

Fertility Responses of Mexican Holstein Cows to US Sire Selection

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ABSTRACT

Genetic relationships between 2 fertility traits and milk production were investigated using mature-equivalent lactation records of 55,162 daughters of 1,339 Holstein sires in Mexico and 499,401 daughters of 663 Holstein sires in the northeastern United States. Data sets contained yields in first and second lactation, age at first calving (AFC), and calving interval (CI). There were 474 US sires in common between countries. A herd-year standard deviation criterion defined nonoverlapping low- ($\leq 1,300$ kg) and high- ($\geq 1,600$ kg) opportunity Mexican herd environments and a low-opportunity ($\leq 1,024$ kg) US environment. Genetic variances for the average Mexican herd (all data) for AFC and CI were 65 and 85% as large as those obtained from half-sisters in the average US herd. Genetic correlations for first-lactation milk in the average US herd and AFC and CI in the average Mexican environment were unfavorable (0.18 and 0.10). Regression coefficients of AFC in Mexican environments on US genetic gain in milk ranged from 2 to 7 d/1,000 kg. However, the favorable predicted response in AFC from genetic gain in milk in Mexican environments, like those in average US herds, ranged from -4 to -7 d/1,000 kg ($r_g = -0.20$). This unequal AFC response may indicate genotype by environment interaction in fitness performance or differential breeding management of high and low yielding Mexican cows. The potential effects of age at first service of breeding females need to be disentangled to accurately assess genetic improvement needs for Mexican Holstein herds. **Key words:** genotype by environment interaction, milk yield, age at first calving, Mexico

INTRODUCTION

Mexico has imported Holstein germplasm especially from the United States and Canada since 1950, primarily because daughters of US sires produce more milk than daughters of sires of other origin (Powell and Dick-

inson, 1977; Blake et al., 1988; Powell and Wiggans, 1991; Stanton et al., 1991a,b; Cienfuegos-Rivas et al., 1999). The effect of this decision on reproductive performance also needs evaluation because of the important unfavorable relationship between fertility and milk production (Hansen et al., 1983; Bonczek et al., 1992; Bagnato and Oltenacu, 1993; Nebel and McGilliard, 1993; Marti and Funk, 1994). After low milk yield and mastitis, unsatisfactory reproduction accounts for about one-third of cow disposals from Mexican herds (Cabello and Ruiz, 1998). In the short term, greater milk sales partially compensate for modest costs of associated health disorders and reduced reproductive performance. However, the accumulation of replacement costs from this genetic trend could curtail net economic returns (Pösö and Mäntysaari, 1996).

Although certain attention has been devoted to genotype by environment interaction in milk yield, unequal genetic relationships between milk and fertility traits across environments also have been suggested (Castillo-Juarez et al., 2000; Windig et al., 2005). Given the disturbance in genetic expression of milk production between herd opportunity groups in the US and Colombia (Stanton et al., 1991a,b), Brazil (Costa et al., 2000), Mediterranean Italy (Raffrenato et al., 2003), and Mexico (Stanton et al., 1991b; Cienfuegos-Rivas et al., 1999), heterogeneous genetic (co)variances should be expected in other traits. For example, genetic expression of age at first calving of Holstein cows (a composite of fertility and physical maturity) differed between Brazilian and Colombian herd environments (Cerón-Muñoz et al., 2004). Consequently, the main objective of this study was to evaluate the impact of US Holstein sires on the fertility performance of their Mexican daughters. To accomplish this, genetic parameters were estimated to determine the influence of US sires on age at first calving and first calving interval in Mexican herds.

MATERIALS AND METHODS

Data and Edits

Data were obtained from the Mexican Holstein Association (Queretaro, Mexico) and from the USDA Animal Improvement Programs Laboratory (Beltsville, MD).

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Mexican data comprised 87,920 first-calving records of 305-d mature equivalent milk yield from Holstein cows calving from 1971 to 1995. These cows were Mexican-born daughters of US (64%), Canadian (14.4%), and Mexican sires (21.6%). The final data consisted of 56,162 Mexican first-calving records from daughters of 1,339 sires in 164 herds. The US data comprised 976,477 first-calving records of 305-d milk yields from Holstein cows calving from 1980 to 1993 in the north-eastern United States. The US data were restricted to the northeastern region to reduce sample size and because most of the common sires were utilized in this region. The final US data comprised 499,401 first-calving records from daughters of 663 US and Canadian sires in 3,685 herds. Sires were required to have at least 3 daughters in at least 2 herds, and each herd was required to provide at least 5 records. There were 474 US and Canadian sires with daughters in Mexico (32,860 records) and in the United States (408,894 records). Age at first calving (AFC) and calving interval (CI) were calculated from dates of birth and first and second calving.

Herd opportunity environments were defined by herd-year phenotypic standard deviation (HYSD) for first-lactation milk yield. As previously indicated, this criterion has been utilized to study differential responses in milk yield and in fertility (Castillo-Juarez et al., 2000; Cerón-Muñoz et al., 2004). The key assumption is that herds with greater expressed variation utilize more management inputs to provide greater opportunity for cows to express more fully their genetic potentials (Raffrenato et al., 2003). Consequently, 2 nonoverlapping opportunity classes were defined for Mexico (HYSD <1,300 kg and HYSD >1,600 kg) and a low opportunity class was defined for the United States (HYSD ≤1,024 kg). These arbitrary limits contained 50 and 22% of all herd-year subclasses (38 and 32% of records) for low- and high-opportunity Mexican environments, respectively. The low-opportunity US environment contained 38% of herd-year subclasses and 25% of all records.

Model and Analysis

Genetic parameters for first-lactation milk yield, AFC, and CI within and between countries were estimated using a multivariate linear mixed sire model with unequal design matrices and missing observations. In matrix notation

$$\mathbf{Y} = \mathbf{X}\beta + \mathbf{W}\mathbf{g} + \mathbf{Z}\mathbf{u} + \mathbf{e},$$

where \mathbf{Y} = vector of record observations; \mathbf{X} = incidence matrix for the herd-year-season contemporary group

effects; β = vector of unknown herd-year-season of calving group fixed effects; \mathbf{Z} = incidence matrix for sire effects; \mathbf{u} = vector of unknown random sire effects; \mathbf{Q} = incidence matrix that relates sires to their respective genetic groups (15 genetic groups were defined based on sire's year of birth and origin); $\mathbf{W} = \mathbf{Z}\mathbf{Q}$ because sires are nested within genetic groups; \mathbf{g} = vector of unknown genetic-group fixed effects; and \mathbf{e} = vector of residual effects.

The joint distribution of \mathbf{u} and \mathbf{e} was assumed to be multivariate normal with mean zero and variance

$$\begin{bmatrix} \mathbf{u} \\ \mathbf{e} \end{bmatrix} \sim N \left(\begin{bmatrix} \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{G} & \mathbf{0} \\ \mathbf{0} & \mathbf{R} \end{bmatrix} \right),$$

where \mathbf{G} and \mathbf{R} are the genetic and the residual (co)variance matrices, respectively.

Estimation of Genetic Parameters

Components of (Co)variance. Variance components for first-lactation milk yield, AFC, and CI within and between countries were estimated by considering performance in each opportunity environment as a separate trait. Variance components were estimated by simultaneously considering 3 or 4 traits at a time including at least 2 fertility traits. For example, the variance components in \mathbf{G} were estimated by considering first-lactation milk yield in the average US herd (all US data) and AFC from the average Mexican herd (all Mexican data), and from low and high opportunity Mexican environments. Therefore,

$$\mathbf{G} = \text{variance} \begin{bmatrix} \mathbf{u}_{1\text{ME U.S. all}} \\ \mathbf{u}_{2\text{AFC Mexico all}} \\ \mathbf{u}_{3\text{AFC Mexico Low}} \\ \mathbf{u}_{4\text{AFC Mexico High}} \end{bmatrix} = \begin{bmatrix} \mathbf{g}_{11} & \mathbf{g}_{12} & \mathbf{g}_{13} & \mathbf{g}_{14} \\ & \mathbf{g}_{22} & \mathbf{0} & \mathbf{0} \\ & & \mathbf{g}_{33} & \mathbf{g}_{34} \\ \text{symm} & & & \mathbf{g}_{44} \end{bmatrix} \otimes \mathbf{A} = \mathbf{G}_0 \otimes \mathbf{A}.$$

where \mathbf{G}_0 = genetic (co)variance matrix between sire effects (\mathbf{u}_i) for the considered traits in different environments ($\frac{1}{4}$ additive genetic variance). \mathbf{A} = numerator relationship matrix among sires, and \otimes is the Kronecker product. Residual covariances among records in different environments were assumed equal to zero. Genetic covariances between all data in Mexico and low and high opportunity environments within the same multivariate analysis were restricted to zero because \mathbf{g}_{23} and \mathbf{g}_{24} are subsets of \mathbf{g}_{22} .

Estimates of (co)variance components and solutions for sire effects were obtained with REML methods (Boldman et al., 1995). The relationship matrix included sire of sire and maternal grandsire pathways. The initial values for sire and residual variance components were obtained from univariate solutions for traits analyzed for alternative opportunity environments. Convergence was assumed when the variance of the simplex values ($-2 \log$ likelihood) was $<10^{-8}$. A global maximum was considered to be achieved when 3 restarts produced convergence without a change in the first 3 decimal places of the F value (Boldman et al., 1995).

Genetic Correlation. Product-moment genetic correlation coefficients between opportunity environments i and j were estimated by

$$r_{g(i,j)} = \frac{\sigma_{ij}}{(\sigma_{ii}\sigma_{jj})^{0.5}},$$

where σ_{ij} = genetic covariance between milk in the i th environment and fertility trait (AFC or CI) in the j th environment; σ_{ii} = genetic variance of milk in the i th environment, and σ_{jj} = genetic variance of a fertility trait in the j th environment.

Bivariate analyses provided estimates of the variance of the simplex value ($-2 \log$ likelihood) for testing genetic correlation coefficients against zero using the likelihood ratio test (Robert et al., 1995). The maximum likelihood function was obtained for 2 models, one without constraint (full model) and a reduced model with genetic correlation set to zero. The difference in twice the log likelihood was used to test the result by χ^2 statistic with 1 degree of freedom.

Fertility Responses to Sire Selection for Milk

Expected changes in AFC and CI were estimated by regressing the EBV for AFC and CI in Mexico and the US on the EBV for milk in the United States.

RESULTS AND DISCUSSION

Genetic Parameter Estimates

Phenotypic means for milk yield and AFC varied with mean HYSD in a manner consistent with our assumption of fewer inputs and less opportunity in low HYSD herds (Table 1). Preliminary analyses of relationships between milk and fertility within Mexico and the US (Table 2) indicated poorer fertility (longer CI) and younger cows at first calving with sire selection for milk. This genetic correlation coefficient agreed with findings by Ojango and Pollott (2001) for Holstein cows in Kenya

($r_g = -0.20$) and by Moore et al. (1991) in Canada ($r_g = -0.29$).

The estimated genetic correlation between milk yield in first lactation in an average Mexican herd and CI in the high opportunity environment was unfavorable ($r_g = 0.10$, $P < 0.0001$). This antagonism may be smaller than in other studies: 0.67 (Pryce et al., 2002), 0.46 (Haile-Mariam et al., 2003), and 0.23 (Kadarmideen et al., 2003). The genetic correlations between milk yield in the average and low opportunity US environments and AFC in Mexican environments were also unfavorable (Table 2).

An important finding was that the genetic covariances between milk yield and AFC analyses within countries differed from analyses between countries: they were negative across Mexican environments (Table 2) but were positive between milk in US and AFC in Mexican herds (Table 3). This outcome implies inconsistent correlated responses to selection for milk between country production systems.

Fertility Responses to Sire Selection

Within-Country Information. The estimated daughter fertility responses across Mexican and US environments are in Table 2. Favorable responses in AFC were predicted when selection is based on milk yield within country with a decrease of 3 to 7 d per 1,000 kg of genetic gain in milk. Thus, predicted AFC responses were similar when selection is based on within-country milk yield information.

Unfavorable CI responses were predicted when selection is based on milk yield within country with a 3-d increase/1,000 kg of genetic gain in milk in the average Mexican herd. In high-opportunity Mexican herds, CI may increase by 2 d/1,000 kg of genetic gain in milk yield. Similarly, a CI increase of 1 to 2 d/1,000 kg of genetic gain in milk may be expected in average- and low-opportunity US herds (Table 2).

Predicting Mexican Fertility Responses with US Information. Predicted genetic responses in fertility of Mexican cows to US germplasm are shown in Table 3. For the average Mexican herd, AFC is expected to increase by about 7 d and CI by about 2 d/1,000 kg of genetic gain in first-lactation milk yield based on information from the average US herd. However, if selection were based on milking performance in low-opportunity US herds, a smaller AFC increase of about 4 d/1,000 kg of genetic gain in milk yield may be expected in Mexican herds. Similarly, CI may increase by 1 to 2 d/1,000 kg of genetic gain in milk yield.

This unequal AFC response to selection for milk production between countries may indicate genotype by environment interaction. Similar to milking ability, the

Table 1. Number of records, means and standard deviations for first-lactation milk yield, age at first calving, calving interval, and herd-year standard deviation (HYSD) for milk in the US and Mexican data sets

Data set	Mature equivalent milk yield (kg)			Age at first calving (mo)			Calving interval (d)			HYSD ⁴		
	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD
Mexico, all data	56,162	7,454	2,134	56,162	27.6	2.9	35,997	406	67	56,162	1,453	278
Mexico, low HYSD ¹	21,524	6,565	1,542	21,410	28.1	2.9	13,388	407	72	21,524	1,102	165
Mexico, high HYSD ²	18,153	8,484	2,470	18,036	26.9	2.8	9,667	408	74	18,153	1,676	298
United States, all data	499,401	9,418	2,436	499,401	27.1	3.1	320,209	401	62	499,401	2,107	205
United States, low HYSD ³	124,421	9,046	2,584	124,421	27.3	3.2	83,810	399	63	124,421	1,853	237

¹Records from herds with HYSD $\leq 1,300$ kg.

²Records from herds with HYSD $\geq 1,600$ kg.

³Records from herds with HYSD $\leq 1,024$ kg.

⁴Average across herd-years.

increased age of Mexican cows at first calving may have resulted from their diminished growth expression compared with US half-sisters. These differences suggest a need for monitoring associations between these traits in Mexican production systems to facilitate genetic decision-making. Alternatively, these results could indicate differential breeding practices. Mexican farmers may have delayed breeding service for high-yielding daughters of high EBV sires to constrain semen cost by ensuring high pregnancy rates. Therefore, it will be important to disentangle the potential effect of age at first service of breeding females to accurately determine genetic improvement needs for alternative Mexican

herds. Daughter pregnancy rate evaluations of US sires were not available when data for this study were obtained. A comparative assessment of daughter pregnancy rate across Mexican opportunity environments and the US should prove useful to dairy industries in Mexico and other Latin American countries.

CONCLUSIONS

Unequal genetic associations between milk yield and fertility traits were identified between opportunity environments in Mexico and the United States. The genetic association between milk yield and AFC was unfa-

Table 2. Within-country estimates of genetic (r_g) and phenotypic (r_p) correlation coefficients and predicted responses (b_{XonY}) from 1,000 kg of genetic gain in milk yield in first lactation for age at first calving (AFC) and calving interval (CI) across Mexican and US environments

Data set		Var _g	COV _g	r _g	r _p	b _{XonY}
Milk yield (X)	Fertility trait (Y)					
Mexico, all data		96,722				
	Mexico, AFC all data	273	-1,028	-0.20 ^a	-0.24	-5.3
	Mexico, AFC low HYSD ¹	200	-712	-0.16 ^a	-0.10	-3.6
	Mexico, AFC high HYSD ²	358	-1,370	-0.23 ^a	-0.26	-6.9
	Mexico, CI all data	81	336	0.12 ^a	0.13	3.4
	Mexico, CI low HYSD	25	31	0.02	0.02	3.0
	Mexico, CI high HYSD	46	211	0.10 ^a	0.06	2.1
United States, all data		129,152				
	United States, AFC all data	415	-1,684	-0.23 ^a	-0.18	-6.5
	United States, AFC low HYSD ³	398	-860	-0.12 ^a	-0.11	-3.3
	United States, CI all data	95	420	0.12 ^a	0.14	1.6
	United States, CI low HYSD	92	345	0.10 ^a	0.10	1.3
United States, low HYSD		124,732				
	United States, AFC all data		-1,367	-0.19 ^a	-0.16	-12.2
	United States, AFC low HYSD		-1,480	-0.21 ^a	-0.17	-5.9
	United States, CI all data		310	0.09	0.05	1.2
	United States, CI low HYSD		373	0.11 ^a	0.06	1.4

^aGenetic correlation coefficients different from zero ($P < 0.001$).

¹Records from herds with herd-year standard deviation (HYSD) $\leq 1,300$ kg.

²Records from herds with HYSD $\geq 1,600$ kg.

³Records from herds with HYSD $\leq 1,024$ kg.

Table 3. Estimates of genetic (r_g) and phenotypic correlation coefficients (r_p) between milk yield in first lactation in the average US herd (all data) and low herd-year standard deviation (HYSD) US herds and age at first calving (AFC), and calving interval (CI) in alternative Mexican herd environments

Data set						
Milk yield (x)	Fertility trait (y)	Var _g	COV _g	r _g	r _p	b _{XonY}
United States, all data		129,152				
	Mexico, AFC all data	273	1,069	0.18 ^a	-0.10	7.2
	Mexico, AFC low HYSD ¹	200	254	0.05	-0.04	1.9
	Mexico, AFC high HYSD ²	358	680	0.10 ^a	-0.10	5.2
	Mexico, CI all data	81	323	0.10 ^a	0.08	2.4
	Mexico, CI low HYSD	25	18	0.01	0.10	3.0
	Mexico, CI high HYSD	46	146	0.06	0.10	1.1
United States, low HYSD ³		124,732				
	Mexico, AFC all data	992	0.17 ^a	-0.11	3.9	
	Mexico, AFC low HYSD	150	0.03	-0.09	0.6	
	Mexico, AFC high HYSD	1,002	0.15 ^a	-0.12	4.0	
	Mexico, CI all data	286	0.09	0.10	2.2	
	Mexico, CI low HYSD	18	0.01	0.05	0.08	
	Mexico, CI high HYSD	216	0.09	0.12	1.1	

^aExceeds zero ($P < 0.001$).

¹Records from herds with HYSD $\leq 1,300$ kg.

²Records from herds with HYSD $\geq 1,600$ kg.

³Records from herds with HYSD $\leq 1,024$ kg.

avorable between milk in the United States and AFC in Mexican environments but favorable within Mexican herds. Differences in direction of this predicted fertility response might be evidence of genotype by environment interaction or differential breeding management. There is a need to disentangle the potential effect of age at first service of breeding females to evaluate genetic improvement needs for Mexican Holstein herds.

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