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Multivariate analysis of test-day and total milk yield in goats

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ABSTRACT. The objective of this study was to estimate genetic parameters for 305-day cumulative milk yield (MY305) and its association with test-day milk yield (TDMY) in Saanen and Alpine goats in order to provide information that allows the use of TDMY as selection criteria. This was done using standard multi-trait and reduced rank models. Data from 1157 lactations, including the first three kiddings, and 5435 test-day records from 683 Saanen and 449 Alpine goats were used. MY305 was analyzed together with TDMY by multi-trait analysis, from the first to tenth test-day, using records of the first three lactations as repeated measures. Three multi-trait models were used: a standard (SM) and two reduced rank models that fitted the first two (PC2) and three (PC3) genetic principal components. Akaike and Schwarz Bayesian information criteria were used to compare models. Heritability for TDMY estimated with the SM ranged from 0.20 to 0.66, whereas the range calculated from the PC2 model was 0.16 to

0.63. Genetic correlations between TDMY and MY305 were positive and moderate to high, ranging from 0.56 to 0.98 when estimated with the SM, and 0.91 to 1.00 when estimated with the PC2. The standard multi-trait model produced estimates that were more accurate than the reduced rank models. Although the SM provided the worst fit according to the two model selection criteria, it was the best in this dataset.

Key words: Heritability; Milk yield; Reduced rank models; Goat

INTRODUCTION

Goat farming is growing in Brazil every year, as a consequence of the initiative of producers with good business vision, and new government programs (Sarmento et al., 2006). There is an increasing demand for goat milk, due to its high nutritional value and low allergenicity compared to cow milk. Goat milk is used for producing cheese, milk powder, and yogurt, among other products. European dairy goat breeds, such as Saanen and Alpine breeds, predominate in Brazil. Although these breeds have been raised in Brazil for some decades, little is known about their performance, and genetic parameter estimates for production traits are scarce.

Test-day milk yield (TDMY) has been proposed as a selection criterion instead of 305-day cumulative milk yield (MY305). For this purpose, test-day models that include all genetic and environmental effects related to TDMY have been developed (Ptak and Schaeffer, 1993). In multi-trait models, TDMY records are considered to be different traits. However, the number of parameters to be estimated with these models increases exponentially with the increase in the number of traits included in the analysis (Meyer, 1997). In addition, a large number of traits may result in over parameterization of the model, demanding time and a large computational capacity for analysis. There are various approaches to reduce the dimension of the covariance matrix, such as principal component analysis (reduced rank models).

Principal component analysis is designed to identify factors that explain a maximum amount of variation, and consists of the transformation of a set of correlated original variables into a new set of variables, which are linear combinations of these originals but are not correlated with one another, thus eliminating redundant information (Kirkpatrick and Meyer, 2004). Recently, studies have applied principal component analysis to beef (Meyer, 2007b) and dairy cattle (Bignardi et al., 2012) systems.

The objective of this study was to estimate genetic parameters for MY305 and its association with TDMY in Saanen and Alpine goats, using standard multi-trait and reduced rank models, in order to provide information that will allow the use of TDMY as selection criteria for milk yield.

MATERIAL AND METHODS

Data from 1104 lactations, including the first three kiddings, and 4970 test-day records of 667 Saanen (offspring of 88 bucks and 413 dams) and 431 Alpine goats (offspring of 83 bucks and 298 dams) were used. Animals were from 26 herds that participated in a goat production and reproduction management program (PROCAPRI) of UNESP, Jaboticabal, São Paulo, Brazil, between 1999 and 2004, and most were located in the southeastern region of Brazil.

The majority of animals used in the study were raised under an intensive milk production system according to recommendations of NRC (National Research Council, 1981). In general,

animals were fed corn silage as forage, and concentrate consisting of corn grain, soybean, roasted soybean, and limestone. Corn silage, mineral salt and water were available *ad libitum* and concentrate was offered during the morning milking. A small group of animals was raised under a semi-feedlot system, within which animals had access to pasture for a few hours. Overall herd management included monitoring and controlling of ecto- and endoparasites. Preventive measures for controlling mastitis consisted of the use of a strip cup; washing the teats before milking; and subsequent teat dipping in iodine and glycerin. Two milkings were performed per day and lactation data were collected at each.

Traits analyzed in the study were the MY305 and TDMY of the first three lactations, each of which was truncated at 305 days. Monthly test-day records, obtained between days 2 and 305 after kidding, were divided into intervals of approximately 30 days, for a total of 10 monthly test-days (TDMY1 to TDMY10).

Two kidding seasons were established based on the concentration of births; one corresponded to the rainy and the other to the dry season. Preliminary analysis using the least squares method was performed in order to determine the influence of fixed effects (including herd, breed, year and season of birth, year and month of test-day, age of goat at kidding, and lactation length) on both traits. Contemporary groups were defined as herd-breed-year-season of birth for MY305, and as herd-breed-year-month of test-day for TDMY. One restriction was that each contemporary group should contain at least three records.

MY305 was analyzed together with TDMY in multi-trait analysis, using the first three lactations as repeated measures. Three multi-trait models were used: a standard multi-trait (SM) and two reduced rank models that fitted the first two (PC2) and three (PC3) genetic principal components. For analysis of MY305 and TDMY, the multi-trait model included the fixed effects of contemporary groups (700 levels); age at kidding (6 levels); lactation length as covariable (for MY305 only; linear effect); and the random effects of direct additive genetic, permanent environmental, and residual. For all models, the covariance matrix of permanent environmental and residual effects was assumed to have full rank. A pedigree file containing 2793 animals in the relationship matrix was used.

The matrix representation of the multivariate model is:

$$y = \boldsymbol{X}\beta + \boldsymbol{Z}u + \boldsymbol{W}p + e \qquad \text{(Equation 1)}$$

where y is the vector of the dependent variable; X is the incidence matrix of fixed effects for the dependent variable; β is the vector of fixed effects; Z is the incidence matrix of direct additive genetic effects; u is the vector of direct additive genetic effects; W is the incidence matrix of permanent environmental effects; p is the vector of permanent environmental effects of the animal; and e is the vector of random residual effects associated with the observations. It was assumed that u represented a vector of genetic effects with $Var(u) = G = \sum \otimes A$, where A was the numerator relationship matrix, and $Var(e) = R$.

The model used for principal component analysis was obtained by reparameterization of the equation used in the SM, generating an equivalent model containing the principal components for direct additive genetic effects. The model in matrix notation is:

$$y = \boldsymbol{X}\beta + \boldsymbol{Z}^{*}u^{*} + \boldsymbol{W}p + e \qquad \text{(Equation 2)}$$

with $Z^* = Z(E \otimes I)$, $u^* = (E' \otimes I)$, $Var(u^*) = (I \otimes A)$, yields an equivalent model, which fits genetic values for the principal components. $\sum = E\Lambda E'$ denotes the eigenvalue decomposition of the matrix of genetic covariances, with Λ the diagonal matrix of eigenvalues, λ_i, and $\boldsymbol{E}$ the corresponding matrix of eigenvalues, $\boldsymbol{e}_i$ with $EE' = I$. It was assumed that λ_i and $\boldsymbol{e}_i$ were in descending order of magnitude of λ_i. To consider only the leading m genetic principal components, replace E with $\boldsymbol{E}_m$, the $k \times m$ matrix comprising the first m columns of E, e_1, ..., e_m. This gives Z^* with number of columns proportional to m rather than k. The number of equations in equation (2) is reduced correspondingly (replacing Λ by its submatrix Λ_m, consisting of the first m rows and columns), and u^* contains m elements for each individual (Meyer and Kirkpatrick, 2005).

Variance components were estimated by restricted maximum likelihood method, using Wombat package (Meyer, 2007a). Models were compared by Akaike (AIC) and Schwarz Bayesian (BIC) information criteria, as reported by Wolfinger (1993). These criteria allow the comparison between non-hierarchical models and penalize models that contain a larger number of parameters; the BIC criterion attributes a more rigorous penalty.

Expected genetic gain and the correlated response to selection for TDMY were obtained using the estimates of heritability, genetic correlations, and additive genetic standard deviations. Selection intensity of 5% for males and an average generation interval of 3.34 based on the literature (León et al., 2005; Lima et al., 2007; Barros et al., 2011) were examined. The expected genetic gain, correlated response to selection and relative selection efficiency were calculated using a common selection index formula that considers a progeny test with 5, 10, 25, and 50 daughters per buck (Van Vleck, 1993).

RESULTS AND DISCUSSION

The number of records at each test-day and the corresponding milk yield means are presented in Table 1. Peak milk yield was observed from TDMY2 to TDMY3, after which, milk yield decreased with days in milk as well as the number of records. Coefficients of variation for milk yield were high, probably due to differences among breeds and herds, although farming and feed management systems were similar.

Table 1. Number of records at each test-day and corresponding milk yield means.

Trait	Number of observations	Milk yield (kg)			LL (days)	
		Mean	SD	CV (%)	Mean	SD
TDMY1	802	2.36	1.30	55	16.2	6.9
TDMY2	844	2.60	1.46	56	44.9	6.4
TDMY3	745	2.58	1.46	57	74.2	6.5
TDMY4	593	2.39	1.34	56	104.7	7.2
TDMY5	536	2.26	1.33	59	133.6	7.1
TDMY6	400	2.26	1.31	58	164.7	7.1
TDMY7	329	2.30	1.28	56	195.3	7.4
TDMY8	277	2.28	1.32	58	225.1	7.6
TDMY9	245	2.33	1.40	60	254.8	7.2
TDMY10	199	2.27	1.36	60	286.1	8.0
MY305	1104	505.5	342.87	68	210.9	73.6

SD = standard deviation; CV = coefficient of variation; TDMY = test-day milk yield; MY305 = 305-day cumulative milk yield; LL = lactation length.

The standard model, containing the largest number of parameters, provided the worst fit

according to the two model selection criteria (Table 2). Both AIC and BIC were lowest for the two reduced rank models, and indicated PC2 as the best model to estimate covariance components and genetic parameters for MY305 and TDMY. An expressive reduction in the number of parameters (45) was observed for PC2 compared to SM, which provided the poorest fit. In addition, PC2 achieved faster convergence than SM and PC3.

Canonical decomposition of the genetic covariance matrix of SM produced the following eigenvalues: 6176.63, 0.45, 0.13, 0.05, 0.03, and 0.01. Thus, the first eigenvalue accounted for most of the genetic variance (99.99%). For PC2, the genetic covariance matrix produced the eigenvalues 5483.69 and 0.12; in this case, genetic variance was totally explained by the first eigenvalue (100.00%).

Table 2. Model conditions.

Model[a]	N	log L	AIC	BIC
PC2	153	-2.516	**5.228**	**5.327**
PC3	162	-2.510	5.234	5.996
SM	198	-2.507	5.301	6.320

[a]PCn = reduced ranked model fitting the first *n* principal components; SM = standard multi-trait model. N = number of parameters; log L = logarithm of the likelihood function; AIC = Akaike information criterion; BIC = Schwarz Bayesian information criterion.

Estimates of additive genetic variance for MY305 and TDMY, obtained using SM, were higher than those estimated with PC2 across lactation (Table 3), but showed the same trend. Estimates of additive genetic variances for TDMY increased until peak lactation (60-90 days) and decreased thereafter, although a marked increase was observed at the end of lactation. The SM and PC2 provided similar phenotypic and residual variances for both MY305 and TDMY. Phenotypic variances for TDMY followed the same trend as the additive genetic variances estimated with the two models. Residual variance estimates (data not shown) increased until peak lactation and declined on subsequent test-days, with a sudden decrease in TDMY10. Permanent environmental variances obtained with the PC2 were slightly higher than those from SM, decreasing with days in milk until TDMY8 and then increased until the end of lactation.

Table 3. Estimates of variance, heritability and repeatability for test-day milk yield (TDMY) and 305-day cumulative milk yield (MY305).

Trait	σ^2_a		σ^2_c		σ^2_p		h^2		t	
	SM	PC2	SM	PC2	SM	PC2	SM	PC2	SM	PC2
TDMY1	0.12	0.09	0.41	0.43	*0.58*	*0.58*	0.20 ± 0.09	0.16 ± 0.02	0.91	0.90
TDMY2	0.16	0.12	0.38	0.42	*0.63*	*0.63*	0.25 ± 0.08	0.19 ± 0.01	0.86	0.86
TDMY3	0.21	0.16	0.32	0.36	*0.61*	*0.60*	0.35 ± 0.08	0.27 ± 0.01	0.87	0.87
TDMY4	0.18	0.15	0.29	0.31	*0.51*	*0.51*	0.35 ± 0.10	0.30 ± 0.01	0.92	0.90
TDMY5	0.17	0.15	0.28	0.30	*0.50*	*0.50*	0.33 ± 0.10	0.31 ± 0.01	0.90	0.90
TDMY6	0.14	0.10	0.29	0.32	*0.47*	*0.47*	0.30 ± 0.11	0.22 ± 0.01	0.91	0.89
TDMY7	0.13	0.12	0.24	0.25	*0.40*	*0.40*	0.31 ± 0.14	0.29 ± 0.01	0.93	0.93
TDMY8	0.30	0.29	0.12	0.14	*0.46*	*0.46*	0.66 ± 0.13	0.63 ± 0.02	0.91	0.93
TDMY9	0.29	0.28	0.31	0.32	*0.63*	*0.63*	0.47 ± 0.19	0.45 ± 0.02	0.95	0.95
TDMY10	0.45	0.17	0.45	0.67	*0.90*	*0.84*	0.50 ± 0.23	0.21 ± 0.01	1.00	1.00
MY305	6,175	5,482	7,442	8,099	*21,780*	*21,764*	0.28 ± 0.07	0.25 ± 0.01	0.63	0.62

Obtained using standard multi-trait (SM) and a reduced rank model fitting the first two genetic principal components (PC2). σ^2_a = additive genetic variance; σ^2_c = permanent environmental variance; σ^2_p = phenotypic variance; h^2 = heritability (± standard error); t = repeatability.

Heritability values (h^2) for TDMY and MY305 estimated with SM were higher than those obtained using PC2 (Table 3) and ranged from 0.20 to 0.66, and 0.16 to 0.63, for SM and PC2, respectively. These estimates indicated that TDMY should respond to selection. However, the estimates standard deviations obtained with PC2 were much lower than those from SM, probably due to decreased sampling variances. The h^2 for TDMY obtained across lactation showed the same trend as reported by Sarmento et al. (2006) and Menezes et al. (2011). The h^2 for MY305 estimated with the SM and PC2 were higher than those reported by Lôbo and Silva (2005) and Torres-Vázquez et al. (2009) who used a repeatability model.

Coefficients of repeatability for TDMY and MY305, estimated with SM and PC2, were similar (Table 3), with the highest estimate in the last month and the lowest in the second month of lactation. Considering repeatability estimates for TDMY were higher than those for MY305 (0.63 and 0.62), test-day records obtained during mid-lactation could be used for culling decisions. Torres-Vázquez et al. (2009) reported repeatability estimates for MY305 lower (0.43) than those obtained in the present study with using the SM and PC2 models.

Genetic correlations between TDMY and MY305 were positive and of moderate to high magnitude, ranging from 0.56 to 0.98 (estimated with SM), and 0.91 to 1.00 (obtained with PC2; Table 4). In Brazil, Bignardi et al. (2008), using Holstein, and Tonhati et al. (2008), using dairy buffalo, found genetic correlations between TDMY and MY305 that ranged from 0.63 to 1.00, and 0.82 to 1.00, respectively. The highest genetic correlations between TDMY and MY305 were observed in mid-lactation and followed the same trend seen in the present study. Genetic correlations between TDMY obtained with PC2 were higher than those estimated with SM, particularly between adjacent test-days in mid-lactation, when genetic correlations were close to one. Genetic correlations between TDMY obtained with SM and PC2 ranged from 0.41 to 0.98, and 0.67 to 1.00, respectively.

Table 4. Genetic correlation between test-day milk yield (TDMY) and 305-day cumulative milk yield (MY305).

	TDMY1	TDMY2	TDMY3	TDMY4	TDMY5	TDMY6	TDMY7	TDMY8	TDMY9	TDMY10	MY305
TDMY1		0.82 ± 0.16	0.74 ± 0.16	0.86 ± 0.18	0.89 ± 0.21	0.80 ± 0.27	0.85 ± 0.35	0.51 ± 0.25	0.52 ± 0.35	0.41 ± 0.38	0.90 ± 0.17
TDMY2	0.86 ± 0.06		0.95 ± 0.08	0.94 ± 0.12	0.93 ± 0.13	0.95 ± 0.21	0.88 ± 0.24	0.72 ± 0.18	0.76 ± 0.29	0.59 ± 0.32	0.97 ± 0.10
TDMY3	0.69 ± 0.09	0.96 ± 0.02		0.88 ± 0.07	0.85 ± 0.10	0.81 ± 0.16	0.82 ± 0.17	0.70 ± 0.14	0.78 ± 0.22	0.44 ± 0.25	0.92 ± 0.08
TDMY4	0.92 ± 0.05	0.99 ± 0.01	0.92 ± 0.03		0.96 ± 0.08	0.95 ± 0.12	0.93 ± 0.15	0.72 ± 0.15	0.74 ± 0.23	0.45 ± 0.27	0.98 ± 0.10
TDMY5	0.95 ± 0.04	0.98 ± 0.02	0.89 ± 0.05	1.00 ± 0.01		0.93 ± 0.12	0.92 ± 0.18	0.77 ± 0.16	0.77 ± 0.22	0.60 ± 0.28	0.98 ± 0.12
TDMY6	0.95 ± 0.04	0.97 ± 0.02	0.87 ± 0.06	0.96 ± 0.01	1.00 ± 0.00		0.91 ± 0.15	0.71 ± 0.14	0.71 ± 0.22	0.61 ± 0.28	0.94 ± 0.15
TDMY7	0.94 ± 0.05	0.98 ± 0.02	0.90 ± 0.05	1.00 ± 0.01	1.00 ± 0.00	1.00 ± 0.01		0.85 ± 0.12	0.85 ± 0.23	0.62 ± 0.28	0.95 ± 0.20
TDMY8	0.75 ± 0.09	0.98 ± 0.02	1.00 ± 0.01	0.95 ± 0.03	0.92 ± 0.04	0.91 ± 0.04	0.93 ± 0.03		0.98 ± 0.13	0.76 ± 0.17	0.76 ± 0.14
TDMY9	0.67 ± 0.09	0.96 ± 0.03	1.00 ± 0.00	0.91 ± 0.03	0.87 ± 0.04	0.86 ± 0.05	0.89 ± 0.05	0.99 ± 0.01		0.72 ± 0.18	0.79 ± 0.21
TDMY10	0.91 ± 0.05	0.99 ± 0.01	0.93 ± 0.02	1.00 ± 0.00	1.00 ± 0.01	0.99 ± 0.01	1.00 ± 0.01	0.96 ± 0.02	0.92 ± 0.02		0.56 ± 0.25
MY305	0.91 ± 0.05	0.99 ± 0.01	0.93 ± 0.04	1.00 ± 0.00	1.00 ± 0.01	0.99 ± 0.01	1.00 ± 0.01	0.95 ± 0.03	0.91 ± 0.04	1.00 ± 0.00	

Estimated using standard multi-trait model (SM, above the diagonal) and a reduced rank model fitting the first 2 principal components (PC2, below the diagonal). Values are the estimate (± standard error).

As expected, for the two models, the direct genetic gain in MY305 increased with the larger number of daughters per buck, as a consequence of higher accuracy of selection (Tables 5 and 6). Using SM, selection for TDMY in the fourth and fifth months of lactation resulted in a higher correlated response in MY305, compared to direct selection for MY305. In contrast, higher correlated responses in MY305 were observed in the fourth, fifth, seventh, eighth, and ninth months of lactation using PC2. For both models, the relative selection efficiency decreased after TDMY3 with the increasing number of daughters per buck, with the exceptions of TDMY6 and TDMY10, obtained using PC2. This finding may be due to the fact that the h^2 estimates for these TDMY were above those expected. An increase in relative selection efficiency in the first two months of

lactation, for the two models, was observed with an increasing number of daughters, probably due to lower h^2 estimates for these TDMY, when compared to h^2 for MY305. Similar results in dairy buffalo were reported by Tonhati et al. (2008), who estimated the correlated response in MY305 using TDMY as a selection criterion.

Table 5. Direct and expected correlated (selecting for test-day milk yield, TDMY) response to selection for milk yield and relative selection efficiency using different number of daughters per buck, obtained by multi-trait model (SM).

Trait	Direct and correlated response in MY305 (kg) Number of daughters per buck				Relative selection efficiency for MY305 (%) Number of daughters per buck			
	5	10	25	50	5	10	25	50
MY305	12.6	15.8	19.5	21.4	100	100	100	100
TDMY1	9.9	12.7	16.4	18.5	79	81	84	86
TDMY2	11.5	14.6	18.3	20.4	91	92	94	95
TDMY3	12.6	15.5	18.6	20.2	100	98	96	94
TDMY4	13.5	16.5	19.9	21.5	107	105	102	100
TDMY5	13.2	16.3	19.7	21.4	104	103	101	100
TDMY6	12.2	15.2	18.6	20.3	97	96	95	95
TDMY7	12.5	15.5	18.9	20.6	99	98	97	96
TDMY8	12.9	14.9	16.7	17.5	102	95	86	81
TDMY9	12.0	14.4	16.7	17.8	96	91	86	83
TDMY10	8.7	10.4	11.9	12.6	69	66	61	59

Table 6. Direct and expected correlated (selecting for test-day milk yield, TDMY) response to selection for milk yield and relative selection efficiency using different number of daughters per buck, obtained with a reduced rank model fitting the first 2 genetic principal components (PC2).

Trait	Direct and correlated response in MY305 (kg) Number of daughters per buck				Relative selection efficiency for MY305 (%) Number of daughters per buck			
	5	10	25	50	5	10	25	50
MY305	11.4	14.4	18.0	19.9	100	100	100	100
TDMY1	8.6	11.2	14.8	17.0	76	78	82	85
TDMY2	10.0	13.0	16.8	19.0	88	90	93	95
TDMY3	10.9	13.7	17.0	18.7	96	95	94	94
TDMY4	12.2	15.2	18.6	20.4	107	106	104	102
TDMY5	12.4	15.4	18.7	20.4	109	107	104	102
TDMY6	10.7	13.6	17.3	19.4	94	95	96	97
TDMY7	12.0	15.1	18.5	20.3	106	105	103	102
TDMY8	15.0	17.4	19.6	20.5	132	121	109	103
TDMY9	12.9	15.5	18.0	19.2	113	108	100	96
TDMY10	10.6	13.6	17.3	19.5	93	94	96	98

The adoption of TDMY4 and TDMY5 as selection criteria permits earlier evaluation of animals, thereby reducing the generation interval and providing higher genetic gain per generation in the herds studied. Moreover, performance-recording costs would be reduced. The use of TDMY, but not MY305, for genetic evaluation of animals permits the quantification of factors specific for each test-day, such as number of milking, pregnancy, or disease. Results found in this study permit to conclude that with using TDMY, it is possible to include incomplete lactations, thus increasing the number of daughters evaluated per buck and, consequently, the reliability of progeny tests.

Principally, AIC and BIC tests alone were regarded as criteria of choice but in fact, the estimates of genetic parameters found also proved to be helpful. Despite the fact that PC2 was the best model based on AIC and BIC criteria, it is not the model that should be used. This conclusion

can be explained by the magnitude of the variances estimated, and it can be clearly seen that some of the genetic variance was re-partitioned to permanent environmental effect (Table 3). This explains the lower estimates of h^2 obtained using PC2, whereas estimates of repeatability are comparable between SM and PC2, since the permanent environmental effect was included. The probability of re-partitioning increased with more than one random effect and few principal components fitted in the model. In the current dataset, PC2 was not optimal due to a loss of valuable additive genetic information, resulting in inaccurate estimates using this model.

CONCLUSION

The adoption of test-day milk yield data from the fourth and fifth months of lactation may be used as selection criteria to increase total milk yield, thereby reducing generation intervals and increasing genetic gain per generation. Although the standard multi-trait model provided the worst fit according to the two model selection criteria, it was the best in the dataset used in the current study. The standard multi-trait model produced estimates that were more accurate than the reduced rank models.

Conflicts of interest

The authors declare no conflicts of interest.

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