

Estimation of covariance components for the first four lactations in Holstein cattle according to different models

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ABSTRACT

Milk production of Cuban Holstein cows was analyzed. There were 15415 lactation records of 9382 cows, which gave birth to the calves of 482 sires. Three models were established to study the milk production for 305 days during each of the first four lactations. Model I was an independent univariate analysis of milk production for lactation. Model II was a repeatability model where lactation was considered the repeated measurement of the same characteristic. Model III was a multivariate analysis in which each lactation was considered an independent characteristic correlated with the rest. The program REMLF90 was used for the analyses. The data show that for the Holstein breed under these study conditions, the estimation of covariance components for milk yield in the first four lactations are best carried out using a multivariate animal model.

Keywords: covariance, heritability, correlations, Cuban Holstein.

Estimación de componentes de covarianza con diferentes modelos para las primeras cuatro lactancias en ganado Holstein

RESUMEN

Fueron analizadas 15415 lactancias de 9.382 vacas Holstein en Cuba, hijas de 482 sementales. Se establecieron tres modelos para estudiar la producción de leche en 305 d durante las primeras cuatro lactancias. El Modelo I fue un análisis univariado de la producción de leche de cada lactancia, el Modelo II fue un modelo de repetibilidad donde cada lactancia se considera una medida repetida de un mismo rasgo y el Modelo III fue un análisis multicarácter donde cada lactancia se consideró un rasgo independiente correlacionado con las restantes. Se empleó para el análisis el programa REMLF90. De los resultados obtenidos se puede concluir que en la raza Holstein bajo las condiciones en estudio, la estimación de componentes de covarianza se pueden llevar a cabo favorablemente mediante un modelo animal multicarácter, siendo éste modelo la mejor opción para la evaluación genética de bovinos Holstein respecto a la característica producción de leche en sus primeras cuatro lactancias.

Palabras clave: covarianza, heredabilidad, correlaciones, Holstein Cubano.

INTRODUCTION

There are various procedures for predicting the milk yield genetic value of dairy cattle (Norman *et*

al., 1991). Generally, the primary goal of evaluation is to obtain precise predictions of the genetic value of an individual, so that the genetic gain of the population can be maximized (Henderson, 1975).

Thus, the correct estimation of genetic parameters that guarantee an accurate prediction of genetic merit is of great importance (Schaeffer, 1984). The basic difference between the procedures is related mainly to the amount of information used, and the possibility of making more frequent evaluations without having to manipulate a great amount of information (Martínez *et al.*, 1999).

In this way, numerous authors have demonstrated that information about the first lactation is a good indicator of the productive performance of a cow. In general, the genes that affect milk production in the first lactation also influence production in the following, and although it is desirable to include more lactations, this can cause a dramatic change in rank of genetic values due to selection effects (Teepker & Swalve, 1988; Albuquerque *et al.*, 1996; Pösö & Mäntysaary, 1996a; Guo *et al.*, 2002). García-Cortés *et al.* (1995) demonstrated that medium to high positive genetic correlations exist among the milk yields of the first lactation and the rest, and recommended a multivariate analysis including the four first lactations.

The present work was conducted to estimate the covariance components of milk yield during 305 days of each of the first four lactations of Holstein cows under Cuban environmental conditions and management, using the BLUP procedure, and univariate, repeatability, and multivariate animal models.

MATERIALS AND METHODS

The information analyzed was collected at several Holstein cattle farms in Havana province, located between 20 and 23° N, and 74 and 85° W. A warm tropical climate prevails in most of Cuba. There are two clearly defined seasons: the rainy (summer) season from May to October, in which 70-80% of rain falls (960 mm), and the dry (winter) season from November to April (240 mm). The average annual temperature is 23.1°C, with relative humidity of 60-70% during the day and 80-90% during the night (Hernández *et al.*, 1998).

There were 15,415 at 305-day milk production records of Holstein cows which calved between 1990

and 2003, distributed in 188 farms. The feeding system was based on grazing by approximately 12 h a day. Cows were fed mainly Stars grass (*Cynodon nlemfuensis*) and Guinean grass (*Panicum maximum*), but during the rainy season, the cows were fed additional natural grass. Cows were milked twice a day, and during each milking they were fed 0.45 kg of concentrate per liter of milk from the fourth liter produced. In the afternoon, the animals were kept in the barn and fed cut forage such as King Grass (*Penisetum purpureum*) and Cane sugar (*Saccharum officinarum*).

Production data were included for any and up to the first four lactations. There were 9,382 first (L1), 3,468 second (L2), 1,604 third (L3), and 961 fourth (L4) lactations recorded. The quarter of the year of calving was used as a time criterion. Contemporary groups were defined by the combination of farm, and the year and quarter of calving. The genealogy file was comprised by 40,591 animals. This included all known individuals up to the second generation of ancestors, and in cases that the identity of an ancestor was not known, it was replaced with a zero. The data were analyzed with the program REMLF90 (Misztal, 1999), which uses a REML procedure with an accelerated EM algorithm. The following statistical models were used.

Model I. Univariate analysis

The lactations were analyzed individually using the following model:

$$y = Xb + Za + e$$

where:

y is the observation vector, in this case the L1, L2, L3, or L4 records.

b is the fixed effects vector of the group of contemporaries (year-farm-quarter) and of the calving cow, as linear and quadratic covariable.

a is the additive random genetic effects vector of the animal.

e is the residual random effects vector.

\mathbf{X} and \mathbf{Z} are the incidence matrices that relate the data to the fixed and random effects, respectively.

It is assumed that

$$\text{var} \begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 \\ 0 & I\sigma_e^2 \end{bmatrix}$$

where: A is the matrix of additive relationships between individuals, I is the identity matrix, and σ_a^2 and σ_e^2 are the additive and residual genetic variances, respectively.

Model II. Repeatability analysis

Milk production records per lactation were used as repeated measurements for a given animal. This assumes genetic correlation equal to 1 among the various lactation measurements, according to the following statistical model:

$$y = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wpe} + e$$

in which y , b , a , e , X , and Z are defined as in Model I, but with the production observations for the different lactations as if they were a single characteristic, pe is the random effects vector of the permanent environment, and W is the incidence matrix that relates the observations in y with the cows in question.

It is assumed that

$$\text{var} \begin{bmatrix} a \\ pe \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 & 0 \\ 0 & I\sigma_{pe}^2 & 0 \\ 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

where: σ_{pe}^2 is the variance of permanent effects in the natural environment.

Model III. Multivariate analysis

The following statistical model was adjusted for the four lactations:

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \end{bmatrix} = \begin{bmatrix} X_1 & 0 & 0 & 0 \\ 0 & X_2 & 0 & 0 \\ 0 & 0 & X_3 & 0 \\ 0 & 0 & 0 & X_4 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 & 0 & 0 \\ 0 & Z_2 & 0 & 0 \\ 0 & 0 & Z_3 & 0 \\ 0 & 0 & 0 & Z_4 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \\ a_3 \\ a_4 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \end{bmatrix}$$

where:

y_i is the production observation vector for the i -th lactation.

b_i is the fixed effects vector (year-farm-quarter, and age at calving as linear and quadratic covariables) for the i -th lactation.

a_i is the random effects vector of the animal for the i -th lactation.

e_i is the random residual effects vector for the i -th lactation.

X_i and Z_i are design matrices that relate the data to the fixed and random effects, respectively.

It is assumed that

$$\text{var} \begin{bmatrix} a_i \\ e_i \end{bmatrix} = \begin{bmatrix} G_0 \otimes A & 0 \\ 0 & R_0 \otimes I \end{bmatrix}$$

where:

G_0 is a matrix of additive genetic variances-covariances of the four lactations, and R_0 is a matrix of variances-covariances of residuals of the lactations. A is the matrix of additive genetic relationships, and I

is the identity matrix. Thus, each lactation was considered as an independent characteristic.

RESULTS AND DISCUSSION

Milk yield

Table 1 shows averages and standard deviations for milk yield of the 305-day lactations, and the calving ages (AC). The averages for milk yield in this study were a little higher than those of Friesian cows in Zimbabwe (2015 kg) in the smallholder sector, in that natural pasture accounted for 90% of feed available during the wet season (Ngongoni *et al.*, 2006). However, the averages for milk yield in this study were lower than those observed in Brazil by other authors for the same breed (Barbosa & Fernandes, 2000; Ferreira *et al.*, 2001; Arione *et al.*, 2005) and for Brown Swiss (Vieira *et al.*, 2003). Milk yield was lower than that observed for Harton from Valley x Holstein Colombian cows, grazing in a tropical environment and feeding on a concentrated supplement during milking (Vargas *et al.*, 2006). These differences, probably due to the downfall of socialism in eastern Europe, had serious repercussions on Cuba's trade situation and undermined development of the livestock sector. Since then, Cuba's livestock sector has emphasized self-sufficiency, based on the utilization of pasture (Pérez, 1999). During the 90s, milk production in Havana province was reduced from 320 to 60 million liters annually, which parallels the importation of cattle feed (Monzote *et al.*, 2005).

Heritability

Variance components and heritabilities obtained with each model appear in Table 2. A larger residual variance for later lactations is observed relative to the first. The univariate and multivariate models showed larger residual variance in the later lactations than the first. This could be caused by factors that do not influence the first lactation, but only the following, such as previous dry period and period of service, among others (Teixeira *et al.*, 1996).

Similarly, heritability was estimated by applying the REML method, using records for

another Cuban Holstein herd from between 1990 and 2000 (González-Peña *et al.*, 2003) and using the DFREML algorithm in Ayrshire cattle in Kenya (0.12) where the poor performance is not only due to the direct effect of climate, but more importantly the poor quality of roughage, low concentrate feed inputs and the high incidence of diseases and parasites and poor economic environment and infrastructure (Amimo *et al.*, 2007).

Table 1. Numbers of observations (N), averages and standard errors (\pm) of milk yield (MY) for each lactation (L1 to L4) and average ages at calving (AC)

Lactation	N	MY	AC
		kg	month
L1	9382	2260 \pm 789	34.3 \pm 8.8
L2	3468	2204 \pm 815	50.7 \pm 10.9
L3	1604	2274 \pm 752	68.9 \pm 13.3
L4	961	2355 \pm 760	82.7 \pm 14.3

In general however, the heritability values determined in each model were below those found in the Holstein breed from Japan (0.30), and Mexico (0.26), in which Mitsuyoshi & Van Vleck (1994) and Palacios-Espinosa *et al.* (2001), respectively, applied DFREML using an animal model with repeated records to estimate variances. A MTDFREML algorithm was used on Holstein cattle from Brazil (Barbosa & Fernández, 2000), and a heritability value of 0.30 was obtained.

A limited number of records used for parameter estimation, which are not confirmed by repeated estimations based on different random samples of data, may lead to misleading results (Strabel *et al.*, 2005). Accordingly, Pool *et al.* (2000) stated that their preliminary results from 8000 lactations were inconsistent and indicated that more data should have been used for estimation. In a study using the AIREML algorithm of lactation records for crossbred Holstein cattle from dairy organizations and smallholders throughout Thailand, heritability was upwardly biased when data from only small herds

were included. This might imply that a small number of records per contemporary group affected the estimate and caused confusion between additive and permanent environmental effects (Chanjivit *et al.*, 2005). Based on these references, the estimated heritability for the third (1604 records) and fourth (961 records) lactations, using the univariate model in this study might be downwardly biased. In other work however, the heritability of milk yield was 0.31 when

274 records were used in a linear regression model (Yang *et al.*, 2005).

The heritability values obtained for each lactation using univariate analysis were lower than those using the repeatability model, but the repeatability model assumed that yields in different lactations had a genetic correlation of 1 (Yang *et al.*, 2005). In this study the genetic correlations between lactations were less than 1.

Table 2. Additive genetic components of variance (σ^2_a), residuals (σ^2_e), and heritabilities (h^2) of milk yield estimated with the studied models.

Model	Lactation	σ^2_a	σ^2_e	σ^2_{pe}	h^2
I	L1	20658	126700		0.15
	L2	22229	158000		0.13
	L3	24744	234300		0.10
	L4	23139	218400		0.10
II		33993	168074	22621	0.16
III	L1	23071	125100		0.17
	L2	27768	159600		0.16
	L3	37450	202300		0.16
	L4	32650	200500		0.14

Using multivariate analysis, the heritabilities for the first and second lactations were close to those estimated by the repeatability model, while those of the third and fourth lactations were higher, possibly due to correction of selection bias made by multivariate analysis.

The performance of the heritability estimates in this study coincides with that of Albuquerque *et al.* (1996), who concluded that the heritability for milk yield in the first lactation was higher than for later lactations. Al-Seaf *et al.* (2007), using a MTDFREML algorithm, obtained heritabilities of milk yield in Holstein cows of 0.18, 0.18, and 0.14 for lactations 1, 2, and 3+, respectively. However, Pösö & Mäntysaary (1996b), using linear multitrait REML, showed that the heritability for the third lactation was higher than for the second. A multiple-lactation model was applied in the first 3 lactations of Polish

Black and White cattle by Strabel & Jamrozik (2006), who found heritabilities of 0.18, 0.16, and 0.17 for 305-day milk yields in the first 3 lactations.

In this study, estimates of heritability for yields in later lactations were a little less than for lactations 1 and 2 (univariate analysis) or lactation 1 (multivariate analysis); this could result from selection in lactations 1 and 2, which could reduce the range of differences of later records (Al-Seaf *et al.*, 2007).

Correlations

The lowest genetic correlations across lactations were between first and third parities (0.62) and the highest between third and fourth parities (0.88); the rest varied between 0.02 and 0.21 (Table 3). Another study reported genetic correlations of

0.69, 0.79, and 0.98 between parities 1 and 2, 1 and 3, and 2 and 3, respectively (Mrode & Swanson, 2003). Carlén *et al.* (2004) found the highest genetic correlations across lactations between second and third parities (0.99) and the lowest between first and third parities (0.90) in Holstein cows. Estimates of genetic correlations above 0.96 between 305-d milk production for different parities were reported in Chinese Simmental cattle (Yang *et al.*, 2005).

In this research, the differences in genetic and residual correlations among lactations varied between 0.47 and 0.63, so application of multivariate analysis is valid according to Schaeffer (1999), who suggested the feasibility of this type of analysis for characteristics where there are large differences between the genetic and residual correlations, preferably greater than 0.50.

Table 3. Genetic (above the diagonal) and environmental correlations (below the diagonal) of milk yield among lactations (L1 to L4), estimated with the multivariate analysis

Lactation	L1	L2	L3	L4
L1	1	0.68	0.62	0.65
L2	0.21	1	0.73	0.80
L3	0.10	0.17	1	0.88
L4	0.02	0.04	0.08	1

Breeding values

Expected progeny difference (EPD) values for the worst and best sires for each lactation and model used appear in Table 4. Notice that the greatest differences appeared with Model II, but this is because the analysis included all lactations from the first to the fourth. Therefore there is a greater variation, and the sires with first lactation calves only could be affected. With the univariate model, higher differences between maximum and minimum breeding values (worst and best sires) were in lactations 1 and 2, whereas with the multivariate model greater differences occurred in the third and fourth lactation. For a given lactation, the greatest difference between maximum and minimum breeding values occurred when multivariate analysis was applied. These differences probably favor a multivariate model, due to correction of selection bias. For example, the predicted breeding values for the third lactation varied from -141.7 to 81.5 kg when

the univariate model was used, indicating that the calves had a genetic amplitude of 223.2 kg, but that amplitude was almost 40% greater when a multivariate model was used.

The correlations of Pearson and Spearman appear in Table 5 above and below the diagonal, respectively, for the estimated genetic values for the sires in the different models. In univariate and multivariate models, the genetic correlations for the different lactations varied from 0.02 to 0.15 and from 0.72 to 0.97, respectively. The residuals went from 0.04 to 0.33 in Model I, and from 0.65 to 0.96 in Model III, showing correlations from 0.02 to 0.98 among the estimated genetic values. Correlations among estimated genetic values in Model II varied from 0.03 to 0.38 with Model I, and from 0.32 to 0.38 with Model III. These results suggest a greater consistency in global response to selection using a multivariate animal model in the prediction of genetic values.

Table 4. Differences in the expected progeny difference (EPD) for milk yield between the best and worst sires obtained with the studied models

Model	Lactation	Minimum	Maximum	Difference
			Kg	
I	L1	-141.5	224.5	366.0
	L2	-59.2	53.8	113.0
	L3	-141.7	81.5	223.2
	L4	-79.4	65.3	144.7
II	All lactations	-339.5	293.5	633.0
III	L1	-172.4	235.7	408.1
	L2	-150.5	151.3	301.8
	L3	-311.7	247.9	559.6
	L4	-266.9	213.4	480.3

Table 5. Correlations of Pearson (above the diagonal) and Spearman (below the diagonal) among estimated genetic values for milk yield obtained with the studied models

Mode	Lactation	Model I				Model II		Model III			
		L1	L2	L3	L4	-	L1	L2	L3	L4	
I	L1	1.00	0.06	0.02	0.30	0.38	0.98	0.68	0.60	0.70	
I	L2	0.04	1.00	0.05	0.14	0.18	0.17	0.66	0.50	0.53	
	L3	0.06	0.33	1.00	0.15	0.03	0.08	0.43	0.68	0.51	
	L4	0.27	0.19	0.09	1.00	0.25	0.33	0.28	0.22	0.37	
II	-	0.33	0.18	0.02	0.29	1.00	0.43	0.40	0.37	0.41	
III	L1	0.97	0.15	0.02	0.31	0.38	1.00	0.79	0.72	0.81	
	L2	0.62	0.64	0.42	0.29	0.36	0.74	1.00	0.93	0.97	
	L3	0.53	0.49	0.66	0.22	0.32	0.65	0.92	1.00	0.97	
	L4	0.65	0.51	0.48	0.36	0.38	0.77	0.96	0.96	1.00	

CONCLUSIONS

The results presented here show that the multivariate animal model was the best for genetic evaluation of milk yield for Holstein cattle in Cuba. This model produced the greatest differences between genetic and residual correlations, the highest heritability values for the four lactations, the highest values of expected progeny difference for the best and worst sires, as well as the greatest correlation among estimated genetic values. In addition, the fact that genetic correlations for milk yields between parities all are not equal to 1 proved adequately that estimation of genetic parameters for milk yields using a multivariate animal model on parities was more

reasonable than a repeatability animal model in Cuban Holstein cattle.

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