

# 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

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## ABSTRACT

The objectives of this study were to estimate from test day records the genetic and environmental (co)variance components, correlations, and breeding values to increase genetic gain in milk yield of Lucerna and US Holstein cattle. The effects of repeated observations (within cow) were explained by first-order autoregressive processes within and across lactations using an animal model. Estimates of variance components and correlation coefficients between test days were obtained using derivative-free REML methodology. The autoregressive structure significantly reduced the model error component by disentangling the short-term environmental effects. The additional information and the more heterogeneous environmental variances between lactations in the multiple-lactation test day model than in the first lactation model provided substantially larger estimates of additive genetic variance (0.62 kg<sup>2</sup> for Lucerna; 14.73 kg<sup>2</sup> for Holstein), heritability (0.13 for Lucerna; 0.42 for Holstein), and individual genetic merit. Rank correlations of breeding values from multiple lactations and from first lactations ranged from 0.18 to 0.37 for females and from 0.73 to 0.89 for males, respectively. Consequently, more selection errors and less genetic gain would be expected from selection decisions based on an analysis of first lactation only, and greater accuracy would be achieved from multiple lactations. Results indicated that substantial genetic gain was possible for milk yield in the Lucerna herd (34 kg/yr). Estimates of genetic variance for Holsteins were larger than previously reported, which portends more rapid genetic progress in US herds also; under our assumptions, increases would be from 173 to 197 kg/yr.

(**Key words:** test day animal model, tropics, autocorrelation, genetic evaluation)

**Abbreviation key:** EPA = expected producing ability, LTE = long-term environmental effect, ME = mature equivalent, STE = short-term environmental effect, TD = test day.

## INTRODUCTION

Many cattle in the tropics come from a gene pool comprising multiple breeds for which the genetic objective capitalizes on breed differences in additive merit for economically important traits. The formation of synthetic or composite breeds for these settings is attractive as a simple alternative to complex strategies of continuous crossbreeding. Studies of breeding strategies in the tropics are scarce, especially for synthetic breeds. Lucerna cattle, a synthetic dual-purpose (milk and beef) Colombian breed that contains about 40% Holstein genes (11), are a product of this alternative strategy to align the genetic potential for milk yield with the modest potentials for feed nutrient supply, mainly from forages, in a tropical environment.

More genetic information and more accurate estimated breeding values may be achievable through the analysis of test day (TD) records of milk yield instead of cumulative lactation totals for genetic evaluation of potential parents. Improved information is especially important in the tropics where data are scarce and costly, thus severely restricting selection gains. Harville (14) suggested a first-order autoregressive process to model the potentially variable permanent environmental effect across repeated lactations of an individual cow. Kachman and Everett (15) included an autocorrelation structure for residuals of the TD records in a lactation. Van Tassel et al. (31) generated 305-d cumulative totals from adjusted TD milk yields using the hypothesis that TD records

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contain less residual variance and similar genetic variance compared with the totals. Wade and Quaas (35) were the first to demonstrate the methodology for incorporating a first-order, autoregressive random effect for year-season into the mixed model equations of a sire model. More milk records per cow ( $\geq 10$  daily yields versus one cumulative total per lactation) are expected to increase the number of unique contemporary groups of animal cohorts: the TD effect.

The use of TD models that accurately disentangle the covariance structure of environmental effects could increase the reliability of estimates of genetic prediction. Gain would also increase because of the reduction in the magnitude of residuals, thus increasing the heritability of a single record or the mean of  $n$  repeated records.

The primary objectives of this study were to compare the effectiveness of alternative (co)variance structures in TD models for partitioning random environmental variation to estimate the components of genetic and environmental (co)variance and to increase daily milk yield, especially for cattle in the tropics. Secondary objectives were to estimate other parameters for daily milk yield, including contrasting Holstein herd environments in the northeastern US. Steps included quantifying the biological responses in different cattle systems, assessing the feasibility of implementing the model and computational algorithms in a multiple-herd scenario, and genetically evaluating Lucerna cows and sires and alternative genetic improvement programs for this breed.

## MATERIALS AND METHODS

### Tropical Climatology and Lucerna Breed Formation

Data were provided under a collaborative research agreement by the Lucerna Cattle Breeders Association (ASOLUCERNA) from the foundation herd, Hacienda Lucerna (Bugalagrande, Valle del Cauca, Colombia). At an altitude of 960 m above sea level, the annual mean temperature at Hacienda Lucerna is about 24°C, and mean temperature minima and maxima range from 19 to 29°C. The annual mean precipitation of about 1100 mm is distributed in two rainy seasons (April to May and October to December), and relative humidity varies from 65 to 80%.

The Lucerna breed is the product of entrepreneurship and a single-herd crossbreeding strategy followed by inter se mating to form a new breed. Starting in 1937, a crossbreeding program for milk was initiated with US Holstein bulls with a local founda-

TABLE 1. Number of records and means for 305-d mature equivalent (ME) milk yield (kilograms) and within-herd standard deviation (SD) class for nine selected Holstein herds.

Class <sup>1</sup>	Records (no.)	Year-season adjusted means for	
		ME yield	
		$\bar{X}$	SD
Low	7266	9281	1508
Medium	9942	9768	1835
High	23,835	9461	2040

<sup>1</sup>Three herds per standard deviation (SD) class: low = <1644 kg of phenotypic SD, medium = 1783 to 1898 kg of phenotypic SD, and high = >2022 kg of phenotypic SD.

tion or Criollo breed, Hartón del Valle. Red Milking Shorthorn bulls were introduced in 1951 for beef and other characteristics. The herd has been closed to outside breeding since 1958. Selection has been based on milking performance (11). The resulting synthetic dual-purpose breed is now mostly reddish in coat color; purportedly, about 40% of its genes come from Holsteins, about 30% come from Milking Shorthorns, and about 30% come from Hartón del Valle cattle (11). Artificial insemination using Lucerna semen was implemented in 1980, and sire selection was based primarily on the dams of sires pathway to increase milk yield. The Instituto Colombiano Agropecuario (Bogotá, Colombia) recognized Lucerna as a dual-purpose breed in 1983.

### Data

The first TD measurement of milk yield for Lucerna cows was taken either on the 1st or the 15th d of the month following calving and thereafter at monthly intervals. Data consisted of 30,256 TD records for the first three lactations of 1819 Lucerna cows calving from 1985 to 1995. The final pedigree file consisted of 2538 animals, including these cows and their ancestors.

Data from Holstein herds in the northeastern US were from first, second, and third lactations of cows calving from 1987 to 1995. Several studies (2, 9, 10, 19, 27, 29) showed that the genetic variance or heritability of milk yield in Holstein cows especially increased with the within-herd phenotypic variance of mature equivalent (ME) yield in US and Latin American herd environments. Phenotypic means and standard deviations for within-herd ME were obtained after adjustment for the effects of year and season of calving. Nine herds with similar mean values for 305-d ME milk yields were chosen to

TABLE 2. Numbers of test day (TD) records, fixed effects, animals, and mean daily milk yield in eight data files for first and multiple lactations for the Lucerna and the Holstein breeds.

Breed	Holstein within-herd SD class <sup>1</sup>							
	Lucerna		Low		Medium		High	
	1 <sup>2</sup>	1 + 2 + 3 <sup>3</sup>	1	1 + 2 + 3	1	1 + 2 + 3	1	1 + 2 + 3
Total TD records, no.	13,998	28,808	14,552	32,526	22,194	46,956	56,567	123,113
TD	120	129	208	217	300	301	282	283
Age, mo	8	10	8	15	9	15	9	15
DIM	33	99	97	291	99	295	99	297
Animals, no.	2326	2538	2748	3126	3753	4136	9958	10,935
Cows with records, no.	1584	1819	1845	2176	2569	2926	7213	8237
Mean TD records per cow, no.	9	16	8	15	9	16	8	15
Mean daily yield, kg	7.9	8.6	29.0	32.1	30.4	32.5	28.5	31.1

<sup>1</sup>Three herds per standard deviation (SD) class: low = <1644 kg of phenotypic SD for 305-d mature equivalent (ME) milk yield, medium = 1783 to 1898 kg of phenotypic SD for 305-d ME milk yield, and high = >2022 kg of phenotypic SD for 305-d ME milk yield.

<sup>2</sup>First lactations only.

<sup>3</sup>First, second, and third lactations.

represent three classes of phenotypic standard deviation (three herds per class; Table 1). The final pedigree files consisted of 3126, 4136, and 10,935 animals for the low, medium, and high classes of phenotypic standard deviation.

For all data, TD observations were deleted if a TD class contained <4 observations or if DIM was >320 d. Lactations were required to have at least 2 TD records per cow. Lactation records were deleted 1) if initiated by abortion, 2) if missing either the date of birth or date of calving, 3) if first reported TD exceeded 75 DIM, 4) if TD intervals were >75 d, or 5) if age at calving for Lucerna cows was not between 20 to 45 mo for first parity (20 to 36 mo for Holstein), 36 to 60 mo for second parity to permit a second lactation for the older primiparous cows (28 to 48 mo for Holstein), and 55 to 90 mo for third parity (40 to 72 mo for Holstein). (The Lucerna management policy was to cull cows that did not conceive within a year of calving.) Other edits removed highly improbable lactation or TD yields.

The Lucerna cows were grouped in 10 classes by age at calving: 1 class each at ≤36 mo, 37 to 38 mo, 39 to 40 mo; 3 classes with 4-mo intervals from 41 to 52 mo; 3 classes with 6-mo intervals from 53 to 70 mo; and 1 class at ≥71 mo of age. Holstein cows were placed into 15 classes by age at calving: 8 bimonthly classes from 20 to 36 mo, 6 classes with 4-mo intervals from 37 to 60 mo, and cows at ≥61 mo of age.

Data from the Lucerna herd and from the Holstein standard deviation classes each provided 2 data files—first lactations only and multiple lactations (first three lactations). These 8 data files are summarized in Table 2.

## TD Models

A genetic TD model partitioning the random environmental component into short-term environmental (**STE**) effects (following a first-order autoregressive process within cow and lactation), long-term environmental (**LTE**) effects (following a first-order autoregressive process across lactations), and independent residuals was used to describe the data. Two animal models differing by the presence (full model) or absence (reduced model) of STE effects were applied to analyze TD observations in data for first lactation and multiple lactations. The full model was as follows:

$$y_{ijklmn} = \text{HTD}_i + \text{age}_j + \text{DIM}(H)_{k(l)} + a_m + p_{m(l)} + t_{n(ml)} + e_{ijklmn}$$

where

- $y_{ijklmn}$  = amount of milk for an individual TD sample from the cow  $m$ ,
- $\text{HTD}_i$  = fixed effect due to cows tested in the same herd TD (HTD),
- $\text{age}_j$  = fixed effect of same age at calving,
- $\text{DIM}(H)_{k(l)}$  = fixed effect for contemporary cows tested in the same lactation and DIM within herd (H),
- $a_m$  = random effect of animal,
- $p_{m(l)}$  = random effect of LTE (only animals with records contribute to this effect) and assumed to follow a first-order autoregressive process across lactations,

$t_{n(ml)}$  = random effect of STE nested within cow and lactation and assumed to follow a first-order autoregressive process, and  
 $e_{ijklmn}$  = random residual term.

In matrix notation, the full model can be represented as

$$y = X\beta + Za + Mp + Qt + e,$$

where  $y \sim N(X\beta, V)$ ,  $\beta$  = unknown vector of fixed effects, which, with known  $X$ , defines the mean;  $a$ ,  $p$ , and  $t$  = vectors representing the random effects of animal, LTE, and STE associated with records in  $y$  by  $Z$ ,  $M$ , and  $Q$  respectively;  $e$  = vector of residuals; and  $V$  = the (co)variance matrix. The expectations and (co)variances for this model are

$$\begin{bmatrix} y \\ a \\ p \\ t \\ e \end{bmatrix} \sim N \left( \begin{bmatrix} X\beta \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}; \begin{bmatrix} V & ZG & MJ & QS & R \\ & G & 0 & 0 & 0 \\ & & J & 0 & 0 \\ & & & S & 0 \\ & & & & R \end{bmatrix} \right)$$

and then (e.g., for  $l = 1, 2, 3$  lactations)

$$V = ZGZ' + MJM + \sum_{l=1}^3 (Q_l S_l Q_l') + R,$$

$$G = A_{q_l} \sigma_a^2,$$

$$J = \sigma_p^2 \begin{bmatrix} 1 & \rho_p & \rho_p^2 \\ & 1 & \rho_p \\ \text{symm} & & 1 \end{bmatrix} \otimes I_{q_2}$$

$$S = \begin{bmatrix} S_1 \\ S_2 \\ S_3 \end{bmatrix},$$

$$S_l = \text{diag}\{F\}_{m(l)} \sigma_{t_l}^2,$$

$$\text{diag}\{F\}_{m(l)} =$$

$$\text{diag} \begin{bmatrix} 1 & \rho_{t1} & \rho_{t1}^2 & \dots & \rho_{t1}^{n-2} & \rho_{t1}^{n-1} \\ & 1 & \rho_{t1} & & \rho_{t1}^{n-2} & \rho_{t1}^{n-1} \\ & & \vdots & & \vdots & \vdots \\ & & & \ddots & \rho_{t1} & \rho_{t1}^2 \\ \text{symm} & & & & 1 & \rho_{t1} \\ & & & & & 1 \end{bmatrix}_{m(l)}$$

$$R = I_N \sigma_e^2,$$

where  $A$  = numerator relationship matrix,  $\sigma_a^2$  = the genetic variance component,  $J$  = LTE (co)variance matrix following a first-order autoregressive process across the three lactations,  $\sigma_p^2$  = LTE variance component,  $\rho_p$  = LTE autocorrelation coefficient (for the single lactation analysis  $J$  reduces to  $I\sigma_p^2$ ),  $S$  = STE (co)variance matrix following a first-order autoregressive process within lactations reflecting the assumption of independence of this effect between lactations,  $F$  = autocorrelated block diagonal matrix corresponding to the cow  $m$  with  $n$  TD samples in lactation 1,  $\sigma_{t1}^2$  = STE variance component 1,  $\rho_{t1}$  = corresponding autocorrelation coefficient (for single lactation analysis,  $S$  reduces to  $\text{diag}\{F\}_{m\sigma_t^2}$ ),  $R$  = residual (co)variance matrix,  $\sigma_e^2$  = residual variance component,  $q_1$  = number of animals being evaluated,  $q_2$  = number of animals having records,  $N$  = the total number of records in the analysis,  $I$  = identity matrix, and  $\otimes$  = Kronecker tensor product.

The reduced model (ignoring the STE effect) had the same assumptions as the full model, except that LTE is the only random environmental effect measuring potential correlations that were due to the cow both within and between lactations.

The parameters were estimated using derivative-free REML (3, 28). Likelihood functions were maximized by the multivariate simplex (polytope) algorithm as described by Nelder and Mead (24). Convergence was assumed when the variance of log-likelihood functions of the polytope was  $<10^{-8}$ , and log likelihoods after restarting did not differ (up to the fourth decimal place). Models were compared by likelihood ratio tests (LRT,  $\chi^2$ ) with 2 df for the analysis of first lactations and 6 df for the analysis of multiple lactations (5).

## RESULTS AND DISCUSSION

### Full Model with STE Effect

Variance components and parameter estimates from analyses of first and multiple lactations for the Lucerna herd and for Holstein standard deviation classes are in Tables 3 and 4. The log-likelihood values,  $-2\log(\mathcal{L})$ , which maximized the likelihood functions for each model, are also given in the tables. Universally large differences between the  $-2\log(\mathcal{L})$  of the full and reduced models clearly indicated that the fit to these data was best for the full model. Differ-

TABLE 3. Estimates of variance components (kilograms per day)<sup>2</sup> for animal ( $\hat{\sigma}_a^2$ ), long-term environment ( $\hat{\sigma}_p^2$ ), short-term temporary environment (STE,  $\hat{\sigma}_t^2$ ), residual ( $\hat{\sigma}_e^2$ ), phenotype ( $\hat{\sigma}_{\text{PHENO}}^2$ ), heritabilities ( $\hat{h}^2$ ), and autocorrelations ( $\hat{\rho}$ ) using test day animal models either including or ignoring a first-order autoregressive process for short-term environmental (STE) effects on daily milk yield in first lactations from a herd of Lucerna cows and from each of the Holstein standard deviation (SD) classes.

Parameter estimate	Holstein within-herd SD class <sup>1</sup>							
	Lucerna		Low		Medium		High	
	Include <sup>2</sup>	Ignore <sup>3</sup>	Include	Ignore	Include	Ignore	Include	Ignore
$\hat{\sigma}_a^2$	0.56	1.01	7.18	7.45	6.22	6.11	8.59	8.94
$\hat{\sigma}_p^2$	<0.00	1.28	8.60	9.72	11.89	13.18	14.80	16.59
$\hat{\sigma}_t^2$	3.24	...	8.96	...	10.14	...	10.49	...
$\hat{\rho}_t$	0.83	...	0.57	...	0.61	...	0.58	...
$\hat{\sigma}_e^2$	1.05	2.48	5.24	12.40	5.50	13.42	7.46	15.71
$\hat{\sigma}_{\text{PHENO}}^2$	4.84	4.77	29.98	29.56	33.74	32.71	41.34	41.24
$\hat{h}^2$	0.11	0.21	0.24	0.25	0.18	0.19	0.21	0.22
-2log( $\epsilon$ )	28,505.40	30,510.43	54,562.03	55,574.30	84,621.29	86,532.82	228,031.92	231,494.89

<sup>1</sup>Three herds per SD class: low = <1644 kg of phenotypic SD for 305-d mature equivalent (ME) milk yield, medium = 1783 to 1898 kg of phenotypic SD for 305-d ME milk yield, and high = >2022 kg of phenotypic SD for 305-d ME milk yield.

<sup>2</sup>Model including the STE effect.

<sup>3</sup>Model ignoring the STE effect.

ences between the log-likelihood values were of multiple orders of magnitude (e.g., chi-squared critical values for  $P = 0.0005$  with 2 and 6 df, respectively, are 15.2 and 24.1; the smallest chi-squared value in this study is 1012). The full model was unequivocally superior for every analysis. Consequently, comparisons of results from the two models are primarily to emphasize the opportunity losses in genetic gain from insufficiently disentangling the environmental effects from the genetic ones.

#### Variance Components, Autocorrelations, and Heritabilities of Daily Yield in First Lactation

The TD records from Lucerna cows were highly correlated (0.83), and most of the nongenetic variance caused by cow was explained by the STE effect. Correlations between TD records in each of the three Holstein classes for phenotypic standard deviation, although smaller than for the Lucerna classes, ranging from 0.51 to 0.61, were similar to the coefficient of 0.58 used in the northeast TD evaluations (12).

The autocorrelation structure was clearly effective in removing STE influences that, if ignored, remained partly confounded with the genetic component, especially in Lucerna data. This confounding caused the genetic component of variance to be overestimated in the reduced model in three of four data files. The

estimated genetic variance from the full model for daily milk yield in primiparous Lucerna cows was 45% smaller than the biased estimate from the reduced model (Table 3), which could mean less genetic progress if the STE effect were ignored, especially in the dual-purpose Lucerna herd.

Family ties in the Lucerna data were fewer than anticipated; 45% of records was from cows with unknown sires. The resulting sparse relationship coefficient matrix probably constrained the estimated heritability ( $\hat{h}^2 = 0.11$ ) because of partial confounding of genotype and environment. More relationship ties for all Holstein data files probably helped to capture relatively more of the genetic variation and gave heritability estimates from full and reduced models that ranged from 0.18 to 0.25 (Table 3). Genetic relationships among the cattle being evaluated are the only data permitting separation of the genetic component from the nongenetic components in the cow effect. Meyer et al. (21) reported that the heritability of milk yield was underestimated for Australian Black and White cows from sire misidentification, which produced a less informative structure of genetic covariance. Insufficiently dense relationship matrices may predispose smaller estimates of genetic variance (4).

Estimates of the phenotypic variance in the single lactation analysis were nearly the same from full and

reduced models (Table 3). This outcome was expected because the models differed only by an environmental effect (STE) that, when ignored, would be contained in LTE and residual effects, if unconfounded with the genetic component.

Heritability estimates for first lactation milk yield from cows in the tropics vary by breed, location, and method of estimation, but tend to be smaller than in temperate regions. For example, Morales et al. (23) found heritability to be 0.12 for 305-d ME milk yield for the Venezuelan Carora breed using REML with a sire model. Stanton et al. (29) reported that estimates for sire (52%) and residual (42%) variances in Colombian Holstein herds were smaller than the estimates from half-sisters of US Holstein sires in US herds, but heritabilities were similar (0.29 vs. 0.24). Mackinnon et al. (17) obtained a heritability estimate of 0.09 for 305-d milk yield in a crossbred dairy herd in Kenya (various percentages of Sahiwal, Brown Swiss, and Ayrshire genes).

**Variance Components, Autocorrelations, and Heritabilities of Daily Yield in Multiple Lactations**

The competency of a statistical genetic model may be measured by how effectively its effects explain the sources of variation contained in the data. The STE component was effective in partitioning important environmental effects in every data file, especially in multiple-lactation analyses. The magnitude of variance component estimates for the STE effects (Table 4) showed that practically all of the nongenetic variation that was due to cow was accounted by this effect. The TD records were consistently highly correlated within lactations ( $\geq 0.72$ ) in all data files.

Persistent environmental effects did not have major impact on the milking performance of Holstein cows in this study. Therefore, the small residual LTE contribution [and small correlation ( $\leq 0.04$ ) between lactations] resulted from an STE effect already accounting for nearly all of the environmental variation.

TABLE 4. Estimates of variance components (kilograms per day)<sup>2</sup> for animal ( $\hat{\sigma}_a^2$ ), long-term environment ( $\hat{\sigma}_p^2$ ), short-term temporary environment (STE,  $\hat{\sigma}_{ti}^2$ ), residual ( $\hat{\sigma}_e^2$ ), phenotype ( $\hat{\sigma}_{\text{PHENO}}^2$ ), heritabilities ( $\hat{h}^2$ ), and autocorrelations ( $\hat{\rho}_p$  and  $\hat{\rho}_{ti}$ ) using test day animal models either including or ignoring a first-order autoregressive process for short-term environmental (STE) effects on daily milk yield in multiple lactations (L<sub>i</sub>) from a herd of Lucerna cows and from each of the Holstein standard deviation (SD) classes.

Parameter estimate	Holstein within-herd SD class <sup>1</sup>							
	Lucerna		Low		Medium		High	
	Include <sup>2</sup>	Ignore <sup>3</sup>	Include	Ignore	Include	Ignore	Include	Ignore
$\hat{\sigma}_a^2$	0.62	0.68	11.37	6.51	12.33	6.00	14.73	8.61
$\hat{\sigma}_p^2$	0.40	1.82	<0.00	16.40	<0.00	20.94	<0.00	20.72
$\hat{\rho}_p$	1.00	0.33	0.01	0.36	0.02	0.40	0.04	0.47
$\hat{\sigma}_{t1}^2$	2.78	...	14.72	...	18.49	...	12.82	...
$\hat{\rho}_{t1}$	0.80	...	0.78	...	0.80	...	0.82	...
$\hat{\sigma}_{t2}^2$	3.70	...	29.22	...	39.11	...	34.08	...
$\hat{\rho}_{t2}$	0.77	...	0.79	...	0.81	...	0.77	...
$\hat{\sigma}_{t3}^2$	4.48	...	39.40	...	48.71	...	52.15	...
$\hat{\rho}_{t3}$	0.74	...	0.78	...	0.80	...	0.72	...
$\hat{\sigma}_e^2$	1.09	2.89	5.36	17.08	4.96	19.41	7.39	24.42
$\hat{\sigma}_{\text{PHENO}}^2$ L <sub>1</sub>	4.88	5.39	31.45	39.99	35.77	46.35	34.94	53.75
$\hat{\sigma}_{\text{PHENO}}^2$ L <sub>2</sub>	5.81	...	45.94	...	56.40	...	56.20	...
$\hat{\sigma}_{\text{PHENO}}^2$ L <sub>3</sub>	6.59	...	56.12	...	65.99	...	74.27	...
$\hat{h}^2$ L <sub>1</sub>	0.13	0.13	0.36	0.16	0.34	0.13	0.42	0.16
$\hat{h}^2$ L <sub>2</sub>	0.11	...	0.25	...	0.22	...	0.26	...
$\hat{h}^2$ L <sub>3</sub>	0.09	...	0.20	...	0.19	...	0.20	...
-2log(£)	62,220.94	66,632.59	128,261.98	134,200.15	188,385.44	199,670.76	263,891.20	277,509.79

<sup>1</sup>Three herds per SD class: low = <1644 kg of phenotypic SD for 305-d mature equivalent (ME) milk yield, medium = 1783 to 1898 kg of phenotypic SD for 305-d ME milk yield, and high = >2022 kg of phenotypic SD for 305-d ME milk yield.

<sup>2</sup>Model including the STE effect.

<sup>3</sup>Model ignoring the STE effect.

These STE effects occurred during the major (i.e., lactating) portion of the productive lifetime of the cow, which afforded relatively smaller impacts from events during juvenile growth and dry periods. The estimates of the LTE autocorrelation coefficient for the reduced model, which ignored STE effects, were not only substantially smaller (0.36 to 0.47) than the estimates for within-lactation correlations in the multiple-lactation analyses (0.72 to 0.82), but also were smaller than within-lactation correlations for a single lactation. In the reduced model correlations between TD records, the data within and between lactations were consolidated in the LTE component; the LTE autocorrelation coefficient was only moderately detectable. This pattern of correlations may be evidence that different factors influence TD variation within (i.e., STE) and between (i.e., LTE) lactations, which implies the need to account separately for STE and LTE.

Chronic environmental constraints may explain the (auto)correlation between lactations of Lucerna cows, which were uncorrelated in US cows (Table 4). A relatively greater contribution from LTE in the tropical setting was associated with near equal lactation curves for cows in all parities. These outcomes may have arisen from persistently less environmental opportunity (e.g., low nutrient intake relative to lactation requirements) and the associated observation errors.

Estimates of genetic variance from multiple lactations were about the same for Lucerna cattle and were larger for Holsteins relative to estimates from the reduced model; this pattern differed from the analysis of first lactations only. This result was yet further evidence that the autoregressive (co)variance structure for STE was highly effective in removing otherwise confounded variation from the genetic component. In addition to larger genetic variances (Holstein only), residual variances were reduced substantially when the STE effects were removed. Residual variances of the Lucerna and the low, medium, and high standard deviation classes of Holsteins were 62, 69, 74, and 70% smaller, respectively, than the variances with the reduced model.

Estimates of the phenotypic variance for each lactation were used to compute corresponding heritabilities. Heritabilities decreased as parity increased because of larger environmental variances in later lactations; these estimates ranged from 0.13 to 0.09 for Lucerna cattle and from 0.42 in first lactation of the high within-herd standard deviation class to 0.19 in third lactation of the medium standard deviation class for the Holstein herds. This pattern and range

in heritability estimates agree with those reported in other studies (1, 6, 11, 18, 27, 29). The full model gave the largest estimates of heritability in every Holstein data file.

Estimates of genetic variance increased as the within-herd phenotypic variance increased. This relationship was especially informative for the Holstein standard deviation classes (with essentially the same genetic composition because of reliance on the same AI sire companies) in corroborating results from a TD animal model: genetic variance especially increases as phenotypic variation within herds increases and decreases as phenotypic variation decreases (8, 15, 19, 20, 27, 29, 33, 36). Therefore, evaluation methods that account for this heterogeneity of variance (or interaction between genotype and environment) are pertinent (8, 16, 20, 33). Furthermore, even if the purported 40% proportion of Holstein genes in Lucerna cattle were the same as the contemporary genes in these Holstein herds, a smaller genetic variation for milk yield should be expected in the tropical environment of the Lucerna cattle, which is more nutrient-limiting (25).

### Predicting Future Daily Milk Yield

Sometimes economic reasons dictate that cows with high expected producing ability (**EPA**) remain in the herd, regardless of genetic merit, because past lactation yields are repeatable in future performances. The EPA is the same as EBV except when genetic and environmental effects exist that are repeated from previous records.

The manner in which repeated environmental effects are partitioned in our full model for multiple lactations permits the prediction of TD yields within and between lactations. These EPA are linear combinations of the EBV of the cows and respective solutions from the STE and LTE vectors.

The covariances for TD records for an individual cow may be represented as

$$\text{cov}(y_{mli}, y_{mli'}) = a_{mm}\hat{\sigma}_a^2 + \hat{\sigma}_p^2 + \rho_{tl}^{(l'-1)}\hat{\sigma}_{tl}^2$$

within lactations ( $i' > i$ ), and

$$\text{cov}(y_{mli}, y_{ml'i}) = a_{mm}\hat{\sigma}_a^2 + \hat{\rho}_p^{(l'-1)}\hat{\sigma}_p^2$$

between lactations ( $l' > l$ ), where  $y_{mli}$  = TD record  $i$  of cow  $m$  in lactation  $l$ .

Estimates of the long-term environmental variance from multiple-lactation analyses for Holsteins were

TABLE 5. Rank correlations between genetic evaluations for daily milk yield from models either including or ignoring a first-order autoregressive process for short-term environmental (STE) effects in the first three lactations of Lucerna cows and Holstein cows in each of three within-herd standard deviation (SD) classes.

Breed	Rank correlation		
	Males	Females	All
Lucerna	0.98	0.98	0.98
Holstein <sup>1</sup>			
Low	0.95	0.94	0.94
Medium	0.95	0.91	0.92
High	0.94	0.93	0.94

<sup>1</sup>Three herds per SD class: low = <1644 kg of phenotypic standard deviation (SD) for 305-d mature equivalent (ME) milk yield, medium = 1783 to 1898 kg of phenotypic SD for 305-d ME milk yield, and high = >2022 kg of phenotypic SD for 305-d ME milk yield.

approximately zero for every standard deviation class. This consistent result implies that subsequent TD yields within a lactation depend only on the genetic and STE effects. Alternatively, TD yields in future lactations covary nearly entirely with the genetic component under the assumption that STE effects are independent between lactations. Consequently, repeatability—the proportion of phenotypic variance that is due to genetic causes and to consistent observation errors from environmental effects across lactations—was identical to the heritability of daily milk yield. Therefore, for Holsteins, the EBV from our TD animal model was the best predictor of daily milk yield in a subsequent lactation.

In contrast, estimates of the LTE variance component from the multiple-lactation model were relatively important for the lower yielding herd of Lucerna cattle. Contributions from environmental correlations between TD yields within and across lactations are needed for the accurate prediction of EPA of Lucerna cows.

Methods of utilizing TD yields to compute 305-d lactation records accumulate STE observation errors and LTE observation errors in a completely confounded manner; these errors can only be partitioned from the genetic component in a large between-lactation component. For production systems with high yielding cattle that require intensive input and that offer producers substantial control over LTE, it seems reasonable that most environmental influences causing correlations between TD records occur while cows are lactating (i.e., the STE effect). This scenario would leave little, if any, residual effect for future lactations, especially in systems with high yields. Consequently, a multiple-lactation TD model effectively provides greater heritability, greater genetic gain in milk, and redefined repeatabilities for

predicting daily yields in current and future lactations.

**Rank Correlations**

Rank correlations between EBV from multiple-lactation animal evaluations using either the full model or the reduced model are in Table 5. Changes in rank with correlations ranging from 0.91 to 0.99 were small (29), as expected, because fixed effects were identical. Consequently, rankings could only be affected by different partitioning of the environmental variance components.

Especially relevant were correlations between evaluations using either single-trait (first lactations only) or multiple-trait (multiple lactations) analysis. Correlations between these analyses disclosed major changes in animal rank (Table 6) from considering additional information on the same cows in an autoregressive process. The largest changes in rank were for Holstein females for which correlations across standard deviation groupings within a herd were 0.18 to 0.24. The rank correlation among Lucerna cows was 0.37, and only 3 Lucerna cows (each with 3 lactation records) were common to listings of the elite 10 females. A closer look at changes in rank between analyses showed that 40% of the 100 Lucerna cows with the highest EBV were primiparous cows. Therefore, multiple-lactation analysis did not favor pluriparous cows having more TD records. Changes in rank were principally from improved predictions from additional pedigree information from dams and sires. The same pattern occurred for Holstein groupings for which 33, 40, and 37% of primiparous cows were among the top 100 cows in the low, medium, and high classes of phenotypic standard deviation.

TABLE 6. Rank correlations between genetic evaluations for daily milk yield using an animal model with a first-order autoregressive process for short-term environmental (STE) effects in multiple lactations and first lactation analyses for Lucerna cows and Holstein cows in each of three within-herd standard deviation (SD) classes.

Breed	Rank correlation		
	Males	Females	All
Lucerna	0.73	0.37	0.38
Holstein <sup>1</sup>			
Low	0.89	0.20	0.26
Medium	0.88	0.24	0.30
High	0.87	0.18	0.23

<sup>1</sup>Three herds per SD class: low = <1644 kg of phenotypic standard deviation (SD) for 305-d mature equivalent (ME) milk yield, medium = 1783 to 1898 kg of phenotypic SD for 305-d ME milk yield, and high = >2022 kg of phenotypic SD for 305-d ME milk yield.

Sires also changed rank but less dramatically than did females; correlations ranged from 0.73 in Lucerna to 0.89 in Holstein cows (Table 6). Among the 10 top sires from each analysis, 7 sires were in common for Lucerna; and 8, 7, and 2 were in common for the low, medium, and high Holstein classes of phenotypic standard deviation, respectively.

The multiple-lactation TD animal model should be effective for genetic evaluation of dairy production systems in both tropical and temperate regions. The addition of more TD records per cow, more daughters per sire, and more pedigree information affects evaluations because EBV is estimated by regressing the adjusted phenotypic record toward the adjusted phenotypic mean of zero (34). This regression coefficient varies with the heritability and repeatability of daily milk yield and with the number of records tied by genetic relationships. The multiple-lactation analysis considered substantially more records from cows with TD in more than one lactation, which permitted adjustments for selection that precluded some cows from having further lactations. Consequently, the bias and sampling error of evaluations were decreased, and concomitant increases occurred in heritability and the accuracy of genetic evaluation.

### Accuracy of Predicting Breeding Values

The histograms in Figure 1 show the accuracies of EBV from evaluations of both multiple lactations and first lactation only for Lucerna and for Holsteins of low phenotypic standard deviation class. This pattern also occurred in the other standard deviation classes. A seemingly bimodal distribution appeared in every data file (Figure 1). Data for animals with the fewest observations and, therefore, lowest accuracies, clustered together around the lower mode. Data for animals with highest accuracies, representing the majority of animals in each data file, clustered around the higher mode. Also illustrated is the expected higher frequency of animals of both breeds with greater accuracies from the multiple-lactation analysis. Accuracies were greater for Holsteins than for Lucerna cattle because the genetic relationships of Holsteins had more ties.

### Genetic Trend in Milk Yield

The mean EBV by year of birth for the animals that were evaluated represent trends in realized genetic progress for the period of this study (1984 to 1992). Figure 2 presents a comparison of these trends

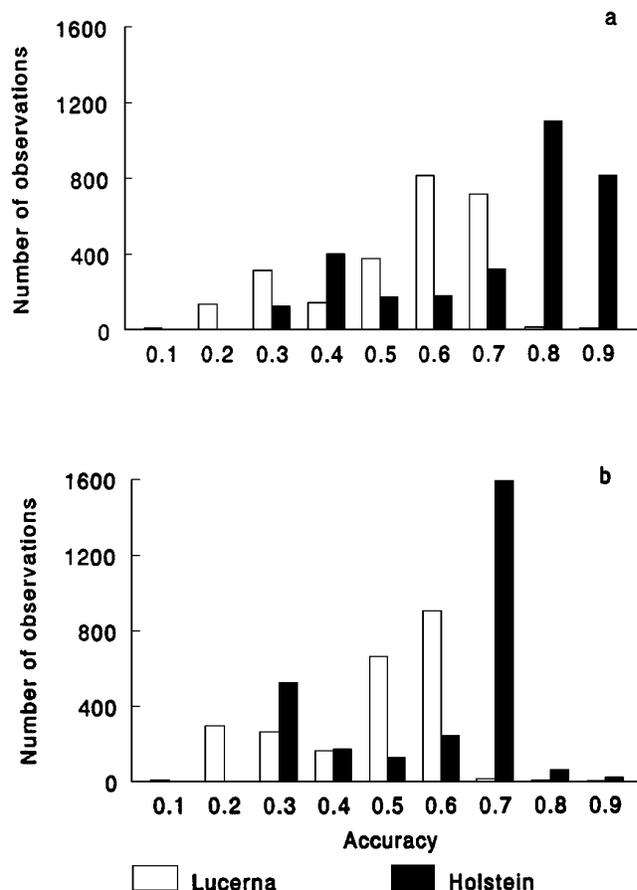


Figure 1. Histograms of the accuracies of EBV obtained from the evaluations for multiple lactations (a) and first lactation (b) evaluations for animals in the Lucerna herd and in the low phenotypic standard deviation Holstein class.

for the Lucerna herd (panel a) and for each of the three Holstein herds in the low phenotypic standard deviation class (panel b). The mean annual genetic trend for the Lucerna herd was nil, except for 1987 to 1989, when average genetic merit for daily milk yield increased by 0.7 kg. Our results indicate that the opportunity for genetic progress in small populations—where nutrients are limited and data are scarce, even for the above average Lucerna situation—is either less available or unavailable unless environmental components can be disentangled to obtain accurate EBV. This collaborative project with ASOLUCERNA yielded the methodology and baseline genetic analyses to enable genetic gains by finding more of the parents with highest EBV.

The genetic trends were heterogeneous among Holstein herds in the low standard deviation class (Figure 2b). Two herds sustained gains throughout the period of the study; one herd hardly advanced

EBV except in 1 yr (herd 1). Trends in genetic merit averaged nearly 1 kg in daily milk yield for this 8-yr period, which was also the outcome in the other within-herd standard deviation classes. The corresponding average annual genetic progress in milk yield was approximately 38 kg (1 kg/8 yr × 305 d in lactation/yr), which was ~16% less than in the literature (12, 32) for the northeastern US Holstein population. Van Tassel and Van Vleck (32) reported a potential annual genetic gain of 96 kg for Holsteins in the northeastern US. When their equations were updated with genetic variance estimates from the present study, the theoretical annual genetic gain for milk yield nearly doubled to 173, 180, and 197 kg/yr for the low, medium, and high standard deviation groups, respectively, which suggests advantages from also using a multiple-lactation TD model in US genetic evaluations.

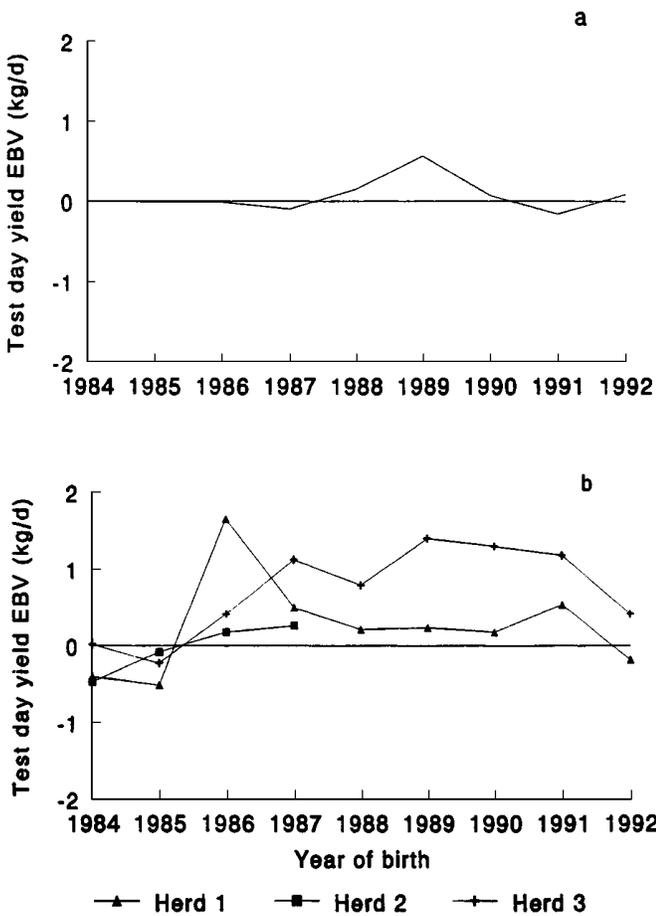


Figure 2. Genetic trends for the period 1984 to 1992 in the Lucerna herd (a) and for each Holstein herd (b) in the low phenotypic standard deviation class.

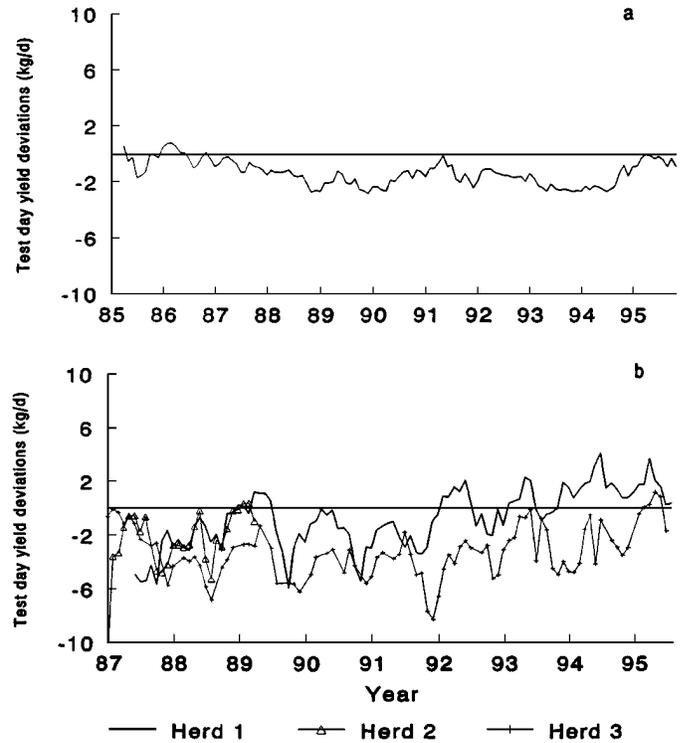


Figure 3. Management trends by test date from January 1985 to November 1995 in the Lucerna herd (a) and from January 1987 to November 1995 for each Holstein herd in the low phenotypic standard deviation class (b).

**Cow Age and Herd Management Effects**

The TD models also help to quantify herd management effects and individual cow productivity. The effects of age and lactation curve were estimated from the data from individual farms. Interactions between Holstein herd and age of cow at calving were not detected ( $P > 0.4$ ). Consequently, a common age at calving effect was fitted.

Figure 3a shows the management trend in the Lucerna herd from 1985 to 1995 and in each Holstein herd in the low phenotypic standard deviation class from 1987 to 1995 (Figure 3b). Within-year variation in average daily milk for Lucerna cows represents changes in production caused by seasonal differences and management, probably reflecting quality, availability and costs of feeds, and other economic factors. There was a long-term decline of ~2 kg in average daily milk yield from 1986 to 1994, followed by a quick recovery in the last year of this study. Overall, there was no net change in the average daily milk yield of Lucerna cows during this 10-yr period. This

lack of net gain from management illustrates the severity of constraints affecting the dual-purpose production systems in the tropics. To increase the milk yield per cow is a major challenge without access to economical resources to increase dietary energy density (26), which typically leads managers to seek profit margins by controlling input costs (25).

Conversely, the US Holstein herds had much greater fluctuations in daily milk yield across years, perhaps from dietary changes and seasonal variation. Herd differences were large (Figure 3b). The consistent rise in average daily milk yield in the winter months may have reflected a seasonal calving policy to take advantage of higher milk prices during this season. Overall, these herds showed a positive management trend of about 8 kg during the 8 yr studied.

The effects of TD were adjusted to a common age and stage of lactation so that fluctuations in adjusted TD milk yield are likely to be caused by feeding and other management effects. The management trend in daily milk yield monitors the efficacy of herd manage-

ment (12), which may help to evaluate promising interventions and to identify bottlenecks in productivity.

### Lactation Curves

The ability to predict future TD records depends on the accuracy of the modeled lactation curves [e.g., I. A. Papjcsik and B. Boderó, 1988, unpublished data; (7, 13, 30)]. Methods to estimate the parameters of the lactation curve have included functional forms such as density functions (e.g., Wood's equation), multiphasic logistic functions, and fourth- or fifth-order polynomial regressions. Lactation curves also can be estimated by obtaining the least squares solutions for TD milk yield on the fixed effect of DIM, which was the method used in this study.

Comparison of lactation curves is another tool for identifying limitations in nutrition and management programs. Figure 4 shows the lactation curves for each of the three parities for the Lucerna herd (Figure 4a), for primiparous Holstein cows in the herds constituting the low standard deviation class

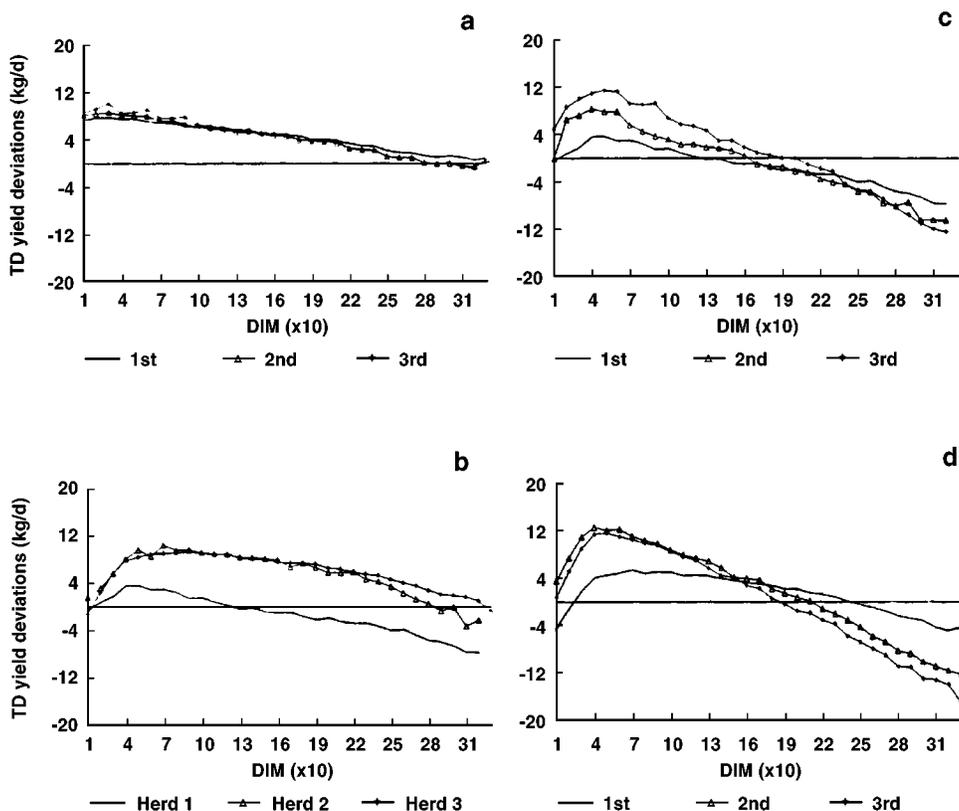


Figure 4. Lactation curves showing milk yield on test days (TD) for each of the three parities in the Lucerna herd (a), for primiparous Holstein cows in the herds constituting the low standard deviation class (b), for each of the three parities in one Holstein herd from the low standard deviation class (c), and for each of three parities in one Holstein herd from the high standard deviation class (d).

(Figure 4b), for each of the three parities in one Holstein herd from the low standard deviation class (Figure 4c), and for each of the three parities in one Holstein herd from the high standard deviation class (Figure 4d).

For Lucerna cows, the nearly identical lactation curves for different parities and a barely discernible early peak (between 30 and 40 d) probably signified a limited nutrient support of milk yield. Coupled with observations that Lucerna cows are chronically thin, these results suggest not only a severe constraint phenotypically (Figure 4a), which may have fostered the autocorrelation between lactations, but also a compression of genetic variance (Table 4).

The lower milk yield of primiparous Holstein cows in herd 1 (Figure 4b) may have reflected less attention to heifer management, which seemed associated with the subsequent large differential for milk yields between second and third lactations in this herd (Figure 4c). Lactation curves in one herd from the high phenotypic standard deviation class (Figure 4d) are typical except for the greater yield of second lactation cows than for older cows. Reasons for these anomalies may be due to differences in the management practices of each farm. This by-product of analysis of TD (i.e., lactation curves adjusted for STE effects) may be especially useful for managing lactation in dual-purpose cattle systems in the tropics.

### Optimizing Genetic Progress in the Lucerna Herd

The effectiveness of a breeding program is measured by genetic achievement in the target population (22), which requires reliable records for genetic analysis. The TD records for Lucerna cattle provide the prerequisite conditions for an effective breeding program. Nevertheless, results from this investigation revealed the need for a proper analytical model to avoid confounding important environmental effects with the genetic component, especially in production settings that restrict genetic expression. For the Lucerna herd, a multiple-lactation TD animal model should be used that considers all TD records, including partial lactation records of cows that were sold or culled, to generate the most accurate EBV.

An appropriate selection goal for dual-purpose cattle might be to maximize net economic returns from increased average daily milk yield per generation without simultaneously decreasing the beef output per cow on a lifetime basis. However, the selection alternatives we considered are only for potential genetic gains in average daily milk yield because of

limitations on available information for this study and the emphasis on milk yield for Lucerna cattle. The herd composition (animals available for the selection process) assumed for this study was based on actual numbers of cattle that are kept on the two ASOLUCERNA farms recording data. Because AI is available, male pathways were unrestricted. For females, a 30% rate of annual substitution (cullings) was assumed for an annual calving rate of 80% (50% female births) and a 90% survival rate from birth to first calving. Consequently, the Lucerna population was assumed to comprise 50 males and 700 females.

To maintain the male population, 97 cows are needed for the dam of sires pathway ( $97 \times 0.5 \times 0.8 \times 0.9$ ), which corresponds to ~14% of the female population. With a substitution rate of 30%, then 210 females need to be born per year; this number already accounts for rates of calving and survival and implies the need for 583 cows (or ~83% of the female population) for the dam of dams path. The selected fraction of males either for the sire of sires path (~10%) or the sire of dams path (~70%), followed the typical recommendation of 1 bull per 20 cows to make available a larger pool of sires to restrict inbreeding. Although current inbreeding is unknown, in closed populations such as Lucerna cattle, care must be taken to avoid detrimental effects from inbreeding, especially in fitness traits.

Table 7 shows the input values corresponding to the genetic gain equations for two, three, and four paths of selection. The assumed generation intervals were based on previous reports (32, 34); an arbitrary inflation was 10% to account partially for later maturity in tropical cattle that were reared on less nutrient-dense diets compared with maturity of cattle in temperate environments. The mean age at first calving was 38 mo for Lucerna cows and 28 mo for Holsteins. The genetic gain for each selection alternative and corresponding theoretical maxima for expected annual gains also are in Table 7. As expected, annual gain is greater when all genetic pathways are utilized. A genetic gain in milk of 34 kg/yr is potentially achievable for Lucerna, which is only 11% less than that obtained by the US Holstein herds in this study.

The usual approach to maximizing genetic gain is to calculate the expected genetic gain for different combinations of records and fractions of animals selected, which influence each other and the generation interval, and then choosing the combination yielding greatest genetic gain (34). More paths of selection, however, imply greater expense (economically and organizationally) in executing a breeding

TABLE 7. Population fractions for selected animals, selection intensities, average prediction accuracies for the estimated breeding values, generation intervals, genetic standard deviation ( $\hat{\sigma}_a$ ), genetic superiority due to the selected path ( $\Delta$ ) and comparative daily and yearly genetic gain in milk ( $\Delta g$ ) obtained by exploiting two, three, or four paths of selection for the Lucerna population.

	Two paths		Three paths			Four paths			
	DS	DD	SD	DS	DD	SS	SD	DS	DD
Fraction selected	0.14	0.83	0.70	0.14	0.83	0.10	0.70	0.14	0.83
Selection intensity	1.51	0.30	0.80	1.51	0.30	1.92	0.80	1.51	0.30
Accuracy of prediction	0.69	0.65	0.72	0.69	0.65	0.76	0.72	0.69	0.65
Generation interval, yr	6.00	7.50	5.00	6.00	7.50	5.00	5.00	6.00	7.50
$\hat{\sigma}_a$ , kg	0.79	0.79	0.79	0.79	0.79	0.79	0.79	0.79	0.79
$\Delta$ , kg/d	0.83	0.16	0.45	0.83	0.16	1.15	0.45	0.83	0.16
$\Delta g$ , kg/d		0.073			0.078				0.110
$\Delta g$ , kg/yr		22			24				34

program. The optimal genetic program for the Lucerna breed (two, three, or four paths of selection), therefore, is the one that maximizes net economic returns to the cost of implementing breedings and storing and analyzing data in a timely manner to inform those persons making selection decisions. Differences in genetic gain from ignoring certain pathways permit the computation of the corresponding opportunity losses in genetic gain.

### CONCLUSIONS

The TD animal models offer the opportunity to improve the genetic evaluation of dairy cattle in tropical and temperate production situations. An obvious advantage is the large increase in information from more records and the ability to account for temporal effects of herd management, which reduces residual variance components, thus increasing estimated heritability and the accuracy of predicting EBV.

The first-order autoregressive structure for residual effects of TD records within a lactation greatly reduced the model error component by better disentangling the random STE effects. The multiple-lactation TD model resulted in the largest estimates of genetic variance and heritability and gave the most accurate estimates of individual genetic merit for daily milk yield by admitting more information and heterogeneous environmental variances between lactations. These findings were confirmed by biological evidence in a wide range of herd environments for which the full model was superior to other approaches relying on a LTE effect but ignoring STE effects. Although these properties of the multiple-lactation TD animal model enhance the value of information from any data base, they are especially important for limited-size data files from production systems in the tropics that are constrained in environment and

resources. Validation of the model would require either an analysis of data subsets in different time frames or, preferably, a comparison of genetic predictions of sires with independent samples of daughters and herds.

The present study showed that substantial genetic progress in milk yield is indeed achievable in small populations that are managed in environments with limited resources (e.g., the nucleus population of two Lucerna herds that we considered) using an animal model that autoregressively accounts for STE and LTE effects. Unbiased estimates and, therefore, genetic gain for dual-purpose cattle systems in tropical settings with few data is likely to be small (or nil) unless TD yields are adjusted for the autoregressive STE structure influencing daily milk production. Autoregressive structures also may be valuable in analyzing other time-dependent livestock traits (e.g., growth, measures associated with disease, and parasite resistance), which may merit further investigation.

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