Inferring Genetic Parameters of Lactation in Tropical Milking Criollo Cattle with Random Regression Test-Day Models

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ABSTRACT

This study inferred genetic and permanent environmental variation of milk yield in Tropical Milking Criollo cattle and compared 5 random regression test-day models using Wilmink's function and Legendre polynomials. Data consisted of 15,377 test-day records from 467 Tropical Milking Criollo cows that calved between 1974 and 2006 in the tropical lowlands of the Gulf Coast of Mexico and in southern Nicaragua. Estimated heritabilities of test-day milk yields ranged from 0.18 to 0.45, and repeatabilities ranged from 0.35 to 0.68 for the period spanning from 6 to 400 d in milk. Genetic correlation between days in milk 10 and 400 was around 0.50 but greater than 0.90 for most pairs of test days. The model that used first-order Legendre polynomials for additive genetic effects and second-order Legendre polynomials for permanent environmental effects gave the smallest residual variance and was also favored by the Akaike information criterion and likelihood ratio tests.

Key words: random regression, lactation, genetic parameter, Tropical Milking Criollo

INTRODUCTION

The quest toward increasing dairy productivity in tropical Latin America has refocused attention on the Tropical Milking Criollo (TMC) cattle (de Alba and Kennedy, 1994; Rosendo-Ponce and Becerril-Pérez, 2002). The current TMC is a *Bos taurus* descendant of Spanish cattle that were brought to tropical America more than 500 yr ago. The TMC breed has greater fertility, survival rate, and longevity than other adapted breeds (Bodisco et al., 1968; Rosendo-Ponce and Becerril-Pérez, 2002), and its milk is high in fat, proteins, and total solids (de

Alba, 1997). These cattle have been under selection for total milk production since the 70s. Initially, selection was based on records of the dam, from which superior bulls were taken and mated, to avoid consanguinity, to unrelated cows of a different family, out of a total of 6 families. Selected sires are used mainly by AI. More recently, genetic parameter estimation and evaluation using an animal model have been performed (Rosendo-Ponce and Becerril-Pérez, 2002). Studies of lactations under hot tropical conditions are very scarce, especially with local breeds. Proper husbandry of these cattle requires consideration of genetic and environmental factors, and characterization of lactation is an important issue. Typically, mathematical functions developed for cows adapted to temperate regions are fitted to data from tropical cows (Osorio-Arce and Segura-Correa, 2005).

Use of test-day yields instead of 305-d lactation production has become common in genetic evaluation of dairy animals (Jensen, 2001). Test-day models have several advantages over traditional lactation models. These include the ability to account for environmental effects on each test day (thus accounting for environmental signals that change over time), as well as the possibility of modeling individual cow lactations (Jensen, 2001; Strabel et al., 2005). Although the use of test-day models implies analysis of larger data sets and possibly more parameters than for a traditional 305-d lactation model, they have already been developed and utilized in many countries (Strabel et al., 2005).

Random regression test-day models (RRTDM), suggested by Schaeffer and Dekkers (1994), are appealing because all test-day records of an animal are utilized and genetic evaluation of persistency is a direct by-product given that breeding values can be predicted at any point of lactation (Jamrozik et al., 1997). In addition, test-day records can be used to derive early predictors of genetic merit (Jaffrézic and Minini, 2003). In tropical areas, where data on milk production are generally scarce, efficient use of all information avail-

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able is especially important (Carvalho et al., 1998; Ilatsia et al., 2007).

Different functions have been applied in RRTDM. Lactation functions, such as Wilmink's function (Wilmink, 1987), are common choices because their parameters can be easily related to the characteristics of the lactation curve shape (Druet et al., 2003; Cobuci et al., 2005; Ilatsia et al., 2007). On the other hand, orthogonal polynomials are appealing in RRTDM, because covariance structures derived from orthogonal polynomials do not involve assumptions about the shape of the trajectory other than those implicit in the choice of order of approximation (Meyer and Kirkpatrick, 2005). Legendre polynomials, proposed by Kirkpatrick et al. (1990), have been used extensively in RRTDM analyses. Legendre polynomials have several attractive features, such as the following: 1) the polynomials are orthogonal, which is useful for analyzing patterns of genetic variation (Kirkpatrick et al., 1990); 2) covariates have small magnitudes (standardized unit of time, from -1 to +1), which decrease problems with rounding errors (Schaeffer, 2004); 3) missing records can be predicted with an acceptable accuracy (Pool and Meuwissen, 1999); and 4) a higher-order regression is often estimable when conventional polynomials fail because of properties that allow for improved convergence in iterative algorithms (Pool and Meuwissen, 1999). The objectives of this research were to infer genetic parameters of lactation in TMC cattle and to compare 5 different random regression functions for test-day analyses.

MATERIALS AND METHODS

Data

Data were collected from 3 TMC herds located in the tropical lowlands of the Gulf Coast of Mexico (within 22°28' and 19°16'N, and nearby to 96°16' W, at an average altitude of 14 m above sea level) and 1 herd in southern Nicaragua (11°25' N and 85°50' W, at 68 m above sea level). The recording scheme used in all herds was unofficial and was supported by the farmers. Climatic conditions are hot subhumid and humid; mean annual temperature ranges between 23.5 and 27.0°C, and rainfall ranges from 935 to 1,546 mm per year. Cows grazed mostly on native and introduced pastures, such as with *Cynodon plectostachyus*, *Brachiaria mutica*, and *Panicum maximum*; cows were manually milked once a day in the morning with the calf at foot.

The initial database contained 2,026 lactations from 588 TMC cows that calved between 1974 and 2006. Records were discarded if they fell in either of the following cases: lactations with fewer than 3 test-day

Figure 1. Distribution of number of test-day records (gray bars) and average daily milk yield (solid line) in 30-d intervals along lactation.

records, observations under disease status, lactations in which the calf was not used to induce let-down, the records of a cow for the same lactation were in 2 different herds, and records before 6 or after 400 DIM. After these edits, 15,377 test-day records from 1,438 multilactations (356 first lactation, 282 second, 238 third, and 562 ≥fourth lactation), of 467 cows were used for the analysis. There were 119 sires and 602 dams in the pedigree. The 11.8% of sires had daughters with records simultaneously in Mexico and Nicaragua, and the 34.5% of the Mexican cows with records were connected directly with at least 1 Nicaraguan cow with records by means of a common parent (i.e., paternal half-sister). The proportion of sires to cows was large because of the importance to avoid mating-related animals and consanguinity, given that this population was small. Moreover, we had eliminated several cows from the original database because they did not have the test-day records (in many cases, the only information available was the total production by lactation). A common practice in TMC is to continue to milk the cow beyond 305 d, because small amounts of milk per cow are still valuable in the tropical dairy unit. Figure 1 shows the distribution of number of test-day records and mean milk yield along lactation. The numbers of test-day records after 305 DIM was smaller than for other stages of lactation.

Statistical Analyses

All random regression models analyzed had the basic structure as:

$$y_{ijklq:t} = HYS_i + TS_j + Parity_k + f_k(t) + \sum_{m=0}^{m_1} a_{lm} z_{1lq:t} + \sum_{m=0}^{m_2} p_{lm} z_{2lq:t} + e_{ijklq:t},$$

where $y_{ijklq:t}$ = the q th observation on the l th animal at time t ; HYS_i , TS_j , and $Parity_k$ = the fixed effects of herd-year-calving season i , test-day season j , and parity k ; $f_k(t)$ = a fixed regression function on time that accounts for an average trajectory of yield across all animals within parity k ; $\sum_{m=0}^{m_1} a_{lm} z_{1lq:t}$ = a random regression function, in which a_{lm} are the animal additive genetic regression coefficients to be estimated, $z_{1lq:t}$ are the covariables related to time t , and m_1 is the order of the regression function (first or second order); $\sum_{m=0}^{m_2} p_{lm} z_{2lq:t}$ = a random regression associated with permanent environmental effects, where p_{lm} are the permanent environmental regression coefficients to be estimated, $z_{2lq:t}$ are the covariables related to time t , and m_2 is the order of the regression function (first or second order). Furthermore, $e_{ijklq:t}$ is a random residu-

al with null mean and variance σ^2 that was assumed to be a constant in the interval from 6 to 400 DIM. All random effects were assumed to be normally distributed.

The fixed effects were the same for all RRTDM and included the following: herd-year-calving season with 165 levels, test-day season with 4 levels (December to February, March to May, June to August, and September to November), and parity with 4 levels (1, 2, 3, and ≥ 4). Because of the limited number of test-day records available for TMC cattle, all available lactations for each cow were considered.

The lactation curve in TMC data seems to be flatter (with an earlier or null peak) than for breeds from temperate conditions. The scatterplots for individual and groups of cows were reviewed, and an earlier examination of lactation curve shapes was carried out using local regression (LOESS), a nonparametric approach (Cleveland and Loader, 1996), in which first- and second-order polynomials (with span = 0.4) seemed to fit the data well. In this form, we decided to decrease the order of polynomials in the random regression models, and 5 random regression functions were chosen for this study. The first model used random regression covariables as in Wilink's function (Wilink, 1987), and the other 4 used covariables defined through Legendre polynomials (Kirkpatrick et al., 1990). In brief: **WI** = Wilink's function for both additive genetic and permanent environmental effects; **L11** = $L_{a(1)} + L_{p(1)}$; **L12** = $L_{a(1)} + L_{p(2)}$; **L21** = $L_{a(2)} + L_{p(1)}$; and **L22** = $L_{a(2)} + L_{p(2)}$, where the number in parentheses gives the order of the Legendre polynomial for the additive genetic effect (L_a) or permanent environmental effect (L_p). Fixed regression functions were Wilink's function for WI ($\beta_0 + \beta_1 \times W_1 + \beta_2 \times W_2$, where $W_1 = \text{DIM}/10$ and $W_2 = e^{-0.05W_1}$)

and second-order Legendre polynomial for models L11, L12, L21, and L22 ($\beta_0 + \beta_1 \times L_1 + \beta_2 \times L_2$). The j th-order Legendre polynomials at time t were calculated as:

$$\varphi_j(t) = \frac{1}{2^j} \sqrt{\frac{2j+1}{2}} \sum_{k=0}^{j/2} (-1)^k \begin{pmatrix} j \\ k \end{pmatrix} x \begin{pmatrix} 2j-2k \\ j \end{pmatrix} q_t^{j-2k},$$

where $[j/2]$ denotes that fractional values are rounded down to the nearest integer, k involves regression coefficients, and q_t is standardized days at time t , ranging from -1 to 1 (Kirkpatrick et al., 1990). The standardized days q_t were computed as

$$q_t = -1 + \frac{2}{t_{\max} - t_{\min}} (t - t_{\min}),$$

where $t_{\min}$ and $t_{\max}$ = the smallest and largest values of time ($t_{\min} = 6$, $t_{\max} = 400$). Fixed regressions were fitted (nested) within parity for each cow.

The residual variance (V_R) and Akaike information criterion (**AIC**; Akaike, 1973) were used for model comparison. In addition, the likelihood ratio test was used to compare nested models using Legendre polynomials. The shapes of estimated variances along lactation and correlations among different DIM were examined. Variance components, solutions of location effects, and likelihoods were estimated using the AIREMLF90 package for Legendre polynomial models. The Wilink function estimations were obtained from the REMLF90 package, because the model did not converge when using AIREMLF90 (Misztal et al., 2002).

Estimates of the (co)variance matrices among random regression coefficients for the additive genetic effects (Σ_a) were utilized to calculate additive genetic (co) variances along lactation from the covariance function $f(t_i, t_j) = \mathbf{z}(t_i)' \Sigma_a \mathbf{z}(t_j)$, where $\mathbf{z}(t_i)$ and $\mathbf{z}(t_j)$ = the vectors of covariates evaluated at times t_i and t_j . An equivalent procedure was applied to calculate the permanent environmental (co)variances.

RESULTS

Variance Components

The magnitudes of daily additive genetic (V_G) and permanent environmental variances (V_{PE}) throughout lactation were given for all models in Figure 2. Values of V_G for all Legendre polynomial models declined from the onset of lactation, attaining minimums at approximately 160 and 250 DIM and increasing thereafter. Wilink's function model had a different shape and

Figure 2. Estimated additive genetic variance (V_G) and permanent environmental variance (V_{PE}) for test-day milk yield along lactation in 5 models: Wilmkink's function (—x—) and Legendre polynomials, with L11 (—♦—) = $L_{a(1)} + L_{p(1)}$; L12 (—■—) = $L_{a(1)} + L_{p(2)}$; L21 (—▲—) = $L_{a(2)} + L_{p(1)}$; and L22 (—○—) = $L_{a(2)} + L_{p(2)}$, where the number within parenthesis gives the order of polynomials for genetic (L_a) or permanent environmental effect (L_p).

magnitude of V_G and V_{PE} along lactation compared with Legendre polynomial models. The Wilmkink model tended to have larger V_G and smaller V_{PE} .

Between the 4 Legendre polynomial models, magnitudes of V_G were similar between 130 and 340 DIM; however, larger differences were observed near the beginning and at the end of lactation. All models had similar V_{PE} values between 100 and 340 DIM. Differences between models at the edges of lactation were less apparent for V_{PE} than for V_G . Model L21 gave the largest estimates of V_G at the beginning of lactation, the smallest V_G in the middle, and intermediate estimates at the end. Model L21 seemed to give the most heterogeneous V_G estimates across lactation among the Legendre polynomial models.

Heritability and Repeatability

As a consequence of different estimates of V_G and V_{PE} , estimated heritabilities and repeatabilities were different between models. In general, heritability of test-day milk yield ranged from 0.18 to 0.45 across lac-

tation. Differences in estimated heritabilities among Legendre polynomials models were observed at the edges of the lactation, which were similar to those in V_G . Standard errors for heritability in the model using first-order Legendre polynomials for additive genetic effect and second-order polynomials for permanent environmental effect (L12) were smaller at the beginning of lactation (0.027 to 0.030) and larger at the ends (0.045 to 0.048). The WI model had a different shape in heritabilities along lactation, and it gave larger heritability estimates. Figure 3 showed the heritabilities and repeatabilities for models WI and L12.

Repeatabilities from different models were less heterogeneous than heritabilities and had the largest values at the beginning (between 0.54 and 0.68 for DIM 10), declined through the middle of lactation (between 0.34 and 0.39 for DIM 220), and increased slowly until the end of lactation (up to 0.47 and 0.51 for DIM 400). Standard errors for repeatability were smaller in early DIM (0.044 to 0.050) and larger from DIM 190 to the end of the lactation (0.071 to 0.103) for model L12. Again, the Wilmkink model gave the largest estimates of repeatability.

Figure 3. Estimated heritability and repeatability for test-day milk yield along lactation in the Wilmkink model (—x—) and first-order Legendre polynomials for additive genetic effect and second-order Legendre polynomials for permanent environmental effect model (—■—).

Genetic and Phenotypic Correlations

Genetic and phenotypic correlations among DIM for most models were, as expected, near unity for adjacent DIM and decreased as the time-lag between the test days increased. Figure 4 displays the genetic correlations between all pairs of DIM throughout lactation for L12 and WI models.

The descending pattern in genetic correlation according to the time distance between DIM was less apparent when using first-order Legendre polynomials for additive genetic effect (and second-order polynomials for permanent environmental effect; model L12), creating a plateau in Figure 4b. Genetic correlations for this model ranged between 0.99 for all adjacent estimated DIM and 0.50 for the pair of DIM having the longest time-lag interval (10 and 400). For the Wilink model, the genetic correlation ranged between 0.97 and 0.99 for adjacent DIM. Model L21 produced a pattern of genetic correlations that departed from the other 4 models. In model L21, the correlation decayed rapidly to 250 DIM and then increased to about 0.75 at 400 DIM. In general, model L12 had the largest genetic correlations among all models considered.

The trends of phenotypic correlations among DIM were similar to those of genetic correlations. Estimates of phenotypic correlations were greater than genetic correlations, and there was less variation among models. An exception was model L11, and it produced a gentler decay pattern in early and midlactation. Model L11 also gave lower phenotypic correlations in the early and later DIM. Overall, the phenotypic correlations ranged between 0.64 and 0.99 across lactation for most models. Both genetic and phenotypic correlations were positive for all models studied.

Model Comparison

The V_R , AIC (Akaike, 1973), and $-2 \log$ likelihood for all models are given in Table 1. Model L12 had the smallest $-2 \log$ likelihood value among models using Legendre polynomials. The likelihood ratio tests among nested Legendre polynomials models favored L12 ($P < 0.01$). In addition, model L12 had the smallest AIC and V_R values among the 5 competing models.

DISCUSSION

Heterogeneity of genetic and permanent environmental variance across DIM was found for milk test-day yields in TMC cattle. The general trend in V_G along lactation is similar to those in Spanish Holsteins (Rekaya et al., 1999; López-Romero and Carabaño, 2003) and in Polish Black and White cows (Strabel et al., 2005). The behavior of increasing patterns of variances at the edges of the lactation observed in this study was also reported by López-Romero and Carabaño (2003), who concluded that this result was from the use of the polynomial functions. The magnitude of the values of V_G and V_{PE} obtained under tropical grazing dairy systems in this study are less than those reported for temperate climates and intensive dairy systems. This is probably a scale effect related to the relationship between mean and variance [i.e., the lower the mean production (tropical conditions), the smaller the variation]. The V_R was similar among all models, being largest for model L11 (Table 1). The models analyzed here distinguish differences in the genetic and permanent environmental components within lactation but ignore differences for both components across lactations (justified by the

Figure 4. Genetic correlations between DIM in a) Wilink model and b) first-order Legendre polynomials for additive genetic effect and second-order Legendre polynomials for permanent environmental effect model.

Table 1. Estimated residual variance (V_R), Akaike's information criterion (AIC), and minus twice log likelihood ($-2\log L$) for the studied models

Model ¹	Free parameters	V_R	AIC ²	$-2\log L^2$
WI	13	1.3320	497.43	—
L22	13	1.3300 ± 0.01128	413.63	403.63 ^c
L21	10	1.3337 ± 0.01130	427.93	427.93 ^d
L12	10	1.3300 ± 0.01128	0.00	0.00 ^a
L11	7	1.3667 ± 0.01145	156.40	166.40 ^b

^{a-d}Values with different superscripts differ using likelihood ratio test ($P < 0.01$) for nested models.

¹Models: WI = Wilmink's function and L = Legendre polynomials, with L11 = $L_{a(1)} + L_{p(1)}$; L12 = $L_{a(1)} + L_{p(2)}$; L21 = $L_{a(2)} + L_{p(1)}$; and L22 = $L_{a(2)} + L_{p(2)}$, where the number within parenthesis gives the order of polynomials for genetic (L_a) or permanent environmental effect (L_p).

²Values are expressed as a deviation from L12.

relatively small number of data available per lactation).

Several studies have discussed levels and patterns of daily milk yield heritability obtained using RRTDM (Misztal et al., 2000; Strabel et al., 2005). We observed different trends between the models studied. Models L11 and L22 had less variation throughout lactation, whereas model L12 had smaller estimates at the beginning and then a monotonically increasing trend until the final part of the lactation. Models L21 yielded greater estimates at the edges of lactation and smaller estimates in the middle of lactation. The latter was also reported in Canadian Holsteins under intensive dairy systems (Jamrozik and Schaeffer, 1997). However, this pattern is opposite to other studies with greater heritability in the middle of lactation and lower at the edges (Rekaya et al., 1999; Druet et al., 2003) in Holsteins. On the other hand, the Wilmink model in this study produced a contrasting pattern compared with model L12, which had larger values at the beginning of the lactation and smaller at the end. Behavior of daily milk yield heritabilities with lower values at the beginning of lactation, as in model L12, seem more acceptable, because the first lactation period is influenced by non-genetic effects cumulated before calving.

One of the earliest studies with test-day milk yield records was that of Van Vleck and Henderson (1961) for Holstein cows in the United States. Their estimates of heritability for monthly records were 0.11, 0.17, 0.22, 0.19, 0.19, 0.15, 0.14, 0.14, 0.12, and 0.08 for mo 1 to 10, respectively. Our estimates were larger, and the declining pattern at the end of lactation detected by Van Vleck and Henderson (1961) was different from what we have found in TMC cattle (with the exception of model WI). Estimated heritability of TMC in the midlactation (ranged between 0.20 and 0.25) was similar to that found with RRTDM by López-Romero and Carabaño (2003) for Holstein in the Andalusia

and Navarre regions of Spain, and our estimates were smaller than those in the Holsteins in Catalonia in the same study (ranged between 0.35 and 0.40).

Studies of lactation under tropical conditions and using RRTDM are scarce. Carvalho et al. (1998) used a first-order autoregressive process within and across lactations to account for effects of repeated observations (within cow) in a test-day animal model. Estimates of heritability were 0.13, 0.11, and 0.09 for first, second, and third lactations in Lucerna cattle, a synthetic dual-purpose breed (about 40% of its genes come from Holstein, 30% from Milking Shorthorn, and 30% from Hartón del Valle Creole cattle). According to the authors, 45% of the records were from cows with unknown sires, and the resulting sparse relationship coefficient matrix hampered their estimation of heritability. Morales et al. (1989) reported heritability estimates of 0.12 for 305-d milk yield for the Venezuelan Carora breed (developed from Amarillo de Quebrada Arriba Creole and Brown Swiss). Mackinnon et al. (1996) reported a heritability estimate of 0.09 for 305-d equivalent mature milk yield in a crossbred dairy herd in Kenya (different percentages of Sahiwal, Brown Swiss, and Ayrshire genes). Ilatsia et al. (2007) estimated heritability between 0.28 and 0.52 for Sahiwal cows in Kenya using both univariate and multitrait fixed regression test-day models.

In earlier research conducted in Turrialba, Costa Rica, using Latin American Milking Criollo, Jersey, and their reciprocal F_1 crosses and backcrosses, de Alba and Kennedy (1985) found estimates of heritability and repeatability for 305-d milk yield of 0.28 and 0.53, respectively. Later on, de Alba and Kennedy (1994) studied TMC and their crosses with several breeds (Holstein, Canadienne, Brown Swiss, Jersey, and native Mexican cows) in Tamaulipas, Mexico, and reported a heritability of 0.17 for 305-d milk yield and a repeatability of 0.44. Recently, Rosendo-Ponce and

Becerril-Pérez (2002) reported heritability and repeatability for 305-d milk yield at 0.17 and 0.50, respectively, for purebred TMC herds in Mexico.

From previous studies, heritability estimates of milk yield from cows in the tropics tend to be smaller than those in temperate regions. However, our estimates for TMC cattle under tropical environments do not differ greatly from other breeds in temperate conditions. This may be attributed to random regression models that better account for variation between environmental conditions in tropical grazing dairy systems.

In our study, model L12 had the greatest genetic correlations between DIM far apart and produced the largest correlations among DIM at the end of lactation. A similar pattern in genetic correlations has been reported in other studies (Van Vleck and Henderson, 1961; Jakobsen et al., 2002; Cobuci et al., 2005). However, our estimates are larger than those reported by Van Vleck and Henderson (1961) and Cobuci et al. (2005) for Holsteins in the United States and Brazil and are similar in magnitudes to those obtained by Jakobsen et al. (2002) in Danish Holsteins. Genetic correlations obtained in this study are much greater than those reported by Ilatsia et al. (2007) for Sahiwal in Kenya. Large and moderate correlations between initial and final DIM suggest that selection for increased milk yield in early lactation will have a positive effect on yield in late lactation.

Although models using higher-order polynomials have been widely used under temperate environments, because they generally improve the model plausibility, authors mention several problems associated with them. The V_G follows more oscillatory patterns, which leads to extreme values at the peripheries of lactation and a negative correlation for the extremes of lactation (Pool et al., 2000; López-Romero and Carabaño, 2003; Strabel et al., 2005). Moreover, the more parameters are used, the less accurately they are estimated, because fewer records are available for each estimate. Unrealistically large estimates of genetic variance for some parts of the lactation may lead to overestimation of the average genetic variance across the whole lactation, and the accuracy in genetic evaluations may be overestimated (Strabel et al., 2005). In this sense, results obtained here for TMC cattle, based on an early exploration of a data set and statistically valid comparison criteria, imply an important first step for alternative RRTDM for tropical dairy conditions in Mexico and Central America.

CONCLUSIONS

Based on the residual variance, AIC, and likelihood ratio test, the model using second-order Legendre

polynomials on fixed regressions, first-order Legendre polynomials for additive genetic effects, and second-order polynomials for permanent environmental effects seemed to fit the data better than the other functions studied. Random regression test-day models allowed estimating milk yield heritability and repeatability at different phases of the lactation of TMC cattle. Although our study is limited in data size, it illustrates the usefulness of test-day models for genetic evaluation of TMC cattle based on daily milk yield. It gives an advantage in tropical dairy systems, where records are scarce and costly to obtain for farmers. Further, the magnitudes of additive genetic variances and heritabilities of test-day records estimated for TMC cattle suggest scope for attaining genetic progress in a selection scheme.

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REFERENCES

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 in *Second International Symposium on Information Theory*. B. N. Petrov and F. Csaki, ed. Academia Kaido, Budapest, Hungary.
- Bodisco, V., A. Carnevali, E. Cevallos, and J. R. Gomez. 1968. Four consecutive lactations in Criollo and brown Swiss cows in Maracay, Venezuela. Pages 61–75 in *Proc. 2nd Meeting Latin American Association of Animal Production (ALPA)*. Vol. 3. ALPA, Lima, Perú. (in Spanish)
- Carvalho, J. G. V., R. W. Blake, E. J. Pollak, R. L. Quaas, and C. V. Durán-Castro. 1998. Application of an autoregressive process to estimate genetic parameters and breeding values for daily milk yield in a tropical herd of Lucerna cattle and in United States Holstein herds. *J. Dairy Sci.* 81:2738–2751.
- Cleveland, W. S., and C. L. Loader. 1996. Smoothing by local regression: Principles and methods. Pages 10–49 in *Statistical Theory and Computational Aspects of Smoothing*. W. Härdle and M. G. Schimek, ed. Springer, New York, NY.
- Cobuci, J. A., R. F. Euclides, P. S. Lopes, C. N. Costa, R. A. Torres, and C. S. Pereira. 2005. Estimation of genetic parameters for test-day milk yield in Holstein cows using a random regression model. *Genet. Mol. Biol.* 28:75–83.

- de Alba, J. 1997. Polymorphism in casein and quality of milk in Tropical Milking Criollo cattle. Pages 21–26 in Proc. Symp. Use of Cattle Breeds and Types Formed and Developed in Latin America and the Caribbean. Vol. 1. Latin American Association of Animal Production (ALPA), Maracaibo, Venezuela. (in Spanish).
- de Alba, J., and B. W. Kennedy. 1985. Milk production in the Latin American Milking Criollo and its crosses with Jersey. *Anim. Prod.* 41:143–150.
- de Alba, J., and B. W. Kennedy. 1994. Genetic parameters of purebred and crossbred milking Criollos in tropical Mexico. *Anim. Prod.* 58:159–165.
- Druet, T., F. Jaffrézic, D. Boichard, and V. Ducrocq. 2003. Modeling lactation curves and estimation of genetic parameters for first lactation test-day records of French Holstein cows. *J. Dairy Sci.* 86:2480–2490.
- Ilatsia, E. D., T. K. Muasya, W. B. Muhuyi, and A. K. Kahi. 2007. Genetic and phenotypic parameters for test day milk yield of Sahiwal cattle in the semi-arid tropics. *Animal* 1:185–192.
- Jaffrézic, J., and P. Minini. 2003. Modelling and analysis of incomplete and short lactations. *Anim. Sci.* 76:19–25.
- Jakobsen, J. H., P. Madsen, J. Jensen, J. Pedersen, L. G. Christensen, and D. A. Sorensen. 2002. Genetic parameters for milk production and persistency for Danish Holsteins estimated in random regression models using REML. *J. Dairy Sci.* 85:1607–1616.
- Jamrozik, J., and L. R. Schaeffer. 1997. Estimates of genetic parameters for a test day model with random regressions for yield traits of first-lactation Holsteins. *J. Dairy Sci.* 80:762–770.
- Jamrozik, J., L. R. Schaeffer, and J. C. M. Dekkers. 1997. Genetic evaluation of dairy cattle using test day yields and random regression model. *J. Dairy Sci.* 80:1217–1226.
- Jensen, J. 2001. Genetic evaluation of dairy cattle using test-day models. *J. Dairy Sci.* 84:2803–2812.
- Kirkpatrick, M., D. Lofsvold, and M. Bulmer. 1990. Analysis of the inheritance, selection and evolution of growth trajectories. *Genetics* 124:979–993.
- López-Romero, P., and M. J. Carabaño. 2003. Comparing alternative random regression models to analyse first lactation daily milk yield data in Holstein-Friesian cattle. *Livest. Prod. Sci.* 82:81–96.
- Mackinnon, M. J., W. Thorpe, and R. L. Baker. 1996. Sources of genetic variation for milk production in a crossbred herd in the tropics. *Anim. Sci.* 62:5–16.
- Meyer, K., and M. Kirkpatrick. 2005. Up hill, down dale: Quantitative genetics of curvaceous traits. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 360:1443–1455.
- Misztal, I., T. Strabel, J. Jamrozik, E. A. Mäntysaari, and T. H. E. Meuwissen. 2000. Strategies for estimating the parameters needed for different test-day models. *J. Dairy Sci.* 83:1125–1134.
- Misztal, I., S. Tsuruta, T. Strabel, B. Auvray, T. Druet, and D. H. Lee. 2002. BLUPF90 and related programs (BGF90). Proc. 7th World Congr. Genet. Appl. Livest. Prod., Montpellier, France. CD-ROM Commun. No. 28-07.
- Morales, F., R. W. Blake, T. L. Stanton, and M. V. Hahn. 1989. Effects of age, parity, season of calving, and sire on milk yield of Carora cows in Venezuela. *J. Dairy Sci.* 72:2161–2169.
- Osorio-Arce, M. M., and J. C. Segura-Correa. 2005. Factors affecting the lactation curve of *Bos taurus* × *Bos indicus* cows in a dual purpose system in the humid tropics of Tabasco, Mexico. *Tec. Pecu. Mex.* 43:127–137.
- Pool, M. H., L. L. G. Janss, and T. H. E. Meuwissen. 2000. Genetic parameters of Legendre polynomials for first parity lactation curves. *J. Dairy Sci.* 83:2640–2649.
- Pool, M. H., and T. H. E. Meuwissen. 1999. Prediction of daily milk yields from a limited number of test days using test day models. *J. Dairy Sci.* 82:1555–1564.
- Rekaya, R., M. J. Carabaño, and M. A. Toro. 1999. Use of test day yields for the genetic evaluation of production traits in Holstein-Friesian cattle. *Livest. Prod. Sci.* 57:203–217.
- Rosendo-Ponce, A., and C. M. Becerril-Pérez. 2002. Productive performance and genetic parameters in the Tropical Milking Criollo cattle in Mexico. Proc. 7th World Congr. Genet. Appl. Livest. Prod., Montpellier, France. CD-ROM Commun. No. 25-25.
- Schaeffer, L. R. 2004. Application of random regression models in animal breeding. *Livest. Prod. Sci.* 86:35–45.
- Schaeffer, L. R., and J. C. M. Dekkers. 1994. Random regressions in animal models for test-day production in dairy cattle. Pages 443–446 in Proc. 5th World Congr. Genet. Appl. Livest. Prod. Guelph, Ontario, Canada. Univ. Guelph, Ontario, Canada.
- Strabel, T., J. Szyda, E. Ptak, and J. Jamrozik. 2005. Comparison of random regression test-day models for Polish Black and White cattle. *J. Dairy Sci.* 88:3688–3699.
- Van Vleck, L. D., and C. R. Henderson. 1961. Estimates of genetic parameters of some functions of part lactation milk records. *J. Dairy Sci.* 44:1073–1084.
- Wilmink, J. B. M. 1987. Adjustment of test day milk, fat and protein yield for age, season and stage of lactation. *Livest. Prod. Sci.* 16:335–348.