estimated for 305-day cumulative milk yield (MY305), test-day milk yield (TDMY), and lactation length (LL) using information from the first lactations of 2816 Guzerat cows selected for milk production in 28 herds in Brazil. Contemporary groups were defined as herd, year and season of the test for TDMY, and as herd, year and season of calving for MY305 and LL. Variance components were estimated with the restricted maximum likelihood method under a multi-trait animal model. Heritabilities estimated for TDMY ranged from 0.16 to 0.24, and were 0.24 and 0.12 for MY305 and LL, respectively. Genetic correlations were high and positive, ranging from 0.51 to 0.99 among TDMY records, from 0.81 to 0.98 between each TDMY and MY305, and from 0.71 to 0.94 between each TDMY and LL. Genetic parameters 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 Guzerat breed. The use of TDMY as selection criteria would result in indirect gains in MY305 and LL. However, the highest response to selection for MY305 would be obtained by direct selection for this trait.

1. Introduction

The extension of Brazil includes the Equator and the Tropic of Capricorn. Thus, there are regions with tropical, subtropical or temperate climates, the last being only in the extreme south of the country. The topography is variable, but usually suitable for cattle breeding. The predominance of the tropical climate imposes management and breeding techniques that differ from what is used for herds in temperate climates, mainly in regard to the use of pasture based systems. Crossbreeding strategies, including *Bos taurus* and *Bos indicus* breeds, are important to achieve the equilibrium between productivity and adaptability of animals to the harsh conditions prevalent in this country.

Nowadays there are a number of elite zebu (*Bos indicus*) herds in Brazil which can provide crossbreeding schemes with genes contributing to milk yield improvement, in addition to the already expected adaptability to harsh conditions. However, some cows tend to drastically decrease milk yield, or even cease lactation much earlier than 305 days, as opposed to what often happens with

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* Corresponding author.
E-mail address: daniel_jordan2008@hotmail.com (D.J.A. Santos).

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http://dx.doi.org/10.1016/j.livsci.2012.12.012

Bos Taurus breeds in temperate systems. This brings a concern about lactation lengths in production systems using zebu animals, which needs to be properly addressed. As published by Peixoto et al. (2012) in the annual dairy genetic evaluation report for the Guzerat breed in Brazil, for instance, the average lactation length was 273 days.

From the Zebu breeds imported to Brazil, the Guzerat is the second most used in milk production systems. Good adaptability to produce under tropical conditions and a high percentage of solids in its milk are some common features of this breed. In addition, the Guzerat breed is often used in crossbreeding for the formation of animals adapted to the tropical conditions of Brazil which are able to maintain economically viable production levels of milk and meat. The Brazilian Breeding Program of Dairy Guzerat Cattle (PNMGuL) has used cumulative milk yield records truncated at 305 days of lactation (MY305) for the genetic evaluation of milk production, while it has been designed to serve the breeders interest on the dual purpose of the breed (Peixoto et al., 2010).

Test-day milk yield (TDMY) is the measurement of the milk produced by a cow over a period of 24 h (Schaeffer and Jamrozik, 1996). Comparisons between lactations models and test-day models for the genetic evaluation of dairy bulls from European breeds can be found in the literature under various perspectives. Schaeffer et al. (2000) presented the Canadian experience with the implementation of test-day models for their national genetic evaluation. They exploited details about the process of changing from a system where 305-days lactations yields were considered as repeated measurements of the same trait and a standard lactation curve was assumed for each cow to a system where each lactation was considered to be a separate trait, where a cow could have different shapes for each lactation curve, and the analyses were on test-day yields. One important discussion within that study was about the extensive efforts that would be required for the producer's acceptance on the changes of methodology and ranking of sires. El Faro and Albuquerque (2003) pointed out some potential advantages for the test-day models, like a better consideration for the systematic effects influencing specific periods of the lactation, which would be intangible under lactation models, or the possibility of inclusion of information from lactating animals. Nevertheless, they concluded that better genetic improvement would be expected from the selection using genetic values obtained under a lactation model, specifically for the Caracu population from their study.

Referring to the Zebu breeds, some studies have been conducted referring to estimates of genetic parameters and comparisons among lactation, repeatability, or random regression models with the Gyr breed (Costa et al., 2005; Herrera et al., 2008; Ledic et al., 2002). Freitas et al. (2010) estimated genetic parameters for TDMY and persistency of lactation measurements for a Guzerat population in Brazil, using random regression models. Nevertheless, studies are still scarce for the Guzerat breed.

The objectives of the present investigation were to estimate variance components and genetic parameters for test-day milk yields (TDMY), their associations with cumulative milk yield (MY305) and lactation length (LL), and expected genetic gains and correlated responses to selection. Those parameters are intended be valuable as a basis for future studies on selection using test-day models within a population of first lactating Guzerat cows.

2. Material and methods

The original data file included 25, 365 test-day records from 3538 first lactating Guzerat cows, with age ranging from 23 to 65 months. Lactations with any interval bigger than 75 days between measurements, from calving to drying off, or with records outside the range between ±3 standard deviations from their contemporary group averages have been removed. The final data file contained 20,524 test-day records from 2816 Guzerat cows, daughters of 371 sires, and belonging to 28 herds. Calving occurred from 1987 to 2009, with this period depending on each herd. Among these cows, there were 2631 with both parents known, 21 with only the sire known, 37 with only the dam known, and 127 with no pedigree information. Considering data used in test-day analysis (TDMY1–TDMY10), sires had an average progeny size of 7.15 and the average number of contemporary groups was 339.5. Number of animals in the average relationship matrix contained 4,148 animals. All information was obtained from the archives of the PNMGuL, a program coordinated by Embrapa Dairy Cattle in partnership with the Brazilian Center for the Genetic Improvement of the Guzerat breed (CBMG) and the Brazilian Zebu Breeders Association (ABCZ).

Test-day records obtained between day 6 and day 305 of lactation were considered in the analyses. Cows whose LL exceeded 305 days had their production records truncated at the last test-day before 305 days. The TDMY were then divided into monthly classes according to days after calving, for a total of 10 classes (TDMY1–TDMY10). Only data from cows with at least four test-day records were maintained. Numbers of observations, means and standard deviations of milk yield and days of lactation, calculated for TDMY1–TDMY10 and MY305 are shown in Table 1.Average lactation length among cows considered in the test-day analyses, was 273.14 days, with a standard deviation of 59.62 days. The frequency distribution of lactation lengths is shown in Fig. 1. Because lactation lengths are short, drying-off is usually done when cows reach low yield levels.

The contemporary groups for MY305 and LL were defined by the concatenation of herd, year and season of calving, and those for TDMY by the concatenation of herd, year and season of test. Seasons were classified into wet (October until March) or dry (April until September).For all traits, contemporary groups that contained fewer than three observations were eliminated.

Variance components were estimated simultaneously for the 12 traits by the restricted maximum likelihood method, under multi-trait animal models, using the Wombat program (Meyer, 2006). For the test-day traits, the model included additive genetic random effects, the fixed effect of contemporary groups, the linear and quadratic regressions of the covariate age at calving and the linear regression of the covariate days of lactation.

TheMY305 and LL models were the same, but adding days of lactation as a covariate. The general model in matrix notation was:

$$y = Xb + Za + e,$$

where y is a vector containing the test-day milk yields, or the 305-day cumulative milk yield or the lactation length, b is the vector of solutions for fixed effects, a is the vector of solutions for direct additive genetic random effects, X and Z are coefficient matrices relating phenotypes to fixed effects and additive genetic random animal effect, respectively, and e is the vector of residual random effects.

Table 1
Number of observations (*N*), means and standard deviations (S.D.) of milk yield and days of lactation for test-day milk yields (TDMY1–TDMY10) and 305-day cumulative milk yield (MY305).

Trait	*N*	Milk yield		Days of lactation	
		Mean	S.D.	Mean	S.D.
TDMY1	1815	8.13	2.94	19.33	6.81
TDMY2	2441	8.39	2.85	45.42	8.70
TDMY3	2452	7.93	2.68	75.96	8.55
TDMY4	2464	7.43	2.63	106.59	8.80
TDMY5	2385	6.94	2.51	136.96	8.44
TDMY6	2288	6.48	2.36	167.19	8.66
TDMY7	2089	6.12	2.25	197.93	8.60
TDMY8	1901	5.69	2.21	228.27	8.60
TDMY9	1508	5.37	2.08	258.67	8.35
TDMY10	1181	5.12	2.04	288.18	8.51
MY305	2816	1,783.20	727.02	254.12	56.30

S.D.: standard deviation.

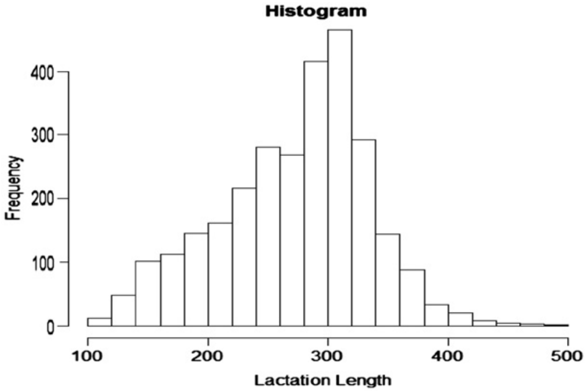

Fig. 1. Frequency distribution of lactation length.

The assumptions about expectations and variances were:

$$E\begin{bmatrix} \mathbf{y} \\ \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{Xb} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix} \; and, \quad \mathbf{V}\begin{bmatrix} \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G} & \mathbf{0} \\ \mathbf{0} & \mathbf{R} \end{bmatrix}$$

where G is the additive genetic (co)variance matrix between traits, and R is the residual (co)variance matrix between traits.

The expected genetic gain (ΔG), correlated response (CR), and relative efficiency of indirect selection (RE), per generation, were calculated for all studied traits considering the same selection intensity (equal to unity). The following equations were used:

$$\Delta G_j = h^2 i \sigma_j$$

$$CR_j = r_a h_j h_k i \sigma_j$$

$$RE = (CR/\Delta G) x\, 100$$

where ΔG_j is the genetic gain due to direct selection for trait j, CR_j is the genetic gain in trait j due to selection on trait k, σ is the phenotypic standard deviation of the trait under selection, i is the selection intensity, r_a is the genetic correlation between traits j and k, h_j and h_k are square roots oh the heritabilities of traits j and k, respectively, and RE is the relative efficiency of indirect selection.

3. Results

Estimates of variance components and heritabilities, and corresponding standard errors for TDMY1–TDMY10, MY305 and LL are shown in Table 2. Variance components for TDMY1–TDMY10 are also illustrated in Fig. 2.Heritabilities for TDMY ranged from 0.16 ± 0.05 to 0.24 ± 0.05, with the highest values in the second and third months of lactation. The lowest heritability estimates for TDMY were observed in the first and eighth months, showing a similar trend to

Table 2
Estimates of additive genetic (σ_a^2), residual (σ_e^2) and phenotypic (σ_p^2) variance components and heritability coefficients (h^2) and their respective standard errors for test-day milk yields (TDMY1 to TDMY10), 305-d milk yield (MY305), and lactation length (LL).

Trait	σ_a^2	σ_e^2	σ_p^2	h^2
TDMY1	0.73 ± 0.22	3.90 ± 0.22	4.63 ± 0.16	0.16 ± 0.05
TDMY2	1.02 ± 0.21	3.30 ± 0.19	4.33 ± 0.13	0.24 ± 0.05
TDMY3	0.86 ± 0.19	3.11 ± 0.18	3.97 ± 0.12	0.22 ± 0.04
TDMY4	0.69 ± 0.17	3.29 ± 0.17	3.98 ± 0.12	0.17 ± 0.04
TDMY5	0.74 ± 0.17	3.15 ± 0.17	3.90 ± 0.12	0.19 ± 0.04
TDMY6	0.69 ± 0.15	2.73 ± 0.14	3.42 ± 0.11	0.20 ± 0.04
TDMY7	0.65 ± 0.15	2.83 ± 0.15	3.48 ± 0.11	0.19 ± 0.04
TDMY8	0.60 ± 0.16	3.15 ± 0.17	3.75 ± 0.13	0.16 ± 0.04
TDMY9	0.78 ± 0.20	3.30 ± 0.20	4.08 ± 0.15	0.19 ± 0.05
TDMY10	0.91 ± 0.26	4.16 ± 0.28	5.07 ± 0.21	0.18 ± 0.05
MY305	77,984 ± 14,573	241,550 ± 13,317	319,530 ± 9,320	0.24 ± 0.04
LL	364 ± 122	2,625 ± 127	2,989 ± 87	0.12 ± 0.04

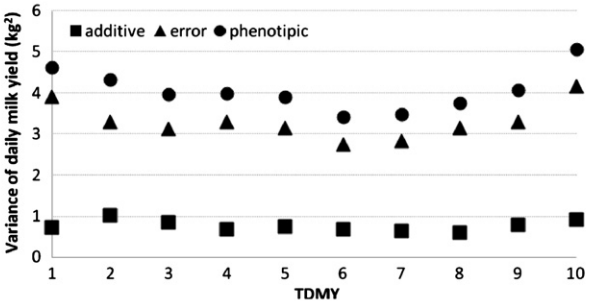

Fig. 2. Estimates of additive genetic, residual and phenotypic variance components for test-day milk yields (TDMY1–TDMY10).

Table 3
Genetic (above diagonal) and phenotypic (below diagonal) correlations between test-day milk yields.

Month	1	2	3	4	5	6	7	8	9	10
1	–	0.91	0.84	0.79	0.77	0.73	0.62	0.68	0.51	0.56
2	0.71	–	0.97	0.94	0.91	0.86	0.80	0.84	0.63	0.65
3	0.67	0.79	–	0.99	0.96	0.92	0.91	0.92	0.77	0.77
4	0.60	0.75	0.80	–	0.98	0.95	0.93	0.94	0.78	0.79
5	0.55	0.69	0.75	0.81	–	0.98	0.92	0.93	0.81	0.82
6	0.52	0.65	0.70	0.76	0.82	–	0.94	0.95	0.86	0.88
7	0.47	0.60	0.66	0.70	0.76	0.82	–	0.99	0.91	0.92
8	0.42	0.52	0.60	0.64	0.71	0.75	0.81	–	0.88	0.91
9	0.40	0.46	0.53	0.56	0.61	0.65	0.73	0.80	–	0.98
10	0.37	0.45	0.49	0.54	0.60	0.63	0.69	0.75	0.85	–

Table 4
Expected responses to selection and genetic correlations in a comparison of direct versus indirect selection on test-day milk yields (TDMY1–TDMY10) or 305-day milk yield (MY305).

Trait	ΔG (kg)	MY305			
		r_a	CR (kg)	RE (%)	CR-cont (kg)
TDMY1	0.34	0.81 ± 0.08	89.79	65.07	0.34
TDMY2	0.49	0.91 ± 0.04	123.29	89.35	0.45
TDMY3	0.43	0.96 ± 0.03	125.16	90.71	0.44
TDMY4	0.34	0.97 ± 0.03	112.13	81.26	0.40
TDMY5	0.38	0.98 ± 0.02	119.05	86.28	0.42
TDMY6	0.37	0.98 ± 0.03	122.25	88.60	0.40
TDMY7	0.35	0.95 ± 0.03	113.99	82.61	0.38
TDMY8	0.31	0.96 ± 0.04	107.08	77.60	0.37
TDMY9	0.39	0.88 ± 0.05	107.49	77.90	0.38
TDMY10	0.40	0.90 ± 0.06	106.11	76.90	0.42
MY305	137.98	1	–	100.00	137.98

ΔG = genetic gain due to direct selection, r_a = genetic correlation between each TDMY and MY305, CR = correlated response on the MY305 when selection is on TDMY, RE = relative efficiency on the MY305 when selection is on TDMY, CR-cont = correlated response on each TDMY when selection is on the MY305.

Table 5
Expected responses to selection and genetic correlations in a comparison of direct versus indirect selection on test-day milk yields (TDMY1–TDMY10) or lactation length (LL).

Trait	ΔG (kg)	LL			
		r_a	CR (kg)	RE (%)	CR-cont (kg)
TDMY1	0.34	0.71 ± 0.19	5.41	81.26	0.21
TDMY2	0.49	0.75 ± 0.14	6.96	104.57	0.26
TDMY3	0.43	0.82 ± 0.14	7.31	109.75	0.27
TDMY4	0.34	0.83 ± 0.13	6.57	98.71	0.24
TDMY5	0.38	0.88 ± 0.11	7.35	110.31	0.27
TDMY6	0.37	0.91 ± 0.11	7.79	117.01	0.26
TDMY7	0.35	0.85 ± 0.10	7.02	105.34	0.24
TDMY8	0.31	0.85 ± 0.10	6.49	97.44	0.23
TDMY9	0.39	0.93 ± 0.08	7.78	116.84	0.29
TDMY10	0.40	0.94 ± 0.09	7.57	113.66	0.31
LL	6.66	1.00	–	100.00	–

ΔG = genetic gain due to direct selection, r_a = genetic correlation between each TDMY and LL, CR = correlated response on the LL when selection is on TDMY, RE = relative efficiency on the LL when selection is on TDMY, CR-cont = correlated response on each TDMY when selection is on the LL.

that observed for the additive genetic variances of these traits.

Phenotypic correlations among TDMY (Table 3, below diagonal) were all positive and ranged from 0.37 (between TDMY1 and TDMY10) to 0.85 (between TDMY9 and TDMY10), with standard errors of 0.01–0.02. Phenotypic correlations between TDMY and MY305(data not shown) were always positive and ranged from 0.67 (first month) to 0.86 (seventh month). Phenotypic correlations between TDMY and LL tended to increase according to the month after calving, ranging from 0.28 (first month) to 0.78 (last month). The phenotypic correlation between MY305 and LL was 0.74.

Genetic correlations among TDMY (Table 3, above diagonal) ranged from 0.51 to 0.99, with standard errors ranging from 0.03 to 0.17 (not shown). Genetic correlations, expected direct or correlated responses to selection and relative efficiencies regarding test-day milk yields and 305-day milk yield are presented on Table 4. Genetic correlations between MY305 and each TDMY were always positive and high, ranging from 0.81 ± 0.08 (first month) to 0.98 ± 0.02 and 0.98 ± 0.03 (fifth and sixth months, respectively). Genetic correlations, expected direct or correlated responses to selection and relative efficiencies regarding test-day milk yields and lactation length are presented on Table 5. Genetic correlations between LL and each TDMY were also always positive, ranging from 0.71 ± 0.19 (first month) to 0.94 ± 0.09 (last month).

4. Discussion

Variances of TDMY tended, in general, to decrease with days in milk until approximately the sixth month of lactation. Heritabilities and additive genetic variances reached a maximum around the second month of lactation. The trend towards an increase in phenotypic and error variances of TDMY after the seventh month (Fig. 2) is probably due to the wide variability in LL seen in the Guzerat breed. In this respect, whereas some animals have good milk yield persistence, others reduce, or even cease, production early in lactation.

Cruz et al. (2006), who also studied TDMY in Guzerat cows, observed a similar trend of variance components during the early period of lactation, including the observation of higher heritabilities compared to mid-lactation. However, the range of heritability values was wider (from 0.03 in the fifth month to 0.29 in the eighth and tenth months). In a study involving dairy Gyr cows, Herrera et al. (2008) estimated heritabilities for first-lactation TDMY ranging from 0.14 (eighth month) to 0.34 (first month). Similar results had been previously reported by Ledic et al. (2002) who analyzed data from the first three lactations of Gyr cows and observed heritabilities ranging from 0.14 in the tenth month to 0.24 in the first month. Although the magnitudes of heritability in the present study were similar to those found by the last authors, the maximum heritability was observed not on the first month, but on the second, which might be explained by differences between breeds in the shapes of lactation curves, particularly during early lactation. Similar magnitudes of heritability for TDMY have been reported by Melo et al. (2005), 0.36, and Bignardi et al. (2008), 0.22, for the Holstein cattle in Brazil, with the highest estimates observed in the fourth and in the third months, respectively.

The heritability for MY305 was 0.24, a value similar to that found in studies with Holstein cattle (Bignardi et al., 2008; Ferreira et al., 2003; Melo et al., 2005). For the Gyr breed, Herrera et al. (2008) reported a heritability of 0.29 and Ledic et al. (2002) of 0.19,but with different data sets and statistical models. El Faro and Albuquerque (2003) found a heritability of 0.27 for a Caracu population. Regarding the Guzerat breed, Peixoto et al. (2006) estimated a heritability of 0.23 for MY305, using a repeatability model. Panetto et al. (2010) obtained a value of 0.27 for MY305, using one lactation per animal, also in the Guzerat breed. The results of most studies conducted in Brazil indicate that the heritability for MY305 obtained in the present investigation was within the range usually found for this trait.

The heritability estimated for LL was 0.12, a value also similar to those usually reported in the literature, ranging from 0.11 for Gyr cattle to 0.19 for crossbred Zebu animals (Balieiro et al., 2000; Vercesi Filho et al., 2007).

Genetic and phenotypic correlations between pairs of TDMY tended to decrease with increasing time distances between test days (Table 3). One hypothesis to explain these results (i.e., correlations of less than unity) is that different genetic and environmental factors act during different periods of lactation. The variation in genetic correlations between TDMY from different periods of the lactation, and higher correlations observed between adjacent tests were also found in other studies (Bignardi et al., 2008; Herrera et al., 2008; Melo et al., 2005; Pander et al., 1992). Although of high magnitude, the estimates obtained in this study were similar to those reported by the cited authors for the Gyr breed, ranging from 0.56 to 1.0, and for the Holstein breed, ranging from 0.3 to 1.0.

Genetic correlations between MY305 and TDMY were all positive and high (Table 4), indicating that the relationships between any of the partial yields and MY305were always favorable. These estimates are similar to those reported by Gadini et al. (1997), Machado et al. (1999) and Ferreira et al. (2003) for the Holstein breed (0.72–1.0), and by Ledic et al. (2002) and Herrera et al. (2008) for the Gyr breed (0.68–1.0). Genetic correlations between LL and TDMY were also high and positive (Table 5) and tended to gradually increase across test days. These results indicate that the relationships between any of the partial yields and LL were also always favorable.

In regard to calculations of genetic responses to direct or indirect selection presented here, the reader should be aware of the possible uncertainty associated with parameters estimated. Considering the estimated genetic correlations and the heritabilities for TDMY, correlated responses on MY305 (CR in Table 4) would be expected be increased for selection with emphasis on TDMY3, TDMY2 and TDMY6, in that order. Relative efficiencies on MY305, based on these TDMY, would be around 90%. Herrera et al. (2008) and Ledic et al. (2002) also found maximum relative efficiencies for test-day records on the improvement of MY305, for the period including the first and second thirds of the lactation, with the Gyr breed. The same have been observed by Ribas and Perez (1990) and Melo et al. (2005), for the Holstein breed.

Contrary correlated responses (CR-cont), i.e. responses on each TDMY obtained by selection on MY305,were generally higher than the genetic gains obtained by direct selection on TDMY in mid-lactation (TDMY4-TDMY8) and almost similar to those obtained by direct selection on TDMY at the beginning or at the end of lactation. These findings indicate that selection on MY305 would provide gains in any TDMY by indirect selection and might be even more effective than direct selection for test-day milk yields if mid-lactation records are to be considered.

For LL, the correlated responses and the relative selection efficiencies were higher than in the case of MY305. The relative efficiencies were even higher than 100% in the case of some test-day milk yields, especially because of the low heritability of LL. As cited before, it is important to remember that these values may include errors associated with the estimations of heritabilities and correlations between traits.

Although results indicate that selection on MY305 would be more efficient as a selection criterion to the improvement of milk production in the Guzerat breed, it can be argued that the use of test-day milk yields brings the possibility of selecting for milk production before the end of lactation (mainly in the first third), allowing the inclusion of animals with unfinished lactations in the genetic evaluations which, in turn, could affect the genetic progress because the evaluation of bulls would include more daughters, improving accuracy, and more young animals, males and females, would be available for selection, which could improve both selection intensity and generation interval. Although this study did not investigate the relationship between test-day milk yields and milk yield persistence, which is an important trait in Guzerat cattle, the positive correlation of any test-day milk yield with LL suggests a selection criterion including TDMY would not negatively interfere with the LL. Madalena (1988) suggested that selecting individuals on an optimum index of lactation yield and length would be more efficient for improving yield than selecting on yield alone, while both criteria would have practically the same efficiency for selection on progeny test, which is the case of the population of this study. Even if LL of the Guzerat breed needs to be improved, present results indicate that a selection program designed to improve milk production would consequently achieve the goal of improving LL, either using test-day milk yields or MY305 as the criterion, without the need of direct selection on this trait.

5. Conclusions

Genetic parameters 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 Guzerat breed. At the same time, no unfavorable relationship was observed between any test-day milk yield (TDMY) and cumulative milk yield (MY305) or lactation length (LL). The use of TDMY as selection criteria would result in indirect gains in MY305 and LL. However, the highest response to selection for MY305would be obtained by direct selection for this trait.

Conflict of Interest

The authors of this paper declare that they have no conflict of interest.

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