Genetic parameters for test-day yield of milk, fat and protein in buffaloes estimated by random regression models

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The test-day yields of milk, fat and protein were analysed from 1433 first lactations of buffaloes of the Murrah breed, daughters of 113 sires from 12 herds in the state of São Paulo, Brazil, born between 1985 and 2007. For the test-day yields, 10 monthly classes of lactation days were considered. The contemporary groups were defined as the herd-year-month of the test day. Random additive genetic, permanent environmental and residual effects were included in the model. The fixed effects considered were the contemporary group, number of milkings (1 or 2 milkings), linear and quadratic effects of the covariable cow age at calving and the mean lactation curve of the population (modelled by third-order Legendre orthogonal polynomials). The random additive genetic and permanent environmental effects were estimated by means of regression on third- to sixth-order Legendre orthogonal polynomials. The residual variances were modelled with a homogenous structure and various heterogeneous classes. According to the likelihood-ratio test, the best model for milk and fat production was that with four residual variance classes, while a third-order Legendre polynomial was best for the additive genetic effect for milk and fat yield, a fourth-order polynomial was best for the permanent environmental effect for milk production and a fifth-order polynomial was best for fat production. For protein yield, the best model was that with three residual variance classes and third- and fourth-order Legendre polynomials were best for the additive genetic and permanent environmental effects, respectively. The heritability estimates for the characteristics analysed were moderate, varying from $0 \cdot 16 \pm 0 \cdot 05$ to $0 \cdot 29 \pm 0 \cdot 05$ for milk yield, $0 \cdot 20 \pm 0 \cdot 05$ to $0 \cdot 30 \pm 0 \cdot 08$ for fat yield and $0 \cdot 18 \pm 0 \cdot 06$ to $0 \cdot 27 \pm 0 \cdot 08$ for protein yield. The estimates of the genetic correlations between the tests varied from $0 \cdot 18 \pm 0 \cdot 120$ to $0 \cdot 99 \pm 0 \cdot 002$; from $0 \cdot 44 \pm 0 \cdot 080$ to $0 \cdot 99 \pm 0 \cdot 004$; and from $0 \cdot 41 \pm 0 \cdot 080$ to $0 \cdot 99 \pm 0 \cdot 004$, for milk, fat and protein production, respectively, indicating that whatever the selection criterion used, indirect genetic gains can be expected throughout the lactation curve.

Keywords: Covariance functions, heritability, Legendre polynomials.

Buffalo milk is mainly used to make cheeses, especially mozzarella. As with any commercially produced milk, the economic value depends not only on the quantity produced, but also on the composition, mainly the fat and protein contents (Seno et al. 2007). In Brazil, as a consequence of improvement in management, infrastructure and feeding practices on buffalo farms, over the last two decades the buffalo milk production per lactation has increased considerably (Tonhati et al. 1996; Malhado et al. 2007; Aspilcueta et al. 2010a). To date, the genetic evaluation

for milking buffaloes is carried out for total milk yield using a repeatability model. This model assumes that genetic and phenotypic variances are constant along the lactation and the lactation curve is equal or the same for all the animals. Moreover, short-length lactations are common in buffaloes, and thus, lactation records must be extended to be included in a genetic evaluation. Alternatively, the production of milk and its constituents by dairy buffaloes can be represented by points that are related to the lactation trajectory, enabling their evaluation by random regression models (RRMs).

RRMs allow the fitting of random lactation curves to each individual, expressed as deviations from a mean curve of the population or groups of individuals. In fitting a RRM, a structure of covariances among the observations is implicitly

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assumed, determined by the covariances of the regression coefficients, so that it can be defined as a covariance function. The implementation of RRMs to estimate genetic parameters for characteristics of the yield of milk and its constituents is widespread in the dairy industry (Schaeffer & Jamrozik, 2008).

Estimates of genetic parameters obtained by using random regression models for dairy buffalo traits are scarce in the literature and those that do exist only consider milk output (Breda et al. 2010; Sesana et al. 2010). These authors report heritability estimates of milk yield ranging from 0·19 to 0·54 during lactation. However, there are no reports of genetic parameter estimates for the constituents of buffalo milk using RRMs. In contrast, in the case of dairy cattle, such estimates of the production of milk and its constituents have been published for a number of breeds (Liu et al. 2000; Jakobsen et al. 2002a, b; De Roos et al. 2004; Silvestre et al. 2005).

Therefore, the objective of this work was to estimate covariance functions for the additive genetic and permanent environmental effects, and subsequently the genetic parameters, for yield of milk, fat and proteins, through the use of random regression models with Legendre polynomials, considering different residual variance structures.

Material and Methods

We analysed test-day results of milk, fat and protein production from 1433 first lactations of Murrah buffaloes, with ages from 24 to 48 months and born between 1985 and 2007, daughters of 113 sires, from 12 herds located in the state of São Paulo, Brazil. The milk yields records were obtained starting on the fifth day after calving and were truncated at 305 days of lactation, since only 12% of females had a lactation length greater than this period. Only cows that had their first test-day record before 45 d after calving were considered in the analyses.

The test-day productions were considered in monthly lactation classes, varying from 1 to 10 classes, and included animals with at least four tests. The contemporary groups were defined as herd-year-month of milk test, with the restriction that each group had to contain at least four animals. After data consistency, the descriptive statistics for milk, fat and protein yield along the lactation (first lactation) are shown in Table 1. A pedigree file containing 10 088 animals was used in all the analyses.

The characteristics of milk, fat and protein production were analysed by means of single-trait random regression models. All the models included additive genetic, permanent environmental and residual effects of the animal. The fixed effects considered were the contemporary group, number of milkings (1 or 2 daily), the linear and quadratic effects of the covariable cow age at calving and the average lactation curve of the population, modelled by a third-order orthogonal polynomial. In matrix form, the model can be represented by:

$$y = Xb + Za + Wap + e$$

where y = vector of observations; b = fixed-effects vector (contemporary group, number of milkings; covariable age of the cow at calving and mean population curve); a = vector of solutions for the random additive genetic regression coefficients; ap = vector of solutions for the random permanent environmental regression coefficients; e = vector of the different residuals; and X, Z, W = incidence matrices for the fixed effects and random additive genetic and permanent environmental effects, respectively. The dimension of the vector a is $k_a N_a$ coefficients, where k_a represents the order of the polynomial and N_a the number of animals in the numerator relationship matrix. The vector ap has dimension of $k_{ap} \times N_d$ coefficients, where k_{ap} represents the order of the polynomial and N_d, the number of animals with phenotypic records.

In the analysis we assumed that the records are distributed with mean Xβ, and for the random additive genetic, permanent environmental and residual effects we considered:

$$E \begin{bmatrix} a \\ ap \\ e \end{bmatrix} \sim N \left(\begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} K_a \otimes A & 0 & 0 \\ 0 & K_{ap} \otimes I_{Nd} & 0 \\ 0 & 0 & R \end{bmatrix} \right)$$

where: K_a and K_{ap} are the matrices of covariances between the random additive genetic regression and permanent environmental coefficients, respectively; A is the numerator relationship matrix among the individuals; I_{Nd} is the identity matrix with dimension N_d; $\otimes$ is the Kroneker product between the matrices; and R represents a diagonal block matrix containing the residual variances. We assumed independence of the residuals.

The random additive genetic and permanent environmental effects were modelled by third- to sixth-order Legendre polynomials. Residual variances were modelled using a step function with 1, 3 (1–3, 4–8, 9–10), 4 (1, 2–3, 4–8, 9–10) or 10 classes for milk production, and with 1, 4 (1, 2–6, 7–8, 9–10), 6 (1, 2, 3–4, 5–6, 7–8, 9–10) or 10 classes for fat production, and with 1, 3 (1, 2–6, 7–10) or 10 classes for protein production.

The citation of the RRMs follows the pattern: $LEGk_a.k_{ap}\_r$, referring to the order of the covariance function for the additive genetic effects (k_a), the permanent environmental effects (k_{ap}) and the residual variances structure (r). For example, the LEG3,4_3 model denotes an analysis fitting a third- and fourth-order Legendre polynomial for the additive genetic and the permanent environmental effects, respectively, and the residual variances modelled with a step function with 3 classes.

The covariances functions were estimated by the restricted maximum likelihood method, employing the WOMBAT statistical program (Meyer, 2006).

The different models were compared by the logarithm of the likelihood function (log L), the likelihood ratio test (LRT) at 1% probability, the restricted maximum likelihood forms of the Akaike information criterion (AIC) and Bayesian information criterion (BIC) of Schwarz and by examining the variances and correlations

Table 1. Description of the production data (kg) of milk per month, fat and protein yield during the first lactation

		Milk				Fat			Protein		
C†	N	Mean	SD	CV, % †	N	Mean	SD	CV, %	Mean	SD	CV, %
1	725	8·24	3·14	38·25	475	0·40	0·15	36·90	0·23	0·09	36·75
2	1352	8·87	3·36	38·41	894	0·47	0·15	30·95	0·26	0·08	30·94
3	1387	8·32	3·23	39·24	854	0·49	0·15	30·78	0·27	0·08	30·33
4	1348	7·96	2·98	37·35	883	0·47	0·14	30·38	0·26	0·08	30·33
5	1322	7·78	2·87	37·61	879	0·43	0·15	33·74	0·25	0·08	33·58
6	1301	7·06	2·63	37·53	800	0·40	0·15	37·29	0·24	0·09	37·33
7	1288	6·68	2·54	38·14	786	0·38	0·14	37·07	0·24	0·09	37·08
8	1173	6·02	2·41	40·21	667	0·34	0·13	38·60	0·22	0·09	38·59
9	966	5·59	2·24	40·23	466	0·31	0·13	39·85	0·22	0·09	39·93
10	807	4·90	1·98	40·45	204	0·30	0·12	38·41	0·22	0·08	38·05

†C: monthly test; N: number of observations; CV: coefficients of variation

Table 2. Number of estimated parameters (N), log likelihood function (Log *L*), Akaike's information criterion (AIC), Schwarz Bayesian information criterion (BIC) and likelihood ratio test (LRT) for the models used comparing the number of classes for the residual variance of milk, fat and protein yields

Model†	N	log L	AIC	BIC	LRT‡
Milk					
(1) LEG3,3_1	13	− 8071·06	16168·12	16262·20	(2–1) 34·05**
(2) LEG3,3_3	15	− 8037·01	16104·01	16212·57	(3–2) 9·40**
(3) LEG3,3_4	16	− 8027·61	16087·22	16203·07	(4–3) 8·63[n.s]
(4) LEG3,3_10	22	− 8018·98	16081·96	16241·17	–
Fat					
(1) LEG3,3_1	13	19458·23	− 38890·46	− 38796·72	(2–1) 112·65**
(2) LEG3,3_4	16	19570·88	− 39109·76	− 38994·38	(3–2) 4·19[n.s]
(3) LEG3,3_6	18	19575·07	− 39114·15	− 38984·35	(4–3) 2·17[n.s]
(4) LEG3,3_10	22	19577·24	− 39110·48	− 39154·48	–
Protein					
(1) LEG3,3_1	13	24077·13	− 48128·25	− 48034·51	(2–1) 97·82**
(2) LEG3,3_3	15	24159·43	− 48288·87	− 48180·69	(3–2) 15·51[n.s]
(3) LEG3,3_10	22	24174·95	− 48305·89	− 48147·24	–

†Models: LEGka.kpe_r or LEGka.kpe_1, corresponding the functions Legendre polynomials (LEG), corresponding to the order of the covariance function for additive genetic (ka) and permanent environmental (kpe) effects and to the residual variance structure of variances modeled by a step function (r) assuming n variance classes or variance homogeneity (1)
‡Verisimilitude ratio test among the hierarchical models.**$P < 0,01$; [n.s]not significant

estimated for the traits. The information criteria can be represented as:

$$AIC = -2 \log L + 2p$$
$$BIC = -2 \log L + p \log(N - r(X))$$

where *p* is the number of parameters estimated, *N* is the number of data, *r*(X) the rank of the coefficient matrix of fixed effect in the model of analysis, and log *L* is the restricted maximum log-likelihood function (Wolfinger, 1993).

Results and Discussion

The average test-day milk yields (Table 1) show a typical lactation curve for buffaloes, starting at 8·24 kg, with increased production until a peak on the second test day

(8·87 kg) and subsequent decline until the end of lactation (4·9 kg). For the yields of fat and protein, the test-day averages were 0·40 and 0·24 kg, with SD of 0·14 and 0·08 kg and coefficients of variation of 35·40 and 35·32%, respectively. As can be observed in Table 1, there was an increase in production in the initial lactation phase (0·40 kg for fat and 0·23 kg for protein) until the third month (0·49 kg for fat and 0·27 kg for protein). These yields both declined as of the fourth month, with the increase in the number of lactation days until the end (0·30 kg for fat and 0·22 kg for protein). There was greater variation in the fat and protein production at the start and end of lactation.

The best fit for the residual variance (Table 2) shows increases in the log-likelihood, significant ($P < 0.01$) according to the likelihood ratio test (LRT), with an increasing number of heterogeneous classes. According to the criteria

Table 3. Number of estimated parameters (N), log likelihood function (Log L), Akaike's information criterion (AIC), Schwarz Bayesian information criterion (BIC) and likelihood ratio test (LRT) for the models used comparing the number of classes for the residual variance of milk, fat and protein yields

Model†	N	log L	AIC	BIC	LRT‡
Milk					
(1) LEG3,4_4	20	− 8000·44	16040·89	**16185·62**§	(2–1) 8·79[n.s]
(2) LEG3,5_4	25	− 7991·65	16033·29	16214·21	(3–2) 13·65*
(3) LEG3,6_4	31	− 7977·99	16017·99	16242·33	–
(4) LEG4,4_4	24	− 7981·55	16011·09	16184·78§	(5–4) 9[n.s]
(5) LEG4,5_4	29	− 7973·01	16004·01	16213·88	(6–5) 13·43*
(6) LEG4,6_4	35	− 7959·58	**15989·16**§	16242·45	–
(7) LEG5,5_4	34	− 7972·52	16013·03	16259·08	(8–7) 6*
(8) LEG5,6_4	40	− 7958·99	15997·97	16287·45	–
Fat					
(1) LEG3,4_4	20	19581·16	− 39122·33	− 38978·10	(2–1) 25·26**
(2) LEG3,5_4	25	19606·42	− 39162·85	**− 38982·57**§	(3–2) 8·53[n.s]
(3) LEG3,6_4	31	19614·96	− 39167·91	− 38944·37	–
(4) LEG4,4_4	24	19592·13	− 39136·26	− 38963·19	(5–4) 24·14**
(5) LEG4,5_4	29	19616·27	− 39174·54	− 38965·42§	(6–5) 8·26[n.s]
(6) LEG4,6_4	35	19624·53	**− 39179·06**§	− 38926·67	–
(7) LEG5,5_4	34	19620·09	− 39172·18	− 38927·01	(8–7) 8·13[n.s]
(8) LEG5,6_4	40	19628·22	− 39176·44	− 38887·99	–
Protein					
(1) LEG3,4_3	19	24169·54	− 48301·08	**− 48163·89**§	(2–1) 10·99[n.s]
(2) LEG3,5_3	24	24180·54	− 48312·71	− 48139·65	(3–2) 20·87**
(3) LEG3,6_3	30	24201·41	− 48342·81	− 48126·48	–
(4) LEG4,4_3	23	24179·64	− 48313·27	− 48147·41§	(5–4) 10·64[n.s]
(5) LEG4,5_3	28	24190·28	− 48324·55	− 48102·64	(6–5) 20·26**
(6) LEG4,6_3	34	24210·53	**− 48353·06**§	− 48107·88	–
(7) LEG5,5_3	33	24192·96	− 48319·91	− 48081·94	(8–7) 19·99**
(8) LEG5,6_3	39	24212·95	− 48347·89	− 48066·66	–

† Models: LEGka.kpe_r, corresponding the functions Legendre polynomials (LEG), corresponding to the order of the covariance function for additive genetic (ka) and permanent environmental (kpe) effects and to the residual variance structure of variances modeled by a step function (r) assuming 3 or 4 variance classes
‡ Verisimilitude ratio test between the hierarchical models. **$P < 0.01$; [n.s] not significant
§ Indicates the best model based on the AIC and BIC

used (AIC and BIC) to assess the goodness of fit, the model considering homogeneity of the residual variances was inadequate. This indicated that the residual variances behaved differently during the lactation period, making it necessary to consider a heterogeneous variance structure for the residuals. The heterogeneous residual variances can be attributed to factors such as the stage of pregnancy, body condition and duration of the lactation interval, among others, since these factors are not easily incorporated in analytic models owing to the lack of information about them (Rekaya et al. 2000; El Faro & Albuquerque, 2003).
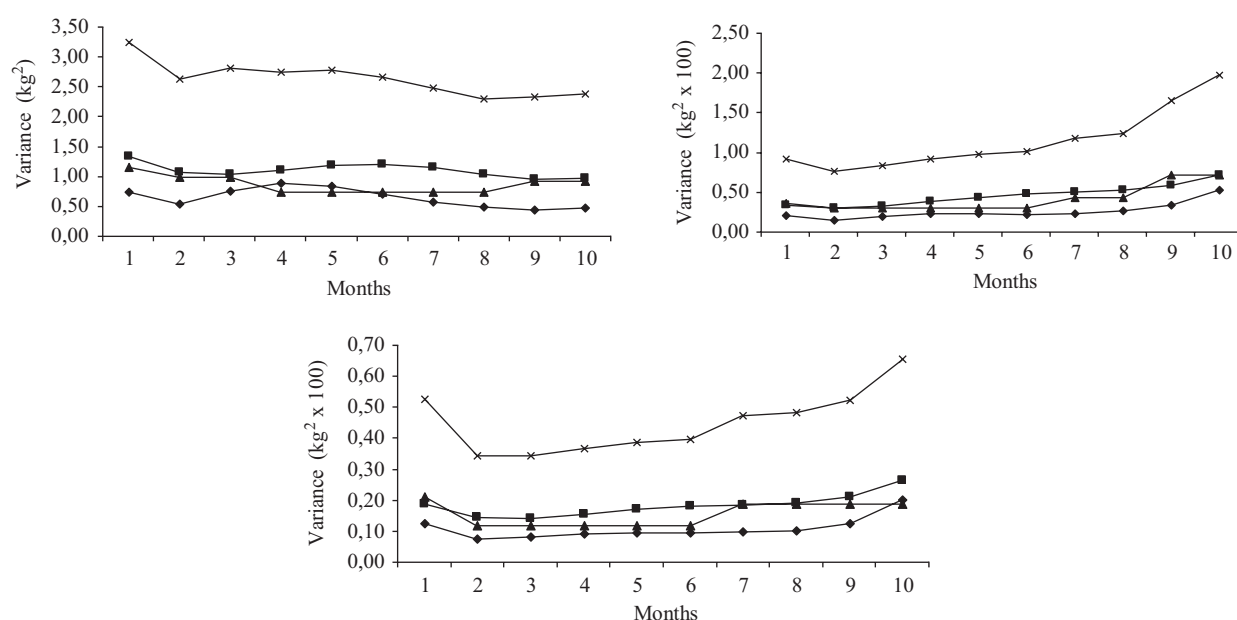
For the traits under study, the models with 10 residual classes should be applied, but for production of milk and fat, based on the LEG3,3_4 model, and for production of protein based on the LEG3,3_3 model, the changes in the log L were small in magnitude and not significant by the LRT ($P > 0.01$). This can indicate that for the milk and fat yield models, four residual classes would be sufficient and three classes would be enough for protein yield to obtain a good residual variance fit. This would avoid using over-parameterized

models, which in general present parameter estimation problems (Bignardi et al. 2009; Sesana et al. 2010).

Random regression models by means of Legendre polynomial functions require definition of the most appropriate order for each random effect considered in the model. For the milk, fat and protein output (Table 3), in general there was an improvement in the Log L criterion ($P > 0.01$, by the LRT) and AIC by increasing the order of adjustment from three to four for the additive genetic variance part associated with order six for the permanent environmental variance. The BIC, more rigorous because of the parameterization, indicated LEG3,4_4, LEG3,5_4 and LEG3,4_3 as the best models for milk, fat and protein yield, respectively. Therefore these are the most suitable models to describe the variation of milk, fat and protein production during lactation. Pool et al. (2000) reported that the lactation curves can be modelled with enough precision using a third-order Legendre polynomial for the additive genetic component and a fourth-order one for the permanent environmental component. Lopez-Romero & Carabaño (2003) also reported that Legendre polynomials of low order for the

Table 4. Percentage of variance explained by eigenvalues of the matrix of random regression coefficients for additive genetic and permanent environmental effects for selected models

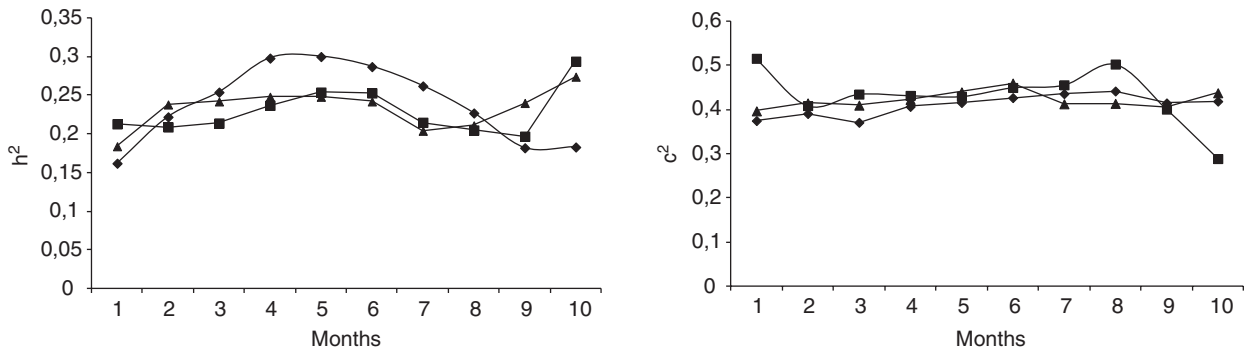| Trait	Random regression coefficient				
	1	2	3	4	5
	Milk LEG3,4_4 and (LEG4,4_4)				
Additive	86·72 (84·05)	10·19 (10·43)	3·09 (5·52)	– (0·00)	–
Permanent environmental	82·75 (84·75)	10·44 (10·55)	5·18 (3·70)	1·63 (1·00)	–
	Fat LEG3,5_4 and (LEG4,5_4)				
Additive	83·34 (83·04)	11·96 (12·07)	4·71 (4·89)	– (0·00)	–
Permanent environmental	79·52 (79·92)	13·79 (13·87)	3·71 (4·36)	2·28 (1·26)	0·71 (0·59)
	Protein LEG3,4_3 and (LEG4,4_3)				
Additive	81·47 (80·26)	13·35 (14·23)	5·18 (5·51)	– (0·00)	–
Permanent environmental	79·12 (79·80)	13·69 (13·72)	5·04 (5·66)	2·15 (0·83)	–

Fig. 1. Estimates of additive variance (◆), permanent environment (■), residual (▲) and phenotypic (x), for test-day milk yield per month, obtained with the LEG3,4_4 (above left), fat yield obtained with the LEG3, 5_4 (above right) and protein yield obtained with the LEG3,4_3 (below).

additive and permanent environmental variances can be most adequate.

Percentage of variance explained by eigenvalues associated with the random regression coefficients matrix for the additive genetic and permanent environmental effects, for the two best models for each of the traits according to the BIC, are presented in Table 4. The models of lower order are sufficient to capture all the variation of the trait, with a fourth coefficient for the additive part being associated with a zero eigenvalue, unlike for the permanent environmental effect. The eigenvalues analysed show that the first was responsible for over 79% of the variance of the data in the models adjusted to the traits under study. The variability of the data for the additive genetic and permanent environmental effects was mainly explained by the first two eigenvalues (more than 90%). According to the results of the eigenvalues, the dimension of the two random effects could be reduced without loss of information, in disagreement with the log L and Akaike information criteria for the additive genetic and permanent environmental effects and in agreement with the Bayesian information criterion for the additive genetic effect. However, Legarra et al. (2004) indicated that one must consider the fact that reducing the dimensionality resulting from eliminating eigenvalues near zero is not advisable in all cases, since adopting this criterion can result in an over-simplistic or inadequate model.

The estimates of the genetic additive, permanent environmental, residual and phenotypic variances for the yields of milk (model LEG3,4_4), fat (model LEG3,5_4) and protein (model LEG3,4_3) on the test day are presented in Fig. 1.

Fig. 2. Estimates of heritability (h^2 – left) and proportion of phenotypic variance due to permanent environmental (c^2 – right) for the milk yield (LEG3, 4_4 (◆)), fat yield (LEG3, 5_4 (■)) and protein yield (LEG3, 4_3 (▲)).

Table 5. Estimated genetic correlations (above diagonal) and phenotypic correlations (below diagonal) between monthly test-day observations for milk yield (LEG3,4_4), fat yield (LEG3,5_4) and protein yield (LEG3,4_3)

	C†	1	2	3	4	5	6	7	8	9	10
Milk	1	–	0·94	0·83	0·73	0·65	0·59	0·53	0·47	0·36	0·18
	2	0·54	–	0·97	0·92	0·87	0·82	0·77	0·69	0·53	0·24
	3	0·44	0·60	–	0·99	0·96	0·93	0·88	0·80	0·62	0·29
	4	0·41	0·59	0·67	–	0·99	0·97	0·94	0·86	0·68	0·33
	5	0·38	0·55	0·64	0·71	–	0·99	0·97	0·91	0·74	0·39
	6	0·36	0·51	0·59	0·67	0·71	–	0·99	0·94	0·80	0·46
	7	0·35	0·47	0·54	0·62	0·67	0·70	–	0·98	0·87	0·57
	8	0·32	0·42	0·49	0·57	0·62	0·66	0·68	–	0·95	0·72
	9	0·24	0·36	0·42	0·48	0·52	0·55	0·58	0·61	–	0·90
	10	0·12	0·27	0·35	0·39	0·40	0·40	0·41	0·46	0·53	–
Fat	1	–	0·92	0·75	0·62	0·55	0·53	0·55	0·59	0·61	0·60
	2	0·51	–	0·95	0·88	0·83	0·80	0·79	0·75	0·66	0·54
	3	0·38	0·60	–	0·98	0·96	0·93	0·89	0·81	0·66	0·47
	4	0·33	0·56	0·64	–	0·99	0·97	0·93	0·83	0·66	0·44
	5	0·31	0·53	0·62	0·67	–	0·99	0·96	0·86	0·69	0·47
	6	0·28	0·50	0·59	0·64	0·68	–	0·99	0·91	0·76	0·55
	7	0·23	0·45	0·53	0·57	0·62	0·66	–	0·97	0·86	0·69
	8	0·18	0·41	0·48	0·51	0·55	0·63	0·67	–	0·96	0·84
	9	0·14	0·34	0·39	0·40	0·43	0·50	0·56	0·63	–	0·96
	10	0·16	0·29	0·31	0·31	0·32	0·37	0·42	0·50	0·53	–
Protein	1	–	0·94	0·82	0·70	0·61	0·56	0·54	0·53	0·50	0·46
	2	0·56	–	0·96	0·89	0·83	0·78	0·74	0·67	0·57	0·44
	3	0·46	0·62	–	0·98	0·95	0·91	0·85	0·75	0·60	0·41
	4	0·38	0·57	0·65	–	0·99	0·96	0·91	0·81	0·63	0·42
	5	0·34	0·53	0·62	0·67	–	0·99	0·95	0·85	0·68	0·46
	6	0·32	0·49	0·58	0·64	0·68	–	0·98	0·91	0·76	0·56
	7	0·28	0·42	0·50	0·56	0·61	0·65	–	0·97	0·86	0·69
	8	0·27	0·38	0·45	0·51	0·56	0·61	0·61	–	0·96	0·84
	9	0·24	0·33	0·38	0·43	0·48	0·53	0·55	0·61	–	0·96
	10	0·17	0·25	0·29	0·31	0·34	0·39	0·42	0·51	0·63	–

†Monthly test day

In the estimates of the additive variance for milk output, there was an increase from the start until the fourth month, after which the yield declined until the end of lactation. The estimate of the permanent environmental variance remained practically constant during the lactation period and was greater than the additive and residual variances. The residual variance estimates declined from the fourth to the eighth month of lactation.

For the fat and protein yields (Fig. 1), the additive genetic variances presented the same tendency as the phenotypic variance, with higher values at the end of lactation. These higher estimates of the constituents might have been due to

the number of data readings obtained or to the higher levels of fat and protein found at the end of lactation. In general, the trends of the additive and permanent environmental variances throughout the lactation period obtained in this study (for the three traits) are comparable to those found by Gengler et al. (1997), Silvestre et al. (2005), Muir et al. (2007) and De Groot et al. (2007) all of whom reported higher additive and permanent environmental variances at the start and end of lactation for milk as well as fat and protein yield.

Figure 2 shows the heritability (h^2) and proportion of the phenotypic variance corresponding to the permanent environmental variance. The estimates of heritability for milk yield fluctuated between $0·16 \pm 0·05$ and $0·29 \pm 0·05$ and were greatest in the fourth and sixth months of measurement.

This result differs from those found by Sesana et al. (2010) and Breda et al. (2010) in which the estimates were higher at the extremes of the lactation curve. This can be attributed to the fact that these authors utilized weekly tests. However, the heritability estimates were near those found by Aspilcueta et al. (2010b, c) who used finite dimensional models. The heritability estimates for production of fat and protein (Fig. 2) showed a similar trend during the lactation, with a sharp increase at the end of this phase. These results follow the same trend observed in the literature by the majority of researchers in dairy cattle (Gengler et al. 1997; Silvestre et al. 2005, De Groot et al. 2007; Muir et al. 2007). The heritability estimates for fat production varied from $0·20 \pm 0·05$ (ninth month) to $0·30 \pm 0·08$ (tenth month). However, the heritability estimates for protein varied from $0·18 \pm 0·06$ (first month) to $0·27 \pm 0·08$ (tenth month). These results are near the estimates obtained by the majority of researchers in dairy cattle using random regression models (Gengler et al. 1997; Liu et al. 2000; De Roos et al. 2004; Muir et al. 2007). Aspilcueta et al. (2010c) used finite dimensional models with monthly data on fat and protein yield of buffaloes and found heritability estimates of lower magnitude than those found in the present study.

The fractions of phenotypic variances referring to the permanent environmental variance of the traits in the present study were greater than the heritability estimates throughout the lactation period, a similar finding to that of El Faro & Albuquerque (2003) in dairy cattle.

The estimates of the genetic and phenotypic correlations for production of milk, fat and protein are presented in Table 5. The genetic correlations for milk production on the test day ranged from $0·18 \pm 0·130$ to $0·99 \pm 0·002$, and were higher the nearer the test days were to each other, declining as the interval between them increased. Among the test days in the middle of the lactation period, these genetic correlations were the highest, near one. This pattern is close to those reported by Sesana et al. (2010) and Breda et al. (2010). Nevertheless, those authors found negative genetic correlation estimates between the first and last test days. Aspilcueta et al. (2010b, c) reported higher estimates, probably owing to the finite dimensional model methodology.

The estimates of the genetic correlations (Table 5) for the fat and protein yields during the lactation period ranged from $0·44 \pm 0·080$ to $0·99 \pm 0·004$ and $0·41 \pm 0·080$ to $0·99 \pm 0·004$, respectively. Most of the estimated correlations were high, approaching one. It can also be seen that the estimates were higher when the test-day fat and protein yields were nearer to each other. Aspilcueta et al. (2010c) reported similar estimates using a finite dimensional model for fat and protein.

For the traits under investigation, the lowest genetic correlation estimates occurred between the yield in the first month and the other test-day months, probably owing to the difficulty of modelling the initial lactation tests, because during this phase the animals suffer post-partum stress and also have negative energy balance.

The phenotypic correlation estimates (Table 5) between the yields for the traits under study were lower as the interval between the test days increased. In general the phenotypic correlation estimates were lower than the genetic ones. This same pattern was reported by Aspilcueta et al. (2010c).

Conclusions

Random regression models employing Legendre polynomials were efficient to describe the genetic variation for test-day yield of milk, fat and protein among buffaloes.

The heritability estimates of the traits were moderate, which can help in the process of selecting animals to obtain genetic gains. The estimates of the genetic correlations were high among the test days, indicating that by either selection criterion, indirect genetic gains can be expected throughout the lactation curve.

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