Original Articles

Estimation of genotype-by-environment interaction for milk traits based on foreign sires used in Colombia^a

Estimación de la interacción genotipo-ambiente para características de producción lechera en toros extranjeros utilizados en Colombia

Estimativa da interação genótipo-ambiente para características de produção leiteira em touros estrangeiros utilizados na Colômbia

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Summary

Background: genotype-by-environment interactions play an important role in genetic improvement programs because they can change the performance of a breeding individual according to the environment where it is evaluated. Objective: to determine the genotype-by-environment interactions for some important traits in dairy farming among countries supplying bovine genetics and assessments conducted in Antioquia, Colombia. Methods: the study was conducted in 135 Holstein herds located in Antioquia. Daughters of 180 sires were evaluated for milk yield and 186 for fat and protein percentages, and somatic cell score. The genotype-by-environment interaction was addressed using Spearman's and Pearson's correlation tests between estimated breeding values in Colombia and those estimated in the sire's countries of origin. Subsequently, the magnitude of the interaction was determined using the regression coefficient between estimated breeding values in Colombia and the foreign estimate for each trait. Results: correlations between estimated breeding values calculated in Colombia and abroad were low, with the highest correlation (0.11) for protein content and the smallest one -(0.06) for milk yield per lactation. The results show a change in the ranking of sires based on their estimated breeding value, depending on whether foreign or domestic breeding values were applied, which indicates a high genotype-by-environment interaction. The results show a regression coefficient between foreign and domestic estimated breeding values of -0.286 L/lactation, with 0.23%, 0.002%, and -0.003 scores for protein percentage, fat, and somatic cell score, respectively. All regression coefficients except that for milk yield were statistically significant (p < 0.05). Conclusion: this study demonstrates a high genotype-by-environment interaction between sires evaluated in Antioquia and abroad, underscoring the need to strengthen the estimation of breeding values adjusted to Antioquia's environment.

Keywords: dairy cattle, estimated breeding values, genetic parameters.

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Resumen

Antecedentes: la interacción genotipo-ambiente juega un papel importante en los programas de mejoramiento genético, ya que dicha interacción cambia el desempeño de un reproductor de acuerdo al ambiente donde es evaluado. Objetivo: determinar la interacción genotipo-ambiente para algunas características de importancia en producción de leche entre los países proveedores de genética bovina y las evaluaciones en Antioquia, Colombia. Métodos: la investigación se realizó en 135 hatos Holstein de Antioquia con información productiva para estimar los valores genéticos. Se evaluaron hijas de 180 toros para producción de leche y 186 para porcentaje de grasa, proteína y puntaje de células somáticas. La interacción genotipo-ambiente fue abordada usando la correlación de Sperman y de Pearson entre los valores genéticos estimados en Colombia contra los foráneos. Se determinó la magnitud de la interacción mediante el coeficiente de regresión para cada característica. Resultados: las correlaciones obtenidas entre los valores genéticos de Colombia y los foráneos fueron bajas, siendo la mayor correlación 0,11 para el caso de porcentaje de proteína y la menor de -0,06 para producción de leche por lactancia. Los resultados obtenidos muestran un cambio en el ranking de los toros con base en su valor genético de acuerdo a si se usan los valores genéticos foráneos o los nacionales, lo que evidencia una alta interacción genotipo-ambiente. Los resultados indicaron un coeficiente de regresión entre valores de cría foráneos y nacionales de -0,286 L/lactancia, 0,23%, 0,002% y -0,003 puntos para producción de leche, porcentaje de proteína, grasa y puntaje de células somáticas, respectivamente. Todos los estimados excepto el coeficiente para producción de leche fueron estadísticamente significativos (p < 0.05). Conclusión: esta investigación demuestra la alta interacción genotipo-ambiente presente entre los toros evaluados en Antioquia y los foráneos, lo que hace evidente la necesidad de fortalecer la estimación de valores genéticos en las condiciones de Antioquia.

Palabras clave: ganado de leche, parámetros genéticos, valores genéticos.

Resumo

Antecedentes: a interação genótipo-ambiente desempenha um papel importante nos programas de melhoramento genético, isto devido a que esta interação altera o desempenho de um touro de acordo com o ambiente onde ele é avaliado. Objetivo: determinar a interação genótipo-ambiente para algumas características de importância na produção de leite entre os países que fornecem avaliações genéticas bovinas em Antioquia, Colômbia. Métodos: o estudo foi realizado em 135 rebanhos de gado holandês em Antioquia com informações produtivas para estimar os valores genéticos. As filhas de 180 touros foram avaliadas quanto à produção de leite e 186 para a percentagem de gordura, proteína e a contagem de células somáticas. A interação genótipo-ambiente foi abordada utilizando as correlações de Spearman e Pearson entre os valores genéticos estimados na Colômbia comparado com os valores estimados no estrangeiro. Determinou-se o grau de interação com o coeficiente de regressão para cada característica. Resultados: as correlações entre os valores genéticos obtidos na Colômbia e os obtidos no país de origem do touro foram baixas, a maior correlação foi 0,11 para o caso da porcentagem de proteína e menos de -0,06 para a produção de leite por lactação. Os resultados permitem observar uma mudança no ranking dos touros com base no seu valor genético, se usado de acordo com os valores genéticos estrangeiros ou nacionais, o que demonstra uma alta interação genótipo-ambiente. Os resultados indicaram coeficientes de regressão entre os valores genéticos dos touros no seu pais de origem e as avaliações desses touros em Antioquia de -0,286 L/lactação, 0,23%, 0,002% e -0,003 para a porcentagem de proteína, gordura e contagem de células somáticas, respectivamente. Todos, exceto as estimativas dos coeficientes de produção de leite foram estatisticamente significativas (p<0,05). Conclusão: esta pesquisa demonstra a alta interação genótipo-ambiente que fica entre os touros avaliados em Antioquia cuja genética é estrangeira, o que torna evidente a necessidade de reforçar a estimativa de valores genéticos nas condições ambientais de Antioquia.

Palavras chave: gado de leite, parâmetros genéticos, valor genético.

Introduction

Since the arrival of artificial insemination to Colombia, the methods used to accelerate genetic progress in dairy herds have been copied from the U.S., Canada and some European countries. Health parameters are included in import policies, but the importers are in charge of the production. Therefore, the cattle entering the country have the same genetics as the cattle used in the countries of origin.

While most genetic progress and increased production levels achieved by stockbreeders in Colombian herds are due to imported animals, it is also true that genetic testing of the sires is conducted under different environmental conditions from those present in most Colombian herds. It is therefore assumed that the results obtained under the specific conditions of each farm do not necessarily coincide with the results based on the country where the sires were obtained (Windig *et al.*, 2006, Hammami *et al.*, 2009).

Genotype-by-environment interactions were described by Falconer (1996) as the performance change in one trait when the trait is measured in two or more environments. This change is expressed as a magnitude of a given parameter or as a ranking of the individual. Commonly, when the change is expressed as a ranking, it is termed an interaction, and when it is expressed as magnitude, is termed a scaling effect.

Genotype-by-environment interactions have become important because, with the implementation of techniques such as artificial insemination and embryo transfer, the genotype of superior individuals is subjected to different environments (countries, herds, etc.). This explains how individuals selected in a particular environment fail to achieve the expected results under a different environment (Krall *et al.*, 2009).

The aim of this study was to determine genotypeby-environment interactions for economically important traits in dairy production among countries that supply bovine genetics to Colombia and some municipalities in Antioquia, Colombia.

Material and methods

The study used information from 135 Holstein herds located in Antioquia. Topography, geographic location, feeding and health management varied among herds. Estimated breeding values of sires were based on the performance of their progeny in Colombia.

The number of sires used for genotype-byenvironment interaction depended on the number of sires with estimated breeding value information available in Colombia. Daughters of 180 sires were used for milk yield and 186 were used for fat, protein, and somatic cell score (SCS). The traits used for the analysis were milk yield per lactation, protein and fat percentages, and SCS.

The statistical analysis of the interaction followed Vargas & Gamboa (2008) based on the Spearman's

rank correlation between breeding values calculated for the sires in this study and the estimated breeding values obtained in Dairy sires for the same sires in the country of origin, where they were tested with greater reliability. The mathematical approximation was as follows:

Pearson's correlation coefficient

$$\rho = \frac{COV(x, y)}{\sigma_x \sigma_y}$$

Where:

cov(x,y): is the covariance of (X,Y).

 σ_X and $\sigma_{Y}\!\!:$ are the standard deviations for the marginal distributions.

Spearman's rank correlation coefficient:

$$r_{S(xy)} = 1 - \frac{6\sum d^{2_{i}}}{n(n^{2} - 1)}$$

Where:

d= is the difference between X – Y values (where X and Y are ordinary columns for each variable sorted from the smallest to the largest).

n= is the number of couples.

Correlations between estimated breeding values of Colombia and other countries were calculated based on the above equations.

After completing this first analysis, breeding values were adjusted for each performance using a regression model between estimated breeding value and reliability. Regression coefficients between foreign and domestic sires were calculated for this adjustment. A new correlation was determined according to the actual interaction between genotype and environment using the adjusted breeding values.

The model used for the regression estimation was:

$$Y = \beta_0 + \beta_1 X_i$$

Where:

Y= estimated breeding value (EBV) for each trait.

 β_0 = intercept.

 β_1 = regression coefficient for reliability effect on the breeding value.

 X_i = reliability of the breeding value.

The same model was applied to each trait using foreign and national data.

From the regression coefficients calculated from the previous model, adjusted breeding values for reliability were calculated in two ways; first, according to the regression coefficients using domestic sire data, and second using foreign sire data.

The predictive models used to estimate adjusted breeding values were:

 $Y = \mu + \beta_1 (X_i - X)$

Where:

 μ = is the breeding value of sire *i*, estimated for a specific trait.

 $\beta_{1=}$ is the regression coefficient of the breeding value as a function of reliability.

 $X_{i=}$ is the reliability of the breeding value of sire *i* for a specific trait.

X: is the mean reliability of the sire for a specific trait in the country where its breeding value was estimated.

Breeding values were adjusted to other countries according to reliability. This method has not been previously reported. We believe that it can be used to improve statistical reliability of the estimates.

Results

A descriptive analysis was carried out to estimate means and standard deviations of the breeding values for each trait (Table 1).

Mean breeding values for milk yield in Colombia were lower but similar to those recorded for other countries. Differences were higher for standard deviation and for maximum and minimum values. This parameter showed much higher variability in the breeding values recorded in other countries compared to those in Colombia. This trend was similar for all parameters except SCS, as standard deviation of breeding values was higher in other countries and maximum and minimum values were extreme.

Reliabilities of estimated breeding values (EBVs) in Colombia were markedly lower than in other countries (p<0.05). This was due to the small amount of information available regarding breeding value estimates in Colombia.

Table 1. Descriptive analysis for estimated breeding values (EBVs) and reliabilities of milk yield, fat and protein percent, and somatic cell score (SCS) in Colombia compared with the country of origin of the sire.

	Milk yield by lactation									
	Number of observations		Mean		Standard deviation		Minimum		Maximum	
	Colombia	Other countries*	Colombia	Other countries*	Colombia	Other countries*	Colombia	Other countries*	Colombia	Other countries*
EBV milk yield (L)	156	180	-27	10	219	346	-583	-1590	709	870
RELIABILITY	156	178	0.32	0.93	0.10	0.142	0.13	0.83	0.69	0.99

	Protein percentage in milk									
	Number of observations		Mean		Standard deviation		Minimum		Maximum	
	Colombia	Other countries*	Colombia	Other countries*	Colombia	Other countries*	Colombia	Other countries*	Colombia	Other countries*
EBV protein percentage (Colombia)	186	180	0.0006	0.004	0.043	0.051	-0.122	-0.18	0.106	0.170
Reliability protein percentage (Colombia)	186	179	0.29	0.93	0.15	0.141	0.13	0.85	0.73	0.99

Continues

				Table1.	Continued							
				Fa	at percent	tage in mi	lk					
	Number of observations		Mean		Standard deviation		Minimum		Maximum			
	Colombia	Other countries*	Colombia	Other countries*	Colombia	Other countries*	Colombia	Other countries*	Colombia	Other countries*		
EBV fat percentage (Colombia)	186	180	-0.0056	-0.0053	0.062	0.108	-0.175	-0.29	0.254	0.580		
Reliability fat percentage (Colombia)	186	179	0.22	0.94	0.16	0.141	0.12	0.83	0.64	0.99		
		Somatic cell score (SCS)										
	Number of observations		Mean		Standard deviation		Minimum		Maximum			
	Colombia	Other countries*	Colombia	Other countries*	Colombia	Other countries*	Colombia	Other countries*	Colombia	Other countries*		
EBV SCS (Colombia)	186	180	1.056	3.00	1.40	0.36	0.07	0.00	5.97	3.57		
Reliability SCS (Colombia)	186	186	0.18	0.90	0.15	0.21	0.12	0.79	0.57	0.99		

* Other countries: Italy, France, USA and Canada.

The Spearman's rank correlation test shows a strong genotype-by-environment interaction between Antioquia and the foreign countries from which semen is usually imported. Spearman's rank correlation for all the traits was low, suggesting a weak relation between both estimates of breeding values. Pearson's correlation revealed the same tendency. Milk protein had the highest Spearman's rank correlation between breeding values (0.11). Conversely, milk yield by lactation had the weakest correlation (-0.06) (Table 2).

Table 2. Spearman's (above the diagonal) and Pearson's (below the diagonal) correlations between estimated breeding values in Antioquia (Colombia; Col), and other countries for milk yield (MY), protein percentage (%P), fat percentage (%F) and somatic cell score (SCS).

Trait	MY Col	MY Other	%P Col	%P Other	%F Col	%F Other	SCS Col	SCS Other
MY Col	1	-0.06	0.01	0.05	-0.04	0.08	-0.27	0.00
MY Other	-0.07	1	0.00	-0.37	-0.12	-0.47	0.15	0.14
%P Col	0.03	0.05	1	0.11	0.36	0.06	0.14	-0.08
%P Other	0.19	-0.34	0.09	1	0.04	0.54	0.00	0.02
%F Col	-0.03	-0.04	0.42	0.08	1	0.07	0.01	-0.02
%F Other	0.19	-0.41	0.03	0.60	0.03	1	-0.08	-0.13
SCS Col	-0.25	0.11	0.10	-0.01	0.08	-0.07	1	0.07
SCS Other	0.02	0.10	-0.04	0.00	0.01	-0.06	0.08	1

Due to differences in EBVs between Colombia and other countries, the breeding estimates of sires were adjusted according to the reliability levels. This adjustment followed procedures described in the Methods section, and the regression coefficients obtained for each trait are presented in Table 3. **Table 3.** Regression coefficients for estimated breeding values (EBVs) for milk yield (MY), protein percentage (%P), fat percentage (%F), and somatic cell score (SCS) as a function of reliability using domestic and foreign data.

Dependent variable	Regression coefficient β_1	Model estimation coefficient r ²
EBV MY Col	-0.89	0.0018
EBV MY Others	9.37	0.1405
EBV %P Col	-0.00017	0.0034
EBV %P Others	-0.00042	0.0135
EBV %F Col	-0.0001	0.0010
EBV %F Others	-0.0006	0.0074
EBV SCS Col	-0.0016	0.0003
EBV SCS Others	0.0170	0.4657

The following equations were developed to estimate breeding values adjusted to reliability of each trait based on estimated regression coefficients:

EBVMAD=EBVM+[(-0.89)*(RM-93.4)]

EBVMAD2=EBVM+[(9.37)*(RM-93.4)]

EBVPAD=EBVP+[(-0.00017)*(RP-93.4)]

EBVPAD2=EBVP+[(-0.00042)*(RP-93.4)]

EBVGAD=EBVG+[(-0.0001)*(RG-94)]

EBVGAD2=EBVG+[(-0.00065)*(RG-94)]

EBVSCSAD=EBVSCS+[(-0.001)*(RSCS-90)]

EBVSCSAD2=EBVSCS+[(0.017)*(RSCS-90)]

Where:

EBVMAD= breeding value for MY adjusted by reliability according to the regression coefficient obtained using data from Colombia.

EBVMAD2= breeding value for MY adjusted by reliability according to the regression coefficient obtained using data from foreign countries.

EBVPAD= breeding value for protein percentage adjusted by reliability according to the regression coefficient obtained using data from Colombia.

EBVPAD2= breeding value for protein percentage adjusted by reliability according to the regression coefficient obtained using data from foreign countries.

EBVGAD= breeding value for fat percentage adjusted by reliability according to the regression coefficient obtained using data from Colombia.

EBVGAD2= breeding value for fat percentage adjusted by reliability according to the regression coefficient obtained using data from foreign countries.

EBVSCSAD= breeding value for SCS score adjusted by reliability according to the regression coefficient obtained using data from Colombia.

EBVSCSAD2= breeding value for the SCS adjusted by reliability according to the regression coefficient obtained using data from foreign countries.

EBVM, EBVP, EBVG and EBVSCS= nonadjusted breeding values for each trait, and RM, RP, RF and RSCS are reliability breeding values for each trait (milk reliability, protein reliability, fat reliability, and SCS reliability, respectively).

Breeding values were adjusted, and correlation between them and foreign breeding values was reestimated. Results are presented in Table 4.

Table 4. Correlation between breeding values (adjusted by reliability using national and foreign data) and estimated breeding values (EBVs) in other countries for milk yield (MY), protein percentage (%P), fat percentage (%F), and somatic cell score (SCS).

	Correlation
EBVMAD	-0.062
EBVMAD2	-0.088
EBVPAD	0.101
EBVPAD2	0.106
EBVGAD	0.071
EBVGAD2	0.050
EBVSCSAD	0.080
EBVSCSAD2	0.088

EBVMAD: Breeding value for milk production adjusted by reliability from Colombia EBVMAD2: Breeding value for milk production adjusted by reliability in foreign sires. EVBPAD: Breeding value for protein percentage adjusted by reliability from Colombia. EBVPAD2: Breeding value for protein percentage adjusted by reliability in foreign sires. EBVGAD: Breeding value for fat percentage adjusted by reliability from Colombia. EBVGAD2: Breeding value for fat percentage adjusted by reliability in foreign sires. EBVSCSAD: Breeding value for somatic cell score adjusted by reliability from Colombia. EBVSCSAD2: Breeding value for somatic cell score adjusted by reliability in foreign sires. The strength of genotype-by-environment interaction calculated in the previous analysis was reinforced after the adjustment. Correlation values were extremely low, providing evidence for a weak association between estimated breeding values of other countries and those obtained in Colombia under different environmental conditions.

Considering the weak correlations and low reliabilities obtained for EBVs in Colombia, we decided to explore the relationship between breeding values for all the traits using breeding values with reliabilities higher than 40% (first) and 45% (second), exclusively for milk yield. Correlations increased considerably; for sires with reliability higher than 40% estimated correlations were -0.177, 0.291, 0.084, and 0.056 for milk yield, protein and fat percentages, and SCS, respectively. For sires with reliabilities higher than 45%, correlation values were -0.251, 0.388, 0.113, and -0.039 for the same traits, respectively.

Regression coefficient between EBVs in Colombia and foreign countries for each trait determined the magnitude of the genotype-by-environment interaction. Regression coefficient for milk yield was -0.286 L/lactation, meaning that a one-liter increase in the foreign breeding value corresponds to a decrease of 2.86 L in the EBV for Colombia. Similarly, estimated regression coefficients were 0.23, 0.002, and -0.003 for protein and fat percentages, and SCS, respectively. All estimates except for milk yield coefficient were statistically significant (p<0.05).

Discussion

The re-ranking effect estimated by Spearman's rank correlation is termed a scaling effect, while the low Pearson's correlations are indicative of a genotype-byenvironment interaction (Falconer, 1996). Correlations (especially Spearman's) obtained in the present study suggest a high genotype-by-environment interaction for all traits considered. That is, sires with higher performance in other parts of the world will not necessarily perform well in the tropical conditions in which Antioquia dairy farming takes place. This highlights the need to estimate breeding values in Colombia to ensure greater progress through genetic selection of sires.

The correlations estimated in this study are lower than those reported by several authors in other countries (Valencia et al., 2008; Krall et al., 2009; Vargas & Gamboa, 2008) and lower than some reported in Colombia (Cerón et al., 2001; Galvis et al., 2001; Cerón-Muñoz et al., 2004). They are similar to those reported by Tsiokos et al. (2009), who evaluated genotype-by-environment interaction between Greece and other countries (Canada, Czech Republic, Denmark, France, Germany, Hungary, Italy, Luxemburg, Netherlands, USA, and New Zealand) where some low correlations were also reported, suggesting that genotype-by-environment interaction is strong even among seasonal countries. Interaction using genome-wide association analysis was recently reported (Streit et al., 2013).

It is clear that there is a low correlation between breeding values estimated in Colombia and other countries. This is mainly due to the strong effect between production systems unique to the tropics and those of seasonal zones, where most foreign sires are evaluated (Zwald *et al.*, 2003).

These results were obtained from dairy herds not belonging to any association, so they reflect what was really happening in the field and yielded reliable results of the genotype-by-environment interactions with sires imported for insemination in Antioquia's dairy region.

Even with the small increase obtained by improving the reliability estimation of the sires, a strong environmental impact on EBVs was still observed. The best way to improve breeding progress across generations is to test sires in the typical conditions of each region to reduce this effect and ensure that the performance of daughters will agree with the breeding values reported for each of the sires (Cerón *et al.*, 2001).

Different methods to estimate genotype-byenvironment interaction between other countries and Colombia showed a high interaction. Spearman's rank correlations between breeding values were extremely low for all traits, indicating a scaling effect, i.e., the ranking of sires based on their breeding value was different if using foreign or Colombian breeding values (Table 2). Similarly, supported by 252

the estimation of Pearson's correlation and regression coefficients between EBVs (Tables 3 and 4), we can conclude that the magnitudes of the breeding values are also different.

Finally, the use of foreign genetics has been the basis of breeding developments for dairy cattle in Colombia. Thanks to the massive use of foreign genetics through artificial insemination, remarkable progress in the production parameters of the country's specialized herds has been achieved. The initial conditions that existed upon the arrival of foreign semen in Colombia ushered in fast improvements. Currently, when livestock conditions are much better in Colombia and the breeding condition of animals has improved, there is a clear need for the sires to be genetically tested based on the specific environment of the Colombian tropics. The results of this study reveal the need to improve our estimations of the breeding values of national and foreign sires, which would improve the quality of information and the reliability of the estimated parameters and enable breeders to offer farmers a variety of genotypes adapted to the specific conditions of each region.

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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