

Variance and covariance components and genetic parameters for fat and protein yield of first-lactation Holstein cows using random regression models[□]

Componentes de varianza y covarianza y parámetros genéticos para grasa y proteína láctea en vacas Holstein de primera lactancia mediante modelos de regresión aleatoria

Componentes de variância e covariância e parâmetros genéticos para gordura e proteína do leite em vacas da raça Holandesa de primeira lactação por meio de modelos de regressão aleatória

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Summary

Background: the genetic parameters of the lactation curve in dairy cattle can be analyzed as longitudinal data using Random Regression Models (RRM). **Objective:** to estimate the (co) variance components and genetic parameters for fat (F) and protein (P) yield in first lactation Holstein cows of Antioquia (Colombia) by RRM based on Legendre polynomials. **Methods:** monthly F and P records (9,479) from 1,210 first-lactation Holstein cows were used. Twenty-two and 24 RRM were used for F and P, respectively, with different orthogonal Legendre-polynomial orders to estimate the fixed-curve population coefficients and predict direct-genetic additive and permanent environment effects. The models considered homogeneous and heterogeneous residual variances of 5, 7, and 10 classes. **Results:** the best fit for F was the fourth order model for the population fixed-curve and the additive genetic effect, and the third order for the permanent environment with seven heterogeneous variances. The best fit for P was the fifth order model for the population fixed-curve and the additive genetic and permanent environmental effects with five heterogeneous variances. The variance for the animals' genetic, phenotypic, permanent environment, and residual effects for both F and P decreased as lactation progressed. F and P heritabilities were between 0.13 and 0.38, and 0.12 and 0.32, respectively. **Conclusion:** first-birth animals can be selected in Antioquia for F and P characteristics. Selection should be done preferably at the beginning of lactation since they reach the highest heritability values at this time.

Keywords: genetic evaluation, heritability, milk quality, solids in milk.

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Resumen

Antecedentes: los parámetros genéticos de la curva de lactancia en ganado de leche pueden ser analizados como datos longitudinales usando Modelos de Regresión Aleatoria (RRM). **Objetivo:** estimar mediante RRM basados en polinomios de Legendre componentes de (co) varianza y parámetros genéticos para producción de grasa (F) y proteína (P) láctea en vacas Holstein de primera lactancia de Antioquia (Colombia). **Métodos:** se incluyeron 9.479 registros mensuales de F y P pertenecientes a 1.210 vacas Holstein de primera lactancia. Para F y P se usaron 22 y 24 RRM respectivamente, con diferentes órdenes de polinomio ortogonal de Legendre para estimar los coeficientes de la curva fija de la población, la predicción de los efectos genético aditivo directo y del ambiente permanente. Los modelos consideraron varianzas residuales homogéneas y heterogéneas de 5, 7 y 10 clases. **Resultados:** para F, el mejor modelo fue el de cuarto orden para la curva fija de la población y el efecto genético aditivo, y de tercer orden para el ambiente permanente con siete varianzas heterogéneas. Para P, el modelo que presentó mejor ajuste fue el de quinto orden para la curva fija de la población, el efecto genético aditivo y el ambiente permanente y 5 varianzas heterogéneas. Para ambas características las varianzas genética aditiva directa, fenotípica, de ambiente permanente y residual disminuyeron a medida que avanzaba la lactancia. Las heredabilidades para F y P estuvieron entre 0,13 y 0,38, y entre 0,12 y 0,32, respectivamente. **Conclusión:** es posible realizar la selección para F y P en animales de primer parto en el departamento de Antioquia, preferiblemente al inicio de la lactancia, ya que ambas características presentan heredabilidades altas en esta etapa.

Palabras clave: *calidad de leche, evaluación genética, heredabilidad, sólidos lácteos.*

Resumo

Antecedentes: os parâmetros genéticos da produção de leite podem ser estimados usando Modelos de Regressão Aleatória (RRM). **Objetivo:** estimar por RRM com base em polinômios de Legendre os componentes de variância e covariância e os parâmetros genéticos para produção de gordura (F) e proteína (P) em vacas leiteiras de primeira lactação da raça holandesa em rebanhos de Antioquia, Colômbia. **Métodos:** foram avaliadas 9.479 registros mensais de F e P pertencentes a 1.210 vacas. Para F e P foram usados 22 e 24 RRM, respectivamente, com diferentes ordens de polinomiais ortogonais de Legendre para estimar os coeficientes da curva fixa da população, os efeitos genéticos aditivo direto, do ambiente permanente e residual. Os modelos consideraram variâncias residuais homogêneas e heterogêneas de 5, 7 e 10 classes. **Resultados:** para F, o melhor modelo foi o de quarta ordem para a curva fixa da população e o efeito genético aditivo, e de terceira ordem para o ambiente permanente com sete variâncias heterogêneas. Para P, o modelo que forneceu o melhor ajuste foi do quinto ordem para a curva fixa da população, o efeito genético aditivo e de ambiente permanente, e com 5 variâncias heterogêneas. Para ambas as características as variâncias genética aditiva direita, fenotípica e residual diminuíram no tempo. As herdabilidades para F e P ficaram entre 0,13 e 0,38 e entre 0,12 e 0,32, respectivamente. **Conclusão:** é possível fazer a seleção de animais da raça holandesa para F e P, de preferência no início da lactação, pois as duas características têm altas herdabilidades.

Palavras chave: *avaliação genética, herdabilidade, qualidade do leite, sólidos lácteos.*

Introduction

Genetic evaluation programs in dairy cattle have been directed towards increasing milk yields, which has led to greater genetic progress in Holstein cattle in developed countries by increasing annual milk yield by an average of 100 kg (Wiggans, 1997). Dairy production systems in the tropics have varying concentrations of metabolites in milk. The changes in fat (F) and protein (P) content are recognized as a response to the environmental and management conditions to which animals are exposed (Hernández

and Ponce, 2006). In spite of this, the price of a liter of milk is determined based on F and P content (MADR, 2012).

The computational capacity achieved in recent years has allowed for the implementation of Random Regression Model (RRM) as an alternative to estimate genetic parameters and variance components in different points throughout lactation. Several authors have used RRM to develop genetic evaluations for milk production characteristics and modeling lactation curves. Fernández *et al.* (2011) estimated genetic

parameters, covariance functions, and lactation curves in first lactation Holstein cows in Cuba through the application of orthogonal Legendre functions comparing different orders in 10 RRM. González-Peña *et al.* (2011) estimated values of heritability and genetic correlations between five measures of lactation persistence using RRM based on Legendre polynomial in first lactation Siboney cows in Cuba. Authors like Swalve (2000) have suggested the RRM for genetic evaluations of longitudinal data such as milk production, F, and P. Several studies have evaluated milk production traits in cattle and buffaloes in different locations and validated the application of the methodology as a model for developing genetic evaluations (Múnera *et al.*, 2013; González-Peña *et al.*, 2011; Herrera *et al.*, 2012; Hurtado-Lugo *et al.*, 2009; Hurtado-Lugo *et al.*, 2006).

RRM allows the calculation of genetic values at any point on the milk production curve, in contrast to the multivariate models that only take into account the points where the characteristic has been measured (Espinoza-Villavicencio *et al.*, 2011). The main practical implication of the RRM is the possibility to change the shape of the milk production curve through selection. In addition, characteristics evaluated on the test day can be used as early predictors of individual genetic merit (Jaffrézic and Minini, 2003).

The aim of this study was to estimate variance components and genetic parameters for F and P using RRM in first lactation Holstein cows in the province of Antioquia (Colombia).

Materials and methods

To estimate the genetic parameters, data from 30 dairy herds were used. Dairy herds were located near the northern and eastern portions of Antioquia where the municipalities of San Pedro de los Milagros, Entreríos, Belmira, Bello, Rionegro, El Carmen de Viboral, and La Ceja are located. Herds participated in the dairy control program of the Corporación Holstein de Antioquia (Antioquia Holstein Corporation) and the Universidad de Antioquia. Dairy herds are situated in a wet, pre-mountain forest life zone, with average temperatures of 16 °C, altitudes between 2,000 and 3,000 m, an annual rainfall between 2,000 and 4,000 mm, with topography

ranging from flat to undulating. The forage base was mostly Kikuyu pasture (*Pennisetum clandestinum*) and some associations with Rye grass (*Lolium perenne*). Animals were supplemented with commercial feeds according to the productive stage and management criteria of each herd. The database included 9,479 monthly records of F and P belonging to 1,210 first lactation Holstein cows with births between November, 2007 and August, 2012. Milk control was conducted using the methodology A4 X2 (ICAR, 2002), which consisted in monthly visits and control at AM and PM milking. The database did not include information from animals with less than 4 controls during the lactation period or animals that had no production records before day 70. Contemporary groups were analyzed with at least 4 animals. The database included 4,951 animals in the relationship matrix.

To calculate genetic parameters of F and P yields, RRM were conducted with different orders of orthogonal Legendre polynomials to predict the coefficients of the population fixed-curve, the additive direct genetic effect, and the permanent environmental effect. Homogeneous and heterogeneous residual variances of 5, 7, and 10 classes were considered.

The random regression model used is represented in the following matrix form:

$$y = X\beta + Za + Wc + e$$

Where:

y = is the vector of N observations for F and P.

β = vector of fixed effects of contemporary group (farm, year, calving season) and the regression coefficients of the population fixed-curve.

a = solution vector of the genetic additive random coefficients.

c = solution vector of the permanent environmental random coefficients.

X , Z , and W = incidence matrices of fixed, additive genetic, and permanent environment effects, respectively.

e = vector of independently distributed residuals, with homogeneity modeling of variance or heterogeneous modeling of variances classes.

Assuming that the model components presented expectations (E) and variances were:

$$E \begin{bmatrix} y \\ a \\ c \\ e \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \\ 0 \end{bmatrix}, V_a = K_a \otimes A, V_c = K_c \otimes I_{N_d} y V_e = R$$

Where:

K_a = the covariance matrix of the random regression coefficients of the additive genetic effect.

K_c = the covariance matrix of the random regression coefficients of the permanent environmental effect.

A = the additive genetic matrix.

I_{N_d} = identity matrix of dimension.

N_d and R = diagonal matrix containing residual variances.

Days in milk (t_i) and (t_j) were standardized in the range -1 to 1. The genetic covariance (G) and permanent environmental (C) between days in milk were estimated by:

$$G = [1, t_i, t_i^2 \dots] K_a \begin{bmatrix} 1 \\ t_j \\ t_j^2 \\ \cdot \\ \cdot \end{bmatrix} \text{ and}$$

$$C = [1, t_i, t_i^2 \dots] K_c \begin{bmatrix} 1 \\ t_j \\ t_j^2 \\ \cdot \\ \cdot \end{bmatrix}$$

Parturition periods were defined in two groups, the first including the months from December to February and June to August, and the second from March to May and September to November, according to the rainfall in the area.

Variance components and genetic parameters of the model were obtained by the restricted maximum likelihood method using the statistical program REML WOMBAT developed by Meyer (2007).

Twenty-two and 24 models with Legendre polynomials were tested for F and P, respectively. F Models are comprised from 333.homountil to 554.het7 and P models are comprised from 333.homo to 555.het10. Different models were compared using the Bayesian information criterion BIC (Schwarz, 1978), which allows the comparison of non-nested models and castigate models with more parameters (Nunez-Anton and Zimmerman, 2000). Lower values of BIC mean a better model fit.

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

Where, p is the number of model parameters; N is the number of observations; $\log L$ is the natural logarithm of the maximum likelihood function; and $r(X)$ is the range of the matrix X (incidence matrix for the fixed effects).

Results

According to the BIC criterion, the best model for F was the polynomial with order 4-4-3 for the fixed curve, the additive genetic, and the permanent environment effects with 7 heterogeneous variances (443.het7). The best model for P corresponded to the polynomial with order 5-5-5 for the fixed curve, the additive genetic, and the permanent environmental effects with 5 kinds of heterogeneous variances (555.het5).

For both characteristics F and P, it was found that the less-fitting adjustments, based on the BIC, corresponded to the less parameterized models and to those models that included homogeneous variances (333.hom and 433.hom). When the order of polynomials was increased in the present study, the difficulty for obtaining convergence was greater. It was impossible to reach convergence with the 555.het5 model for F, and with the 655.het5 model for P.

Estimated variances for F obtained with the 443.het7 model are shown in Figure 1. The variance for direct genetic, phenotypic, permanent environment,

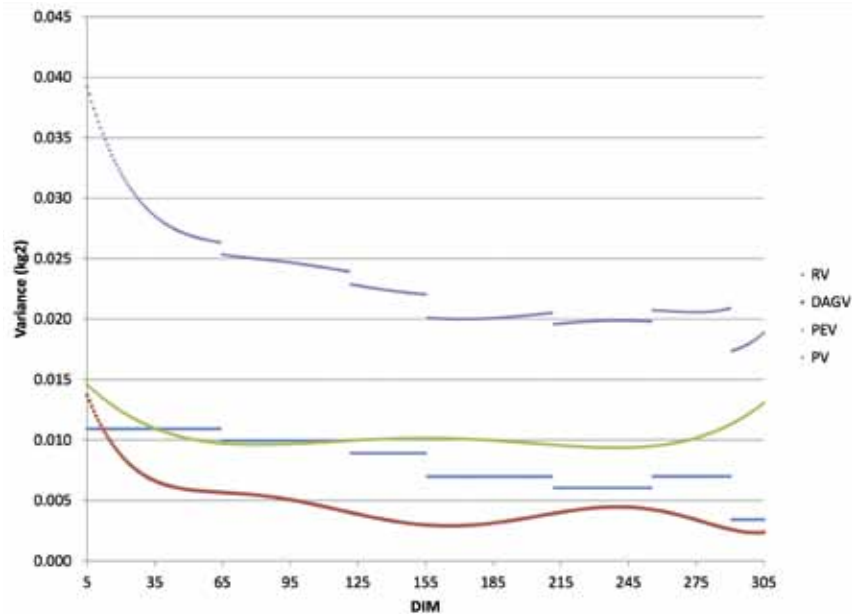


Figure 1. Direct additive genetic variance (DAGV), Phenotypic variance (PV), permanent environmental variance (PEV), and residual variance (RV) for fat yield obtained during lactation in first lactation Holstein cows of Antioquia.

and residual effects showed the highest values at the beginning of the lactation period and decreased as the production period progressed. The direct genetic variance was between 0.002 kg^2 and 0.016 kg^2 . The permanent environmental variance decreased from 0.015 kg^2 , in early lactation, to 0.009 kg^2 at day 254, and ended with 0.013 kg^2 at day 305.

Phenotypic variance values found were 0.017 kg^2 for day 293 and 0.042 kg^2 at the beginning of lactation. The residual variance presented a similar behavior to the phenotypic variance, with values falling between 0.003 kg^2 and 0.011 kg^2 .

The trajectory of the estimated variances for P is shown in Figure 2. The highest values for the direct

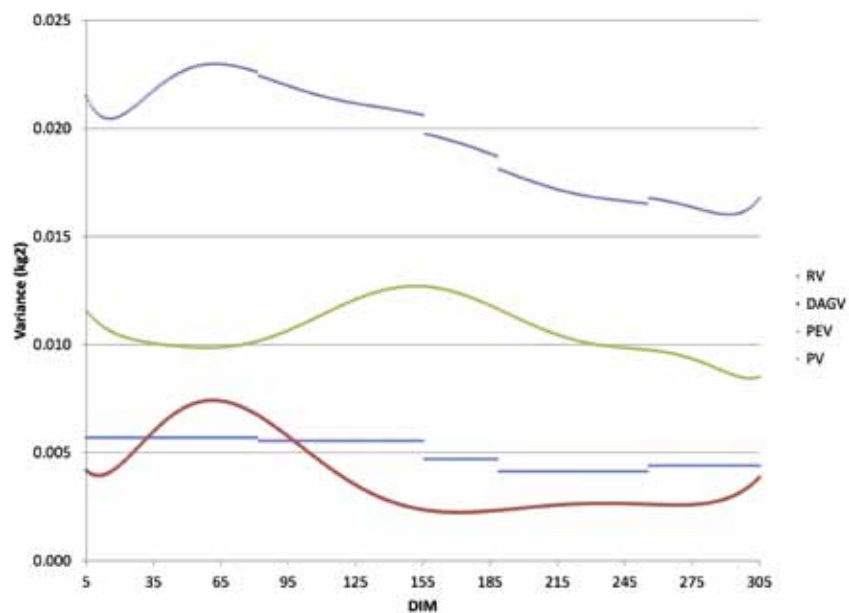


Figure 2. Direct additive genetic variances (DAGV), phenotypic variance (PV), permanent environmental variance (PEV), and residual variance (RV) for protein yield obtained during lactation in first lactation Holstein cows of Antioquia.

genetic and phenotypic variances were around day 60, coinciding with the period of higher milk production. For the additive genetic variance, values were 0.002 kg^2 for 149 to 205 days, and 0.007 kg^2 for 45 to 85 days of lactation.

The highest values for the phenotypic variance were 0.023 kg^2 from day 48 to 81, a period that corresponds to milk production peak and coincides with the highest level of supplementation of the studied population. As lactation progresses variances decrease, reaching 0.016 kg^2 at day 290.

For the permanent environmental variance, the highest values (0.013 kg^2) fell between days 137 and 167. The residual variance presented a downward trend as lactation progresses with values falling between 0.004 kg^2 and 0.006 kg^2 .

For F heritability, the highest values were observed at the beginning of lactation, with 0.38 dropping to 0.14 at day 155. While lactation progressed, an increase to 0.23 in heritability was observed on day 239, which then declined again to the lowest value obtained (0.13 at day 305) (Figure 3).

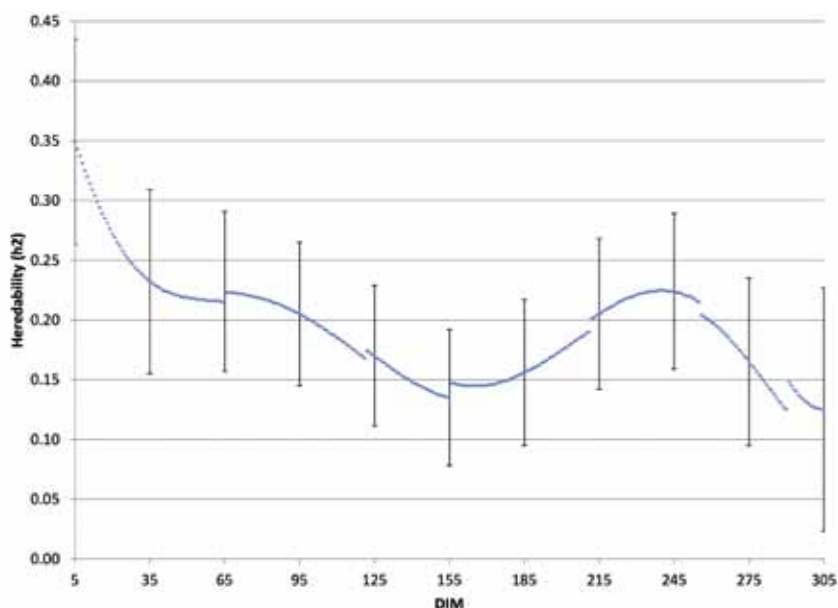


Figure 3. Heritabilities (h^2) for fat yield along lactation in Holstein cows in Antioquia.

Heritability for P ranged from 0.12 to 0.32 (Figure 4). Values obtained at the beginning of lactation were 0.20, which increased until 0.32 from days 51 to 72, afterwards descending as lactation progressed until heritability was 0.12 between days 146 and 188. Towards the end of lactation, there was a slightly increase to 0.23 at day 305.

The correlations for F decreased while the intervals of days increased. The genetic (Figure 5) and phenotypic (Figure 6) correlation between day 1 and day 5 was 0.99 and 0.99, respectively; and between day 1 and day 305 was 0.38 and 0.65, respectively.

Correlations for P decreased while the intervals of days increased. The genetic (Figure 7) and phenotypic (Figure 8) correlation between day 1 and day 5 was 0.98 and 0.99, respectively; and between day 1 and day 305 was -0.11 and 0.29, respectively.

Discussion

It was found that the less fitting adjustments for both F and P traits, based on BIC, corresponded to the less parameterized models and those that included homogeneous variances. Studies have tried different orders of Legendre polynomials to analyze

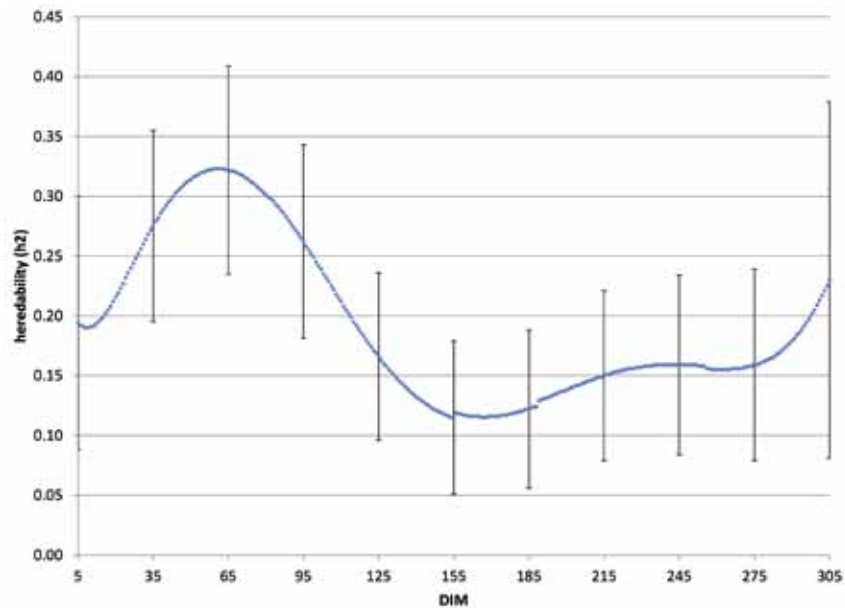


Figure 4. Heritabilities (h^2) for protein production along lactation in Holstein cows in Antioquia.

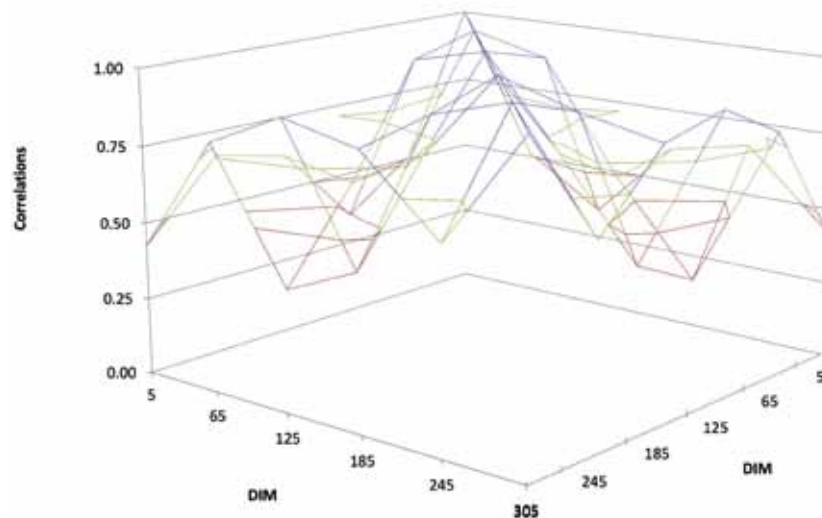


Figure 5. Additive genetic correlations for fat yield in Holstein cows in Antioquia.

F and P yields, especially tri-characteristic analysis including milk volume for Holstein populations in different countries, and have found that models with homogeneous variances showed no satisfactory adjustments for data analysis throughout lactation (Abdullahpour *et al.*, 2013; Hammami *et al.*, 2008; De Roos *et al.*, 2004; Strabel and Misztal, 1999). In the present study, it was more difficult to obtain

convergence when the order of polynomials was increased making it impossible to reach it with the 555.het5 model for F and the 655.het5 model for P. The flexibility of the curve can increase, raising the computational requirements and the difficulty of convergence, when models with high orders of Legendre polynomials are considered (Meyer, 1998; Kirkpatrick *et al.*, 1994).

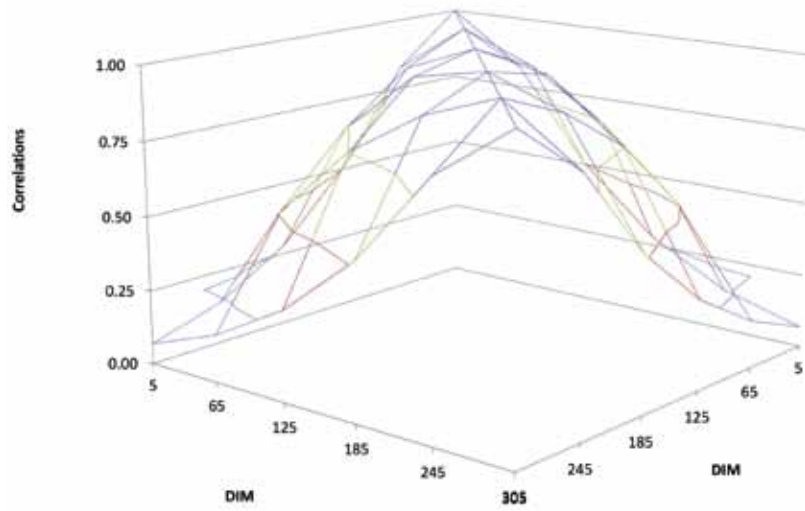


Figure 6. Phenotypic correlations for fat yield in Holstein cows in Antioquia.

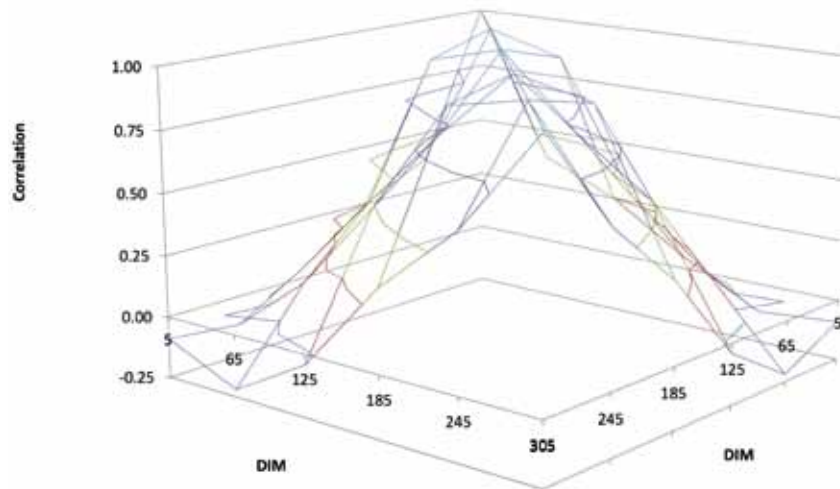


Figure 7. Additive genetic correlations for protein yield in Holstein cows in Antioquia.

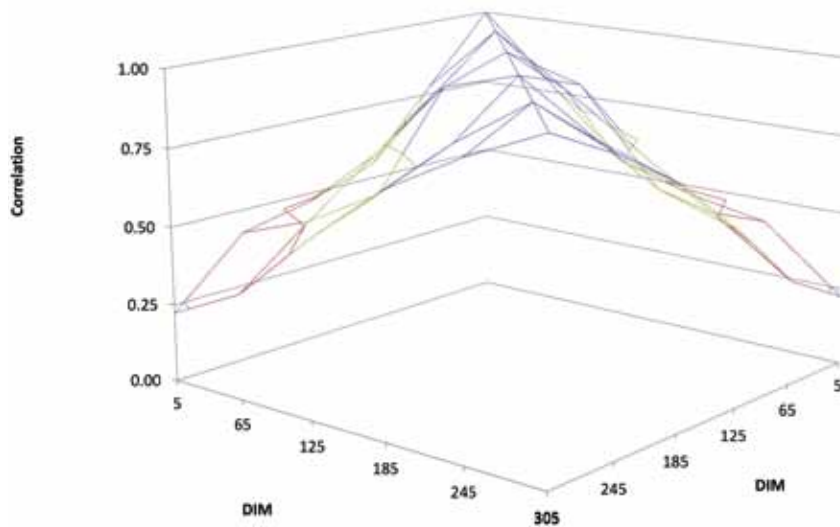


Figure 8. Phenotypic correlations for protein production in Holstein cows in Antioquia.

Other model structures have been used assuming homogeneous residual variances. Strabel *et al.* (2004) used the 5-4-4 model to estimate variance components in a Holstein population in Poland. Strabel and Misztal (1999) used model 333-Het5 for F and P characteristics, while Hammami *et al.* (2008) and Roos *et al.* (2004) used models 333-het6 and 444-het10, respectively. Abdullahpour *et al.* (2013) tested models with 9-4-4 polynomial orders with 11 kinds of heterogeneous residual variances.

The direct genetic variance for F was between 0.002 kg² and 0.016 kg² (Figure 1). These results agree with those reported by Roos *et al.* (2004) who used Legendre polynomials of fourth order for the additive genetic effect with 10 kinds of heterogeneous variances, finding the highest values at the beginning of lactation, followed by a slight decline as it progressed. Abdullahpour *et al.* (2013) used Legendre polynomials of ninth order for the additive genetic effect with heterogeneous variances of 11 classes and reported high variances at the beginning of lactation but with lower values between days 50 and 60, followed by a slight increase towards the end of the production period.

Abdullahpour *et al.* (2013) used Legendre polynomials of fourth order with 11 kinds of heterogeneous variances for permanent environmental variance. Their data presented similar results to the present study but with higher values at the beginning of lactation, followed by a marked decline around day 50. Zampar (2012) and Khabat *et al.* (2013) using Legendre polynomials of sixth and second order, respectively, with homogeneous variances obtained similar results for the permanent environment effect.

The phenotypic variance values found fell between 0.017 kg² for day 293 and 0.042 kg² at the beginning of lactation. Similar trends were reported by Abdullahpour *et al.* (2013) who found the same behavior at the beginning of lactation although with a slightly increase towards the end of the production period from day 270.

The additive genetic variance values found for P were higher in the days close to the production peak, contrary to what was reported by Khabat *et al.* (2013) and Abdullahmmad *et al.* (2013) who found

the largest variances at the end of lactation and the lowest variation near day 60.

Phenotypic variances showed that the highest values correspond to the peak of milk production were the highest supplementation levels were offered to the population. Similar results are reported by Zampar (2012) who found higher values at the beginning of lactation with a rapid decline by day 20 of lactation, followed by slight variations until day 300, after which there is an increase in variance until the end of lactation.

The heritabilities for F found in this study (Figure 3) were higher than those reported by authors such as Strabel and Misztal (1999) for a Holstein population in Poland. Khabat *et al.* (2013) and Abdullahpour *et al.* (2013) found that heritabilities were lower near the milk production peak between days 60 and 130 for Holstein cows in Iran. Higher values were reported by Roos *et al.* (2004), who found heritabilities exceeding 0.40 around day 220 of lactation, and the lowest heritabilities (0.29) on day 50.

Heritabilities for P ranged from 0.12 to 0.32 (Figure 4). The heritabilities found corresponded to those reported by other authors (Abdullahpour *et al.*, 2013; Hammami *et al.*, 2008; De Roos *et al.*, 2004; Strabel and Misztal, 1999; Khabat *et al.*, 2013) who reported heritabilities between 0.10 and 0.20 using RRM. Nevertheless, they described higher values during the last third of lactation, contrary to the trend found in the present study.

F and P had higher heritabilities near the milk production peak and lower heritabilities towards the end of lactation, which also had the highest errors. Given the production conditions in the evaluated herds and the nutritional management, there are higher solid yields, reactivation of the ovarian cycle, and recovery from the negative energy balance during the first third of lactation and near the milk production peak. These physiological events influence milk production and milk metabolites towards the end of lactation, depending on the physiological stage and days in pregnancy, resulting in marked variations in production levels between animals during this period. Variations between animals can generate higher values of environmental variance that decrease the additive genetic proportion in this period.

The genetic and phenotypic correlations for F in extended intervals of days were low; this can be explained by the high error values in the calculated heritabilities at the beginning and end of lactation. These low correlations can result from the changes in production levels and differences in management and nutrition programs of each herd, similar to what happened with P.

This study showed that it is possible to select first-birth animals for F and P in Antioquia. The selection should preferably be performed close to the production peak since this is the time when they reach the highest heritability values. However, other heritability values in other points of the lactation period have to be taken into account if selection for persistence in both F and P is needed. A genetic variability was found for F and P in the studied population. High genetic and phenotypic correlations were found for consecutive days in each characteristic, but low in extended intervals of days.

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Conflicts of interest

The authors declare they have no conflicts of interest with regard to the work presented in this report.

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