

GENETIC AND ENVIRONMENTAL VARIANCE COMPONENTS FOR MILK YIELD ACROSS REGIONS, TIME PERIODS AND HERD LEVELS FOR HOLSTEIN CATTLE IN MEXICO

Componentes de Varianza Genética y Ambiental para Producción de Leche a Través de Regiones, Períodos de Tiempo y Nivel de Hato en Ganado Holstein en México

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ABSTRACT

Additive genetic, permanent environmental, and temporary environmental variance components were estimated for 86,812 milk yield records for different regions, time periods and herd-years according their standard deviation levels for Holstein cattle in Mexico. Variances were estimated using REML and an animal model. Additive genetic and residual variances were bigger in the Northern region and for the most recent period 1991-1997, both being associated with higher production levels. Heritability estimates for regions were from 0.27 to 0.31 ± 0.02 , and for time periods were from 0.20 to 0.27 ± 0.03 using all lactations. Heritability values for region and time periods in first lactation cows were from 0.21 to 0.25 ± 0.02 and 0.21 to 0.31 ± 0.02 , respectively. Heritability according to the standard deviation levels were from 0.21 to 0.24 ± 0.01 . Repeatability values ranged from 0.36 to 0.51. Differences ($P < 0.05$) in the additive and environmental variances were found classifying herds-years for milk yield standard deviation level, through regions, periods of time and their combinations. Different degrees of heterogeneity of variances were found according to the classification criterion used. Results obtained in this study suggest the need to let genetic evaluation procedures account for these differences in variance according to region, in order to reduce bias and to increase the accuracy of predicted breeding values.

Key words: Heterogeneous variance, genetic variance, heritability, repeatability.

RESUMEN

Fueron analizados 86.812 registros de producción de leche para estimar componentes de varianza genética aditiva, de ambiente permanente y de ambiente temporal para diferentes regiones, periodos de tiempo y hatos-años de acuerdo a su nivel de desviación estándar en ganado Holstein en México. Las varianzas fueron estimadas utilizando la metodología de máxima verosimilitud restringida con un modelo animal. Las varianzas genética y residual fueron grandes en la región Norte y para el período más reciente 1991-1997, siendo ambas, asociadas con alto nivel de producción en los hatos. Utilizando todas las lactancias, las heredabilidades estimadas para la región oscilaron en el rango entre $0,27$ a $0,31 \pm 0,02$ y para períodos de tiempo $0,20$ a $0,27 \pm 0,03$. En primeras lactancias las heredabilidades para región y período fueron de $0,21$ a $0,25 \pm 0,02$ y de $0,21$ a $0,31 \pm 0,02$, respectivamente. Las heredabilidades estimadas por nivel de desviación estandar fueron de $0,21$ a $0,24 \pm 0,01$. La repetibilidad tuvo un rango de 0,36 a 0,51. Se encontraron diferencias significativas ($P < 0,05$) en las varianzas genética aditiva y ambiental clasificando los hatos-años de acuerdo a su nivel de desviación estándar, para regiones, períodos de tiempo y sus combinaciones. Fueron detectados diferentes grados de heterogeneidad de varianzas en función del criterio de clasificación de registros utilizado. Los resultados obtenidos en este estudio sugieren la necesidad de efectuar evaluaciones genéticas que consideren las diferencias en las varianzas entre regiones, con el objeto de reducir el sesgo e incrementar la precisión de los valores genéticos predichos.

Palabras clave: Heterogeneidad de varianzas, varianza genética, heredabilidad, repetibilidad.

INTRODUCTION

Prediction of breeding values in dairy cattle using mixed lineal models, assumes the knowledge of variance components for genetic and environmental effects [7]. In practice, these variances have preferably been obtained with methods that assure accurate and unbiased estimates, using data obtained from the population to be improved [8]. The use of accurate estimations of the variances allows obtaining predictors that rank the animals better on the basis of its breeding values and therefore improve the selection response [6].

Currently, the restricted maximum likelihood procedure, associated to the use of an animal model (REML-AM), is the reference method for variance components estimation in dairy cattle due to their convenient properties of maintaining estimates within the parametric space and to take into account the selection bias when the pedigree is complete [7, 8, 18].

Estimates of genetic and environmental variances for milk yield in cattle available in Mexico has been obtained using a relatively limited number of records and herds, using ANOVA-derived algorithms such as the Henderson’s method 3 [15, 17, 22], and using a sire model [1, 15]. Compared to an animal model such procedures consider only partially the genetic relationships among the animals in the population and do not correct for all possible selection biases [8].

In order to implement more effective models for genetic evaluation of dairy cattle, it is important to investigate whether variances are homogeneous through geographical regions and herd levels, which are implicit assumptions done in simple models of genetic evaluation. Changes on variances are expected also to occur through time [5, 27, 28].

Studies to establish the degree of variance heterogeneity and appropriate methods to predict breeding values for milk yield according for variance heterogeneity have not been made in Mexico. The first step toward this goal is to detect and evaluate the source and degree of these differences.

The objectives of this study were to obtain estimates of genetic parameters needed for genetic evaluations of Holstein cattle in Mexico and to evaluate the effects of potential sources of variance heterogeneity such as region, period and herd level.

MATERIAL AND METHODS

Data were obtained from the milk production recording system of the Mexican Holstein Association, for the period 1970-1997. Lactations had been standardized to 305 days of lactation and were corrected to age-month of calving [26]. Records without lactation number, those without first lactation information, herds with less than 5 cows, records with lactation codes indicating lactations initiated with abortion, sale, death, illness or lesions or cows with less than 1500 kg of milk production, and with less than 18 months of age at first calving were eliminated. Total numbers of used records were 86.812.

Milk production records were classified by geographical region and by time period. The regions were defined as Northern, Central and Southern, according to the location of the herds. The Northern region included the States of Baja California Norte, Chihuahua, Sinaloa, Coahuila and Durango; the Central region consisted of the states of Aguascalientes, Guanajuato, Michoacán, Jalisco, Querétaro, San Luis Potosí and Zacatecas, and the Southern region included the states of Mexico, Hidalgo, Tlaxcala, Puebla and Veracruz.

With the intention of maintaining an appropriate number of records, the periods were defined as 1973-1983, 1984-1990 and 1991-1997.

In order to evaluate whether differences exists in the additive genetic and residual variances between first and later lactations, first lactations data were also analyzed separately.

Groups of herds-years according to their standard deviation values (SD) for milk yield were defined as well. Herd-years SD were defined as high, medium and low (TABLE I).

The number of observations of data by region and period for all and first lactations are shown in TABLES II and III.

Variance component estimation was made with the REML method using the derivative free procedure with the program MTDFREML [4].

A univariate animal model was used [7] to analyze milk production. The model included the fixed effect of herd-year and the random effect of the animal. In the analysis of data including all lactations, the model also included a random permanent environment effect. The model used for first lactation data was:

$$y = Xb + Zu + e$$

where:

- y = vector (nx1) of observations for milk yield,
- X = incidence matrix (nxp) of fixed effects, that included the effect of herd-year,
- b = vector (px1) of fixed effects,
- Z = incidence matrix (nxq) of random effects that included the animal effect
- u = vector (qx1) of random effects,
- e = random vector (nx1) (error).

TABLE I
HERDS-YEARS GROUPS ACCORDING TO THEIR
AVERAGE STANDARD DEVIATION VALUES (SD) FOR
MILK YIELD

Data Base	Number of observations
Low SD (F kg)	24.466
Medium SD (from 1240 to 1490 kg)	26.403
High SD (1520 kg)	28.911

TABLE II
NUMBER OF OBSERVATIONS AND VARIANCE COMPONENTS FOR REGION, PERIOD AND REGION-PERIOD OF TIME FOR MILK YIELD IN HOLSTEIN CATTLE IN MEXICO FOR ALL LACTATION DATA

Data	N	Additive genetic variance	Permanent environment variance	Residual variance	$h^2 \pm se$	r
Northern	13.420	742.895	345.427	1.287.305	0.31 0.02	0.46
Central	51.468	487.550	420.083	1.207.547	0.23 0.01	0.43
Southern	21.924	351.925	446.785	1.182.891	0.18 0.02	0.40
Period 1973-1983	26.998	421.899	346.583	790.597	0.27 0.02	0.49
Period 1984-1990	27.105	364.374	425.267	1.053.383	0.20 0.02	0.43
Period 1991-1997	32.709	614.437	450.750	1.713.265	0.22 0.01	0.38
Northern 1973-1983	6.954	433.714	500.844	1.026.211	0.22 0.03	0.48
Northern 1984-1990	2.834	348.370	495.959	1.010.160	0.19 0.05	0.46
Northern 1991-1997	3.632	1.464.289	82.956	1.936.013	0.42 0.05	0.44
Central 1973-1983	13.035	406.854	304.508	688.736	0.29 0.03	0.51
Central 1984 -1990	17.003	369.170	393.036	1.047.751	0.20 0.02	0.42
Central 1991-1997	21.430	572.485	456.927	1.693.921	0.21 0.02	0.38
Southern 1973-1983	7.009	456.710	222.429	762.385	0.32 0.04	0.47
Southern 1984-1990	7.268	344.109	485.887	1.079.323	0.18 0.03	0.43
Southern 1991-1997	7.647	365.952	558.181	1.646.034	0.14 0.03	0.36

N= number of observations; h^2 = heritability; se= standard error; r = repeatability.

TABLE III
NUMBER OF OBSERVATIONS AND VARIANCE COMPONENTS FOR REGION, PERIOD AND REGION-PERIOD OF TIME FOR MILK YIELD IN HOLSTEIN CATTLE IN MEXICO USING FIRST LACTATIONS

Data	Number of observations	Additive genetic variance	Residual variance	$h^2 \pm se$
Northern	5.275	471.542	1.481.704	0.24 0.03
Central	21.772	464.124	1.379.212	0.25 0.02
Southern	9.739	363.388	1.402.639	0.21 0.02
Period 1973-1983	12.125	431.453	970.463	0.31 0.03
Period 1984-1990	11.227	422.793	1.270.002	0.25 0.02
Period 1991-1997	13.434	497.025	1.851.787	0.21 0.02
Northern 1973-1983	3.229	396.521	1.406.912	0.22 0.04
Northern 1984-1990	1.075	261.707	1.480.034	0.15 0.07
Northern 1991-1997	971	880.093	1.761.287	0.33 0.06
Central 1973-1983	5.546	451.804	777.190	0.37 0.04
Central 1984 -1990	7.082	402.423	1.223.060	0.25 0.03
Central 1991-1997	9.144	514.516	1.847.445	0.22 0.03
Southern 1973-1983	3.350	456.628	843.401	0.35 0.05
Southern 1984-1990	3.070	509.240	1.306.695	0.28 0.05
Southern 1991-1997	3.319	408.451	1.805.515	0.18 0.04

h^2 = heritability; se= standard error.

Usual assumptions were made about 'u' and 'e', where 'u' and 'e' were non correlated and were normally distributed; $E(\mathbf{u})=0$, $E(\mathbf{e})=0$, $\text{Var}(\mathbf{u})= \mathbf{A}^2_a$ and $\text{Var}(\mathbf{e})= \mathbf{I}^2_e$ [e.g. 28, 30, 31].

Convergence of the models was assumed when the -2 log likelihood was equal or smaller to 10^{-6} . If at least three re-starts with different initials values obtained convergence to the same value, it was supposed that the global maximum was attained [4].

The Bartlett test was used [21] to test the differences among the variances.

RESULTS AND DISCUSSION

All lactation data

In TABLE II variance components estimates are presented by region and period of time for all lactations. Additive genetic variance for the Northern region was 2.1 and 1.4 times bigger than the additive genetic variance of the Southern and Central regions, respectively. The additive genetic variance showed a tendency to increase through time, with a slight decrease in the intermediate period of the study (1984-1990). The additive genetic variance for the period 1991-1997 was 69% bigger than for period 1973-1983.

The additive genetic variance in the Northern region and period 1991-1997 was 4.2 times than those for period 1984-1990 in the same region. The differences for other region-period combinations, in the additive genetic variance were smaller compared to those observed by regions or periods. It is probable that an overestimation of the additive genetic variance has occurred in the Northern region, because with a repeatability model it is sometimes difficult to separate the additive genetic variance and the permanent environment variances when the number of lactations in each cow is relatively low, just as it occurred with the data of this study. This situation would probably propitiate a negative correlation between the estimators and a possible overestimation of the additive genetic variance (L.D. Van Vleck, 2000, personal communication).

The increment in the additive genetic variance with time could be related to the importation of foreign genetic material that can differ in the frequency of some alleles compared to the local population. This is more likely to occur at the beginning of the period under study and lesser afterwards. Selection of sires and dams used could have propitiated an increment in the genetic merit observed for milk production in the Mexican Holstein population in the considered period. Valencia *et al.* [26] estimated a genetic trend for this same population of 29 kg of milk per year for the period 1970-1997. This increase can also have as a basis the increase in the production level, as a scale effect. Moreover, the increase of the production level associated to the improvement in environmental conditions observed with these different subsets of data could have contributed also to this scale effect.

Ibáñez *et al.* [10] found increments in the additive genetic variance of around 70% through time (from 1988-1989 compared

to the base period 1980-1984) in Holstein cows in Spain. These results shown the same tendency as obtained in this study.

The permanent environment variance did not show important changes except for the Northern region and periods 1973-1983 and 1991-1997, with values of 82,956 and 500,844, respectively.

Residual variances were also increased through time, from 790,597 to 1,713,265 for periods 1973-1983 and 1991-1997, respectively. It was observed that in combinations the residual variances showed the same tendency by regions and periods. The changes in the variances can be explained by changes in management practices that have occurred in this population with a tendency toward more intensive and more efficient production systems and also probably a scale effect.

Heritability values by region and period were from 0.14 to 0.42, with standard errors from 0.01 to 0.05. The heritability for the Northern region was 1.7 times that for the Southern region and the heritability in the period 1973-1983 was 1.35 times that for the period 1984-1990. The larger heritability found was for the Northern region and period 1991-1997 (0.42). The distribution of records was examined according to the lactation number trying to explain this high heritability value. The percentage of first lactations was smaller in the Northern region for the period 1991-1997 compared to the other files in average (27% vs. 42%), then the additive genetic variance was probably increased, considering that the additive genetic variance for first lactations was smaller. Another probable reason are a relatively high estimate error associated to the smallest number of observations in this combination, and possibly convergence problems associated to the derivative free REML used or possible limitations in the models used in this study related to the nature of data.

In Mexico, Abubakar *et al.* [1], Ruíz and Apodaca [17] and Torres [25], obtained heritabilities of 0.36, 0.40 and 0.23, respectively for milk yield in Holstein cattle, values that are within the range of estimators obtained in this study. Also, the heritabilities obtained in this study are within the range of the values obtained by several authors using REML and an animal model [2, 14, 20, 24].

Mirande and Van Vleck [13] found a decrement in the heritability with time, similar to results obtained in this study. These decrements in the heritability of this study were related to the greater increments in the environmental variances, compared to genetic variances through time.

Repeatabilities estimates in this work ranged from 0.36 to 0.51 for all subsets data. According the classifying for region, repeatabilities were from 0.40 to 0.46 and for time period from 0.38 to 0.49. Estimates obtained in this study are similar as reported values for milk yield in others dairy cattle populations [11], and range with a superior limit slightly under the estimators of Montaldo and Torres [15] for Holstein cattle in Mexico (0.53) and of Suzuki and Van Vleck [24] for Holstein cattle of Japan (0.53).

The lowest repeatability value was obtained for the Southern region and period 1991-1997 (0.36) and the highest for the Central region and period 1973-1983 (0.51). These extreme values probably were due to an association between the permanent environment and the residual variances estimates. For example, for the same regions and periods previously indicated, the biggest permanent environment variance estimate was for Southern region and period 1991-1997 (558.181), while the lowest residual variance estimate was obtained for the Central region and period 1973-1983 (688.736).

First lactations data. The estimates for first lactations variances are presented in TABLE III. The additive genetic variance did not show important changes, except in the Northern region and periods 1984-1990 and 1991-1997. The variance was found to be 3.3 times greater for period 1991-1997 than for 1984-1990.

Residual variances also showed a tendency to increase through time. The variance for period 1991-1997 was 1.9 times that one for period 1973-1983. In the period 1991-1997 for Central and Southern regions, residual variances were 2.4 and 2.1 times bigger than in the period 1973-1983, respectively. These results agree with increases in residual variance with time observed by Wiggans and VanRaden [31] with data from United States, and Van der Werf *et al.*, [27] with data from The Netherlands.

Heritabilities ranged from 0.15 to 0.37 (TABLE III). Excepting for the Northern region, heritabilities for first lactation by region were slightly higher than for all lactations in agreement with trends observed by Majjala and Hanna [11]. Heritabilities obtained for first lactation milk yield in Holstein cattle from the United States didn't change importantly when comparing the regions of New York, California and Wisconsin [2, 28, 30]. In this study, the heritabilities among regions for first lactations were also approximately similar.

In TABLE IV, simple averages of milk yield mature equivalent are presented for region and period of time in first and all lactations. The main difference in milk yield average was observed among the Southern regarding the Northern region in the analyses of all lactations (675 kg), probably due to environmental factors that could benefit to milk production, as more appropriate or intensive intra herd nutritional and management practices, in the Northern region. Another possible reason could be climate differences and the probable existence of a genotype x environment interaction across regions. Some previous results show evidences of genotype x environment interaction between the Northern and Southern regions of Mexico (Valencia, P.M., 2003, not published data)

In this study, the increments of the residual variance through the time can be explained also by the change in milk production averages, because the feeding and the management systems have also evolved with time.

The differences among first lactation milk productions between regions and periods of time were smaller compared to es-

TABLE IV
SIMPLE AVERAGES OF MATURE EQUIVALENT MILK YIELD AND 305 DAYS FOR REGION AND PERIOD OF TIME IN FIRST AND LATER LACTATIONS

Data	Average for all lactations (kg)	Average for first lactations (kg)
Northern	8.550	7.908
Central	8.275	8.184
Southern	7.875	7.835
Period 1973-1983	6.837	6.635
Period 1984-1990	7.684	7.688
Period 1991-1997	9.797	9.636

timates for all lactations, due probably to scale effects and because first lactation milk production may be less influenced by environmental factors than production of later lactations [11].

Dong and Mao [5] found that milk productions were increased through time, from 6,640 kg in period 1976-1979 to 7,181 kg for period 1984-1987. This trend is approximately similar to those obtained when information of all lactations was used (6,837 and 7,684 kg for periods 1973-1983 and 1984-1990, respectively).

Several authors suggest that residual variance increases in proportion to the increase of milk production average [3, 5, 9, 10, 13]. Powell *et al.* [16] found more "elite" cows in herds with high productions than in herds with low productions and they suggest that the increment in the variation is associated to the increment in the average milk production.

Production level

Variance components estimates are shown in TABLE V, according to their milk yield standard deviation level. Additive variances, permanent and residual environmental variances were increased as the variability of the milk production increased, similar to the results found by Stanton *et al.* [23] in herd-years classified according to the milk yield standard deviation level in Colombia, Mexico and Puerto Rico. For the residual variances, Ibáñez *et al.* [10] found increases from 40 to 80% when the level of milk production of the herd changed from low to high in Spain.

The additive genetic, permanent environment and residual variances were 2.8, 2.1 and 3 times bigger, respectively, for high than low standard deviation level. Heritabilities had similar values, 0.23, 0.21 and 0.24 for herds-years with low, medium and high standard deviations, respectively. Other authors, however, observed increases in heritability with increases in the production level of the herd. Boldman and Freeman [3] grouped herds-years according to the milk yield average, low, medium and high, and they observed that the variance components increased with the production level as well as the heritabilities (0.18, 0.22 and 0.24 respectively). Heritabilities estimated by Short *et al.* [19] showed a similar tendency

TABLE V
VARIANCE COMPONENTS FOR MILK YIELD BY LEVEL OF HERD-YEAR IN HOLSTEIN CATTLE IN MEXICO

Database	Additive genetic variance	Permanent environment variance	Residual variance	Heritability ± standard error	
Low SD 1,210 kg	266,414	243,946	629,964	0.23	0.01
Medium SD 1,240-1,490 kg	386,572	427,626	1053,458	0.21	0.01
High SD 1,520 kg	754,596	502,560	1920,692	0.24	0.01

SD= Standard deviation.

to the Boldman and Freeman [3] using first lactation, found the lower heritability of 0.15, in the herd-years with low standard deviation, compared to herd-years with medium and high standard deviations (0.26 and 0.22 respectively).

In this study also was found heterogeneity of additive genetic variances, of permanent environment and of residual variances, when classifying herds-years by standard deviation level ($P < 0.05$).

The model used to predict breeding values for milk yield for the Holstein cattle in Mexico, assumes homogeneity of genetic and environmental variances, utilizing a single heritability value (0.29) for all regions and levels of milk production of the herds of the country [26]. A similar assumption has also been made in Spain [9] but several studies showed evidences for heterogeneity of variances through environments and production levels of the herds [3, 5, 13, 27].

Predicted breeding values can be biased when the heterogeneity of variances is not accounted for in the evaluation model [29]. This can reduce the selection response, particularly from incorrect cow ranking [6, 12].

The knowledge of the variances as well as the detected heterogeneity and other parameters obtained in this study may help to the design of more appropriate genetic evaluation models for the Holstein population in Mexico. In practical conditions, the assumptions of homogeneity of variances in the evaluation model were often used to reduce the computing and parameter requirements to obtain genetic breeding values. However, Garrick and Van Vleck [6] observed in its results that in large populations with homogeneous variance this approach is likely to be satisfactory. If variances differ by environment, the difficulty arises in determining which components to use for each environment. When heritability increases with the residual variance, there is a loss in efficiency of selection from assuming homogeneity. The effect of incorrect variance components is greatest when the most variable environment has the lowest heritability. However, when heritabilities increase with production herd level, ignoring the heterogeneity could cause only a small reduction in the selection efficiency. Used parameters favors the selection of sires with progeny in high environments, but often this is the environment with the greatest heritability and therefore a preferred environment for selecting animals because the accuracy of evaluation could be greater.

CONCLUSIONS

For all lactations, additive genetic and residual variances were larger for the Northern region and for the period 1991-1997. For first lactations, the additive genetic and residual variances were also larger in the Northern region and during the period 1991-1997, although the differences among the classes were smaller than in the analyses of all lactations.

Heritabilities and repeatabilities for milk yield estimated in this study are inside the range found in the literature. Heritabilities values were from 0.14 to 0.42 using all lactations and from 0.15 to 0.37 for first lactations. Heritabilities increased across region, 0.18, 0.23 and 0.31 for Southern, Central and Northern regions, and diminished across time from 0.27 to 0.22 for 1973-1990 and 1991-1997 periods, respectively, using all lactation. Heritabilities showed a similar trend across time using first lactations (from 0.31 to 0.21 for periods 1973-1990 and 1991-1997, respectively). Heritabilities were similar when classifying herd-years by standard deviation level, around 0.23. Repeatability values were from 0.36 to 0.51.

Differences ($P < 0.05$) in the additive and environmental variances were found classifying herds-years for milk yield standard deviation level, through regions, periods of time and their combinations. Heterogeneity of variances was different according to the classification criterion used. In spite of the differences found in the variances when classifying herds-years by milk yield standard deviation level, the heritabilities were similar. Estimates of heritabilities across regions using information of first lactation were also similar.

Results obtained in this study suggest the need for making studies to account for differences in the variances, probably using more complex genetic evaluation models for milk yield that account for the heterogeneity of variances, and to evaluate in the model the possible consideration of regional differences, in order to reduce the bias and to increase the precision when obtaining the predicted breeding values, in order to increase the selection response.

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