Genetic parameters for test-day milk yield, lactation persistency, and fertility in low-, medium-, and high-production systems in Kenya

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ABSTRACT

Genetic parameters for test-day milk yield, lactation persistency, and age at first calving (as a fertility trait) were estimated for the first 4 lactations in multiple-breed dairy cows in low-, medium-, and high-production systems in Kenya. Data included 223,285 test-day milk yield records from 11,450 cows calving from 1990 to 2015 in 148 herds. A multivariate random regression model was used to estimate variance and covariance components. The fixed effects in the model included herd, year, and test month, and age as a covariate. The lactation profile over days in milk (DIM) was fitted as a cubic smoothing spline. Random effects included herd, year, and test month interaction effects, genetic group effects, and additive genetic and permanent environmental effects modeled with a cubic Legendre polynomial function. The residual variance was heterogeneous with 11 classes. Consequently, the variance components were varied over the lactation and with the production system. The estimated heritability for milk yield was lower in the low-production system (0.04–0.48) than in the medium- (0.22–0.59) and high-production (0.21–0 60) systems. The genetic correlations estimated between different DIM within lactations decreased as the time interval increased, becoming negative between the ends of the lactations in the low- and medium-production systems. Low (0.05) to medium (0.60) genetic correlations were estimated among first lactation test-day milk yields across the 3 production systems. Genetic correlations between the first lactation test-day milk yield and age at first calving ranged from 0.27 to 0.49, 0 to 0.81, and −0.08 to 0.27 in the low-, medium-, and high-production systems, respectively. Medium to high heritabilities (0.17–0.44) were estimated for persistency, with moderate to high (0.30–0.87) genetic correlations between 305-d milk yield and persistency. This indicates that genetic improvement in persistency would lead to increased milk yield. The low to medium genetic correlations between test-day milk yield between production systems indicate that sires may be re-ranked between production systems. Therefore, we conclude that sires should be selected based on a genetic evaluation within the target production system.

Key words: genetic parameters, test-day milk yield, age at first calving, production systems

INTRODUCTION

Modeling the systematic environmental and genetic effects along the lactation trajectory using test-day milk yield records has been widely used for dairy cattle genetic evaluation, because it provides higher accuracy than genetic evaluation based only on total lactation yield or 305-d milk yield. Additionally, the estimated variance or covariance components can be used to derive variance components and genetic parameters for 305-d milk yield without the need to extend the milk yield (Ptak and Schaeffer, 1993). Furthermore, genetic parameters for the shape of the lactation curve can be used to estimate lactation persistency; that is, the ability of a cow to continue producing milk at a high level after the lactation peak (Gengler, 1996; Dekkers et al., 1998). Higher persistency is typically associated with a lower peak production in early lactation, resulting in reduced physiological strain due to high daily milk yield, and risk of reproductive and metabolic disorders (Sölkner and Fuchs, 1987).

Random regression models are commonly applied to account for environmental effects and to model variation in the lactation curve (Schaeffer et al., 2000). Legendre polynomials, in particular, have been widely applied using higher-order polynomials. These high-order polynomials, however, frequently result in erratic and implausible estimates of variance components (genetic parameters) and are influenced by the number and dis-

tribution of observations (Meyer, 2005). Spline models are an alternative to high-order polynomial models (Meyer, 2005). The application of spline models for the analysis of test-day records in dairy cows was initially presented by White et al. (1999). They applied a cubic spline model and demonstrated its flexibility and ability to model the lactation curve better than by using polynomial regression.

A dairy performance recording scheme using test-day milk yield has been implemented by the Dairy Recording Services of Kenya in Naivasha. The participating herds represent quite diverse production environments and have been grouped into low-, medium-, and high-production systems based on their level of production (Wahinya et al., 2020). Holstein-Friesian and Ayrshire are the dominant breeds, with crosses making up 50% of the total herd (Muriuki, 2011). Other breeds include Guernsey, Jersey, Sahiwal, Brown Swiss, and their crosses (Bebe et al., 2003). Genetic improvement in this population is currently implemented using males and females selected in the high-production system, based on 305-d milk yield (Kahi and Nitter, 2004; Wasike et al., 2014). This is likely to result in an inefficient genetic evaluation in the presence of heterogeneity of variance and genotype × environment interaction (Meuwissen and van der Werf, 1993).

The profitability of dairy enterprises is heavily dependent on milk yield and fertility. Among the fertility traits, age at first calving, in particular, influences the heifer rearing cost, the productive life of a cow, and the replacement policy, and, thereby, the productivity of a herd (Kahi and Nitter, 2004). Understanding the nature of the genetic association between age at first calving and test-day milk yield in different production systems could be used as a management tool to optimize the genetic improvement of milk yield and reproductive efficiency.

Unbiased genetic parameters are important for the development of any genetic improvement program. Several studies have estimated genetic parameters for test-day milk yield in Sahiwal and Holstein-Friesian populations in Kenya using Legendre polynomials (Ilatsia et al., 2007; Muasya et al., 2014b). Lactation curve parameters, however, have not been previously evaluated for different production systems in Kenya and are needed to facilitate optimum utilization of the production systems. Moderate genetic correlations between lactation yields suggest that milk yield is controlled by different genes in later lactations (Powell et al., 1981; Ilatsia et al., 2007; Meseret and Negussie, 2017). Therefore, in a multitrait analysis, repeat lactations should be treated as different but correlated traits. Multivariate genetic evaluation models, using information from multiple lactations, would also increase the accuracy

of genetic evaluation and, therefore, the efficiency of selection (Beaumont, 1989).

This study estimated the genetic variance components of milk yield and lactation persistency over the first 4 lactations using test-day milk yield records from multi-breed cows under 3 production systems in Kenya. It also examined the genetic association of milk yield with age at first calving.

MATERIALS AND METHODS

Data

A total of 337,465 test-day milk yield records, collected between 1990 and 2015 from multi-breed cows reared under diverse production environments in Kenya, were obtained from the Livestock Recording Centre in Kenya in Naivasha. The test-day milk yield records were the sum of milk yields recorded in the morning and evening. Test-day yields greater than 0.5 kg per day, within 4 standard deviations of the mean for each test-day, and recorded from d 5 to 305 after parturition, were used in this study. Records from cows with both parents unknown or with an age at first calving earlier than 640 d were deleted. Contemporary groups with fewer than 3 cows were not considered in this analysis. The final data set consisted of 223,285 records from 11,450 cows, representing 148 herds. The cows were descendants of 1,934 sires and 7,634 dams. The pedigree extended over 4 generations, and 78% of the cows in the data set had both parents identified.

Herds were classified into low-, medium-, and high-production systems based on their mean 305-d milk yield (Wahinya et al., 2020). Herd effects were predicted for 305-d milk yield in a linear mixed model, with calving year, parity, and breed group as fixed effects and herd and residual as random effects.

Statistical Analysis

Data were analyzed with a random regression test-day model within each production system, considering the 4 lactations' milk yields as separate traits. The mean lactation curve was modeled using a cubic spline function with 12 knots at 5, 15, 30, 60, 90, 120, 150, 180, 210, 240, 270, and 305 d of the lactation. This spline is fitted as a fixed slope, and 10 random covariates were calculated from DIM t_{jk} and fitted as described by White et al. (1999). The additive genetic and permanent environment effects were fitted using covariance functions with third-order orthogonal Legendre polynomials. The third-order orthogonal Legendre polynomial was selected based on the log-likelihood of models with varying degrees using the Bayesian information criteri-

on. Contemporary group was fitted as the combination of herd, test year, and month (**HYM**) fitted as fixed main effects and their 3-way interaction as a random effect. Genetic group was fitted as a random effect and age at calving in days as a covariate. Residual variance was assumed to be heterogeneous across 11 classes of 5 to 15, 16 to 30, 31 to 60, 61 to 90, 91 to 120, 121 to 150, 151 to 180, 181 to 210, 211 to 240, 241 to 270, and 271 to 305 d in milk. The model was fitted in ASReml software (Gilmour et al., 2015) as follows:

$$y_{jk} = \mu + H + Y + M + GG + Age + \beta t_{jk} + z_l(t_{jk})$$
$$+ HYM + \alpha_{km}\varphi_m(t_j) + p_{km}\varphi_{nm}(t_j) + e_{jk},$$

where y_{jk} is the test-day milk yield sampled on animal k at t_{jk} DIM; μ is the intercept; H, Y, and M are the herd, year, and month of each test-day milk recording, respectively, fitted as a fixed effect; GG is the genetic group the animal represents, fitted as random; Age is the age at calving fitted as a linear and quadratic covariate; βt_{jk} is the fixed linear component of the spline; $z_l(t_{jk})$ denotes the random curvature component of the cubic spline; HYM is a random interaction term between herd, test year, and month; α_{km} and p_{km} are the regression coefficients for the covariance functions based on DIM for the additive and permanent environmental random effects of each cow k, respectively; $\varphi_m(t_j)$ is the covariate of the regression function of mth Legendre polynomial order for the DIM; and e_{jk} is the residual term. We defined 74 genetic groups separately for sires and dams, based on year of birth (before 1986, between 1986 and 1990, 1991 to 1995, 1996 to 2000, 2001 to 2005, and after 2005) and breeds (Friesian, Ayrshire, Guernsey, Jersey, Sahiwal, Brown Swiss, and unknown breeds) using the Westell-Quaas method (Westell et al., 1988). In matrix notation, the model can be expressed thus:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_G}g + \mathbf{Z_S}s + \mathbf{Z_C}c + \mathbf{Z_A}a + \mathbf{Z_U}u + e,$$

where **y** is a vector of test-day milk yield; **b** is a vector of fixed effects for herd, year, and month, covariate for age at calving and fixed regression of DIM; **g** is a vector of random genetic group effects; **s** is a vector of 10 cubic spline coefficients; **c** is a vector of random (herd × year × month) contemporary group effects; a is $m_1 + 1$ additive genetic regression coefficients for each animal in the pedigree; u is $m_2 + 1$ permanent environmental regression coefficients for each animal with data; and e contains the temporary environmental effects. **X**, $\mathbf{Z_S}$, $\mathbf{Z_C}$, $\mathbf{Z_A}$, and $\mathbf{Z_U}$ are design matrices associating observations with fixed effects, cubic spline, contemporary groups, animal, and permanent environmental random

effects, respectively. $\mathbf{Z_G}$ is the matrix of genetic group proportions for all animals in the pedigree, calculated as described above, and m_1 and m_2 are the order of polynomials for additive and permanent environmental effects, respectively. It is assumed that

$$\text{var}\begin{pmatrix} g \\ s \\ c \\ a \\ u \\ e \end{pmatrix} = \begin{pmatrix} \mathbf{I} \otimes \sigma_g^2 & 0 & 0 & 0 & 0 & 0 \\ 0 & \mathbf{I} \otimes \sigma_s^2 & 0 & 0 & 0 & 0 \\ 0 & 0 & \mathbf{I} \otimes \sigma_c^2 & 0 & 0 & 0 \\ 0 & 0 & 0 & \mathbf{A} \otimes \mathbf{G} & 0 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{I} \otimes \mathbf{U} & 0 \\ 0 & 0 & 0 & 0 & 0 & \mathbf{R} \end{pmatrix},$$

where **I** is an identity matrix, σ_g^2 is the genetic group's variance, σ_s^2 is the variance component for the cubic spline, σ_c^2 is the herd, test year, and month contemporary group variance, **G** is the variance-covariance matrix of the additive genetic random regression coefficients of order $m_1 + 1$, **U** is the variance-covariance matrix of the permanent environmental random regression coefficients of order $m_2 + 1$; and **R** is a matrix of temporary environmental variances for the 11 residual classes previously described. Genetic variance for different test-days along the lactation trajectory was calculated from **G** as $\sigma_{aii}^2 = t_i \mathbf{G} t_i'$, and genetic covariance as $\text{Cov}_{aij} = t_i \mathbf{G} t_j'$, where $t_i = \varnothing_i$ is the ith row vector of a matrix with Legendre polynomials, the row pertaining to the particular test-day.

Age at first calving was modeled using a univariate animal model fitting herd, birth year, and season as fixed effects and their interaction as a random effect. Heritability was estimated as a ratio of additive variance to phenotypic variance. Multivariate random regression models were used to estimate the variance-covariance components for test-day milk yield within and between the first 4 lactations under the 3 production systems. Bivariate random regression models were used to estimate the genetic correlations between the first lactation test-day milk yield between the production systems and between test-day milk yield and age at first calving within the production systems.

Genetic correlations (r_{ij}) were estimated as

$$r_{ij} = \frac{\text{Cov}_{aij}}{\sqrt{\sigma_{aii}^2 + \sigma_{ajj}^2}},$$

where σ_{aii}^2 and σ_{ajj}^2 are the genetic variances for the ith and jth test day.

Heritability, additive $\left(V_{a_{305}}\right)$, and permanent environment variances $\left(V_{pe_{305}}\right)$ for 305-d milk yield were obtained as follows:

$$V_{a_{305}} = \mathbf{t}_{305}\mathbf{G}\mathbf{t}'_{305} \text{ and } V_{pe_{305}} = \mathbf{t}_{305}\mathbf{P}\mathbf{t}'_{305}$$

$$\text{with } \mathbf{t}_{305} = \sum_{i=5}^{305}\sum_{j=0}^{3}\varnothing_{ij},$$

where $\mathbf{t}_{305}$ is a row vector of order q, with the jth elements equal to the sum of the jth orthogonal polynomial from d 5 to 305, and $\mathbf{G}$ and $\mathbf{P}$ are the variance-covariance matrices of additive genetic and permanent environment random regression coefficients of order $m_1 + 1$. Heterogeneous residual variance was obtained by summing residual variance estimates from d 5 to 305 along the lactation. Genetic parameter estimates for lactation persistency were estimated using the method developed by Jakobsen et al. (2002) and recommended by Cobuci and Costa (2012), Jakobsen et al. (2002), Khorshidie et al. (2012), and Padilha et al. (2019). The additive and permanent environmental variance components (V_{per}) for lactation persistency were estimated thus:

$$V_{per} = \sum_{dim=60}^{279}\left(V_{dim} - V_{280}\right),$$

where dim is days in milk, and V_{dim} and V_{280} are the estimated additive or permanent environmental variance on a particular DIM between d 60 and 280, respectively. Pearson correlations between 305-d milk yield and lactation persistency in different lactations were calculated in R software (R Foundation for Statistical Computing, Vienna, Austria). The heritability for 305-d milk yield $\left(h_{305}^2\right)$ and persistency $\left(h_{per}^2\right)$ were estimated as

$$h_{305}^2 = \frac{V_{a_{305}}}{\left(V_{a_{305}} + V_{pe_{305}} + \hat{V}_e \times k_i\right)}$$

and

$$h_{per}^2 = \frac{V_{a_{per}}}{\left(V_{a_{per}} + V_{pe_{per}} + \hat{V}_e \times k_j\right)},$$

where $\hat{V}_e$ is the average residual variance of the heterogeneous residual variance estimated from d 5 to 305 for

305-d milk yield and d 60 to 280 for persistency and k_i and k_j are constants 90,601 and 48,841, respectively, derived using the number of days over which the variances are summed 301 and 221 (Prakash et al., 2017).

RESULTS

Data Structure

Table 1 shows the breed proportions of the cows under the low-, medium-, and high-production systems. The dominant breeds in the low-production system were Friesian (32%), Ayrshire (15%), Guernsey (10%), and Sahiwal (6%), with 36% unknown. The dominant breeds in the medium-production system were Jersey (30%), Friesian (25%), and Ayrshire (24%), with 20% unknown. Most of these cows were crossbred. Finally, 78% of the cows in the high-production system had a Friesian breed component, and 21% had unknown breed composition.

Table 2 presents the number of records, herds, animals, sire, dam, and average test-day milk yield for the first 4 lactations under low-, medium-, and high-production systems. The high-production systems had the greatest numbers of records, cows, and herd sizes. Based on the clustering method, average test-day milk yield increased with the intensity of production, whereas age at first calving decreased with the intensity of production. The number of common sires between low–medium, low–high, medium–high, and all the production systems were 97, 84, 107, and 40, respectively (Table 3). These sires had from 133 to 686 progeny, with 1,214 to 6,466 records. The average number of progeny per sire ranged from 3 to 10 across production systems, with a minimum of 1 and a maximum of 44 progenies.

Lactation Curves

Lactation curves in the low-, medium-, and high-production systems are shown in Figure 1. The aver-

Table 1. Mean breed composition for the cows with test-day milk yield records under the low-, medium-, and high-production systems

| Breed | Breed proportion | | |
	Low	Medium	High
Ayrshire	14.61	23.81	0.74
Friesian	32.23	25.38	77.57
Guernsey	10.06	0.23	0.08
Jersey	1.35	30.49	0.04
Sahiwal	6.01	0.03	0
Brown Swiss	0.03	0.03	0.09
Unknown	35.71	20.03	21.48

Table 2. Numbers of records, herds, cows, sires, dams, average test-day milk yield, and age at calving (SD) for 4 lactations in low-, medium-, and high-production systems

Lactation	System	Records	Herds	Cows	Sires	Dams	Milk, kg	Age, d
1	Low	9,734	46	1,029	383	911	8.13 (3.63)	1,113 (277)
	Medium	17,076	42	1,640	440	1,265	12.63 (4.79)	990 (229)
	High	23,770	35	2,484	626	1,578	16.89 (5.76)	909 (139)
2	Low	11,340	42	1,189	412	982	8.96 (4.08)	1,516 (402)
	Medium	16,143	38	1,551	443	1,209	12.92 (5.20)	1,368 (279)
	High	23,745	32	2,460	616	1,469	19.00 (7.26)	1,314 (219)
3	Low	11,134	42	1,179	406	967	9.29 (4.50)	1,920 (460)
	Medium	13,926	38	1,362	428	1,060	13.70 (5.53)	1,806 (346)
	High	17,232	27	1,807	520	1,070	20.13 (7.81)	1,737 (264)
4	Low	8,841	34	952	368	773	9.22 (4.75)	2,317 (491)
	Medium	11,063	29	1,085	358	869	14.00 (5.46)	2,246 (391)
	High	12,493	24	1,300	429	751	20.18 (8.04)	2,135 (291)

age milk yield under the high system was twice that of the low system. The medium- and high-production systems curves show a peak at 21 to 73 d after calving, which was not evident under the low system. Milk yield tended to be higher in later lactations.

Variance Components and Genetic Parameters

Figures 2 and 3 show the variance components for different DIM of the first 4 lactations under the 3 production systems. Variance components varied between production systems. Additive, permanent environment, and residual variances increased with the level of production. Within the production systems, variance components did not differ between lactations, except in the high-production system, where the additive genetic and permanent environment variances in the first lactation were considerably lower than in the other lactations. In the low-production system, the additive variance was highest at the beginning of the lactation and then decreased gradually until the end of the lactation. In the medium-production systems, higher additive variances were observed around the peak or at the ends of the lactation curve. The highest additive variance in the

high-production system was estimated around the peak of milk yield. Additive variance in the high-production system increased from the first to the third lactation and decreased in the fourth lactation. However, in the low- and medium-production systems, no clear trend was observed over the lactations.

Permanent environmental variances increased with the level of production (Figure 3). In the low-production system, the variances were uniform within and between the lactations. In the medium-production system, the variance gradually increased as the lactation progressed. Higher permanent environmental variance was estimated at the extremes of the lactations in the high-production system. The first lactation had the lowest permanent environmental variance in all production systems. The third and fourth lactations had higher permanent environmental variances in all 3 production systems.

Table 4 shows the HYM and genetic group variance components for the first 4 lactations under the 3 production systems. The HYM variances estimated under the high-production system (1.75–2.01) were approximately double those estimated under the low- (0.80–1.06) and medium-production (0.80–1.01) systems. The

Table 3. Number of common sires between low-, medium-, and high-production systems, their progeny, records, and average numbers of progeny per common sire (with minimum and maximum number of progeny in parentheses) within production systems

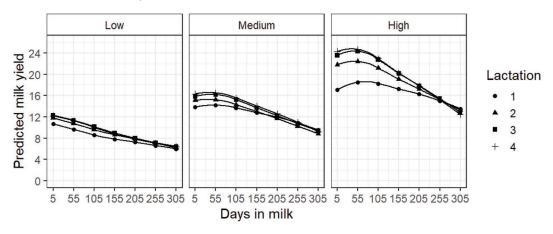| System[1]	Sires	Progeny			Records			Average no. of progeny per sire (minimum–maximum)		
		L	M	H	L	M	H	L	M	H
L-M	97	319	597	—	2,976	5,946	—	3.3 (1–17)	6.1 (1–46)	—
L-H	84	239	—	612	2,174	—	5,762	2.9 (1–12)	—	7.3 (1–44)
M-H	107	—	444	686	—	4,288	6,466	—	4.2 (1–31)	6.4 (1–44)
L-M-H	40	133	235	419	1,214	2,271	3,896	3.3 (1–12)	5.9 (1–29)	10.4 (1–44)

[1]L = low; M = medium; H = high.

Figure 1. Lactation curves for different lactations in low-, medium-, and high-production systems.

genetic group variances ranged between 1.62 to 9.49, 1.75 to 3.91, and 1.40 to 2.40 under the low-, medium-, and high-production systems, respectively.

Figure 4 shows the change in the estimated heritabilities for DIM in the first 4 lactations under low-, medium-, and high-production systems. The heritability estimated for test-day milk yield varied between 0.08 and 0.60 along the lactations in the 3 production systems. Heritability estimates varied within lactations, between lactations, and between production systems. Higher heritabilities were estimated around the peak of milk production in the medium- and high-production systems. Under the low-production systems, heritability estimates at the beginning and end of the lactations were erratic. Compared with the other lactations, the first lactation had higher heritabilities, especially toward the end of the lactation, in all 3 production systems. The fourth lactation, on the other hand, had lower heritabilities, except under the low-production

system. The standard errors for the heritability estimates ranged from 0.04 to 0.08, 0.03 to 0.06, and 0.02 to 0.04 for the low-, medium-, and high-production systems, respectively. Although the results are not shown here, test-day milk yield in these data was highly repeatable, with repeatabilities ranging from 0.65 to 0.90 in the 3 production systems.

Table 5 shows the variance components for 305-d milk yield and persistency for the first 4 lactations in low-, medium-, and high-production systems. Variance components for 305-d milk yield and persistency varied between production systems and lactations. The additive, permanent environment, residual, and phenotypic variances increased with the level of production. Low to high heritabilities were estimated for 305-d milk yield (0.18–0.52) and medium to high for lactation persistency (0.17–0.44). The heritability for persistency decreased from the first lactation under the low-production system. Under medium- and high-production
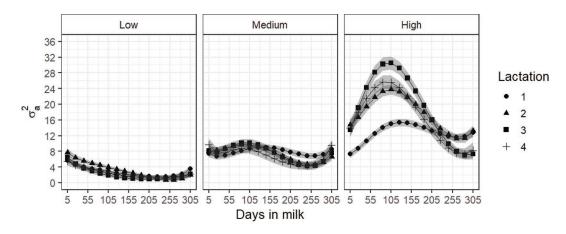

Figure 2. Additive genetic variances $\left(\sigma_a^2\right)$ with SE (gray bands) for test-day milk yield in 4 lactations under low-, medium-, and high-production systems.

Table 4. Variance components for herd, year, and month interactions and genetic group effects in 4 lactations under the low-, medium-, and high-production systems

Lactation	HYM[1]			Genetic group		
	Low	Medium	High	Low	Medium	High
1	0.80	0.80	1.75	1.62	3.91	1.40
2	0.92	0.82	1.89	2.10	1.75	2.40
3	1.06	0.90	1.99	4.88	1.91	1.22
4	1.02	1.01	2.01	9.49	3.25	1.83

[1]HYM = herd, year, and month of calving interaction effect.

systems, the heritability increased from the first to the fourth lactation. Both 305-d milk yield (0.65–0.77) and persistency (0.54–0.69) were highly repeatable. Genetic correlations between 305-d milk yield and persistency ranged between 0.38 to 0.55 under the low-production system and 0.32 to 0.60 and 0.30 to 0.87 under the medium- and high-production systems, respectively.

Table 6 shows the additive and phenotypic variances for age at first calving under low-, medium-, and high-production systems. The additive and phenotypic variances decreased with the level of milk production. Heritability for age at first calving in the low-production system (0.35) was more than double the heritability in the medium- (0.14) and high-production (0.09) systems.

Genetic Correlations

Between Test-Days Within Lactations. Figure 5 shows the change in genetic correlations between test-day milk yields of the first 4 lactations under the low-, medium-, and high-production systems. Genetic correlations between DIM in all production systems decreased as the time interval increased. The lowest correlations were estimated between yields at the beginning and end of the lactations. Although the esti-mated genetic correlations were all positive in the high-production system, they were negative between yields at the beginning and end of the later lactations in the low- and medium-production systems.

Between Lactations. Figure 6 shows the genetic correlations between milk yields in different lactations. The correlations ranged from −0.07 to 0.91, 0.04 to 0.93, and 0.31 to 0.96 under the low-, medium-, and high-production systems, respectively. Lower genetic correlations were observed at the beginning and end of lactations, except in the low-production system, where the correlations between lactations were higher at the beginning than at the end of the lactation. In the low-production system, the highest genetic correlations were estimated between the first and second lactations. The second and third lactations had the highest correlations in the medium-production system, whereas the third and fourth lactations had higher genetic correlations under the high-production system. The last 3 lactations had higher correlations compared with the first and later lactations under the medium- and high-production systems.

Between Milk Yield in Different Production Systems. The genetic correlations for milk yields between production systems for the first lactation (Figure
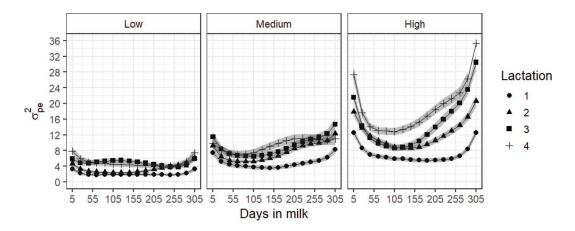

Figure 3. Permanent environmental variances $\left(\sigma^2_{pe}\right)$ with SE (gray bands) for test-day milk yield in 4 lactations under low-, medium-, and high-production systems.

Table 5. Variance components ($\times 10^3$), heritabilities, and repeatabilities for 305-d milk yield and persistency of genetic correlations for the first 4 lactations under low-, medium-, and high-production systems[1]

Lactation	System	305-d milk yield					Persistency					
		V_a	V_{pe}	V_P	h^2	r	V_a	V_{pe}	V_P	h^2	r	r_g
1	Low	174	157	507	0.34	0.65	77	60	218	0.36	0.63	0.38
	Medium	538	359	1,159	0.46	0.77	150	123	401	0.37	0.68	0.32
	High	1,123	452	2,148	0.52	0.73	104	231	619	0.17	0.54	0.30
2	Low	232	208	666	0.35	0.66	108	97	310	0.35	0.66	0.55
	Medium	396	586	1,339	0.30	0.73	234	138	545	0.43	0.68	0.60
	High	1,460	751	3,069	0.48	0.72	241	327	971	0.25	0.58	0.55
3	Low	159	338	739	0.22	0.67	74	123	308	0.24	0.64	0.48
	Medium	377	724	1,493	0.25	0.74	243	158	582	0.42	0.69	0.55
	High	1,585	901	3,494	0.45	0.71	232	455	1,176	0.20	0.58	0.87
4	Low	210	307	780	0.27	0.66	86	129	329	0.26	0.65	0.47
	Medium	279	801	1,513	0.18	0.71	261	126	587	0.44	0.66	0.47
	High	1,305	1,253	3,559	0.37	0.72	326	402	1,210	0.27	0.60	0.70

[1]V_a = additive variance; V_{pe} = permanent environmental variance; V_P = phenotypic variance; r = repeatability; r_g = genetic correlation.

7) were positive but not significantly different ($P \leq$ 0.05). They ranged from 0.05 ($\pm$ 0.07) to 0.25 ($\pm$ 0.16) between low and medium systems, 0.19 ($\pm$ 0.19) to 0.60 ($\pm$ 0.21) between low and high systems, and 0.10 ($\pm$ 0.10) to 0.35 ($\pm$ 0.17) between medium- and high-production systems. Again, the correlations were lower at the beginning and end of the lactations. The genetic correlations between the low- and high-production systems were higher than for the other system contrasts.

Between Milk Yield and Age at First Calving. Genetic correlations between test-day milk yield in the first lactation and age at first calving are shown in Figure 8. They ranged from -0.17 to 0.59 and were not significantly different ($P \leq 0.05$) between production systems. Estimated genetic correlations were all positive under the low-production system, with a peak around d 125. The correlation generally declined over the lactation for the medium and high systems, becoming negative at the end.

DISCUSSION

Test-day milk yield records from multiple-breed cow populations in Kenya were analyzed in this study to estimate genetic parameters. Herds were grouped into low-, medium-, and high-production systems based on mean production level (Wahinya et al., 2020). Multivariate random regression models were then used to estimate (co)variance components for test-day milk yield and lactation persistency in the first 4 lactations. A series of bivariate random regression models were used to estimate genetic correlations between the first-lactation test-day milk yields under the 3 production systems and between first-lactation test-day milk yields and age at first calving within the production systems. To account for the base population and breed effects, genetic groups were fitted into the model as a random effect. The variance components and genetic parameters estimated in this study were used to discuss the
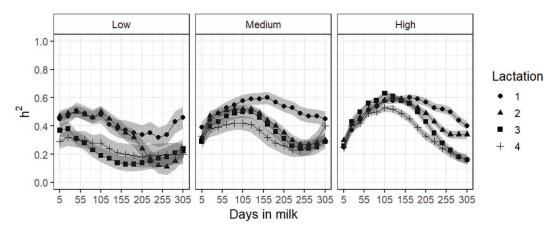

Figure 4. Heritability estimates with SE (gray bands) for test-day milk yield in 4 lactations under low-, medium-, and high-production systems.

Table 6. Variance components and heritability for age at first calving in low-, medium-, and high-production systems

Production system	Records	Variance		h^2
		Additive	Phenotypic	
Low	1,016	9,801	28,201	0.35 ± 0.14
Medium	1,635	2,427	17,969	0.14 ± 0.08
High	2,480	756	8,189	0.09 ± 0.06

genetic control of milk yield, lactation persistency, and age at first calving.

Test-Day Milk Production

The average test-day yield in this study was higher than that reported previously for smallholder herds in Kenya (Ojango et al., 2019). Wasike et al. (2014) reported a peak milk yield for Ayrshire, Holstein, and Jersey population in Kenya similar to that observed in the high-production systems in this study. Test-day milk yields similar to those reported in this study for medium- and high-production systems were reported by Muasya et al. (2014b) for Holstein-Friesian cattle in the nucleus (breeding herds) and commercial herds of Kenya. Higher yields than those reported in this study were reported for Holstein populations in Tunisia (Hammami et al., 2008) and Brazil (Bignardi et al., 2009). The milk yield of animals in the low-production systems declined across the whole lactation, as was also reported by Ojango et al. (2019) for low-producing smallholder herds. The environment in the low-production systems, therefore, does not support an increase in milk yield to a peak in the lactation.

Variance Components and Genetic Parameters

Additive, permanent environmental, residual, and phenotypic variances in this study increased with the level of production. The variances along the lactation trajectory also differed among the lactations. This shows that the influence of genes on test-day milk yield differs along the lactation trajectory in low-, medium-, and high-production systems. The additive variances reported for the low-production system in this study concur with those reported in previous studies (Silvestre et al., 2005; DeGroot et al., 2007) for dairy cows in North Carolina and Portugal, respectively, using cubic spline models. Bignardi et al. (2011, 2012) reported additive variance in Brazilian Holstein cows within the range we estimated in the medium- and high-production systems. Additive variances estimated in this study are higher than those reported in studies analyzing records from multiple lactations of Tunisian Holsteins (Hammami

et al., 2008), smallholder dairy production systems in Kenya (Ojango et al., 2019), Sahiwal cattle in Kenya (Ilatsia et al., 2007), and Holstein-Friesians in Ethiopia (Meseret and Negussie, 2017), using Legendre polynomial functions. The higher additive variance estimated around the peak under the high-production systems indicates that cows in such systems are more genetically diverse at the peak lactation stage. Conversely, genetic differences fail to be expressed under the more stressful low- and medium-production systems. Permanent environmental variances similar to those reported here have been reported by DeGroot et al. (2007) and Silvestre et al. (2005) using spline animal models and by Hammami et al. (2008) and Meseret and Negussie (2017) for Holstein cattle in Tunisia and Ethiopia, respectively. The effect of permanent environment is constant in the low-production system, although it increases gradually in the medium-production system along the lactation trajectory. The high permanent environment variance at the start and end of lactation in the high-production system is probably overstated and an artifact of the random regression model fitted, because less information is available at the extremes.

The HYM variances estimated under the high-production system were similar to those reported by Strabel et al. (2005) for Polish Black and White cattle. These estimates represent the changes in environmental conditions that have an influence on lactation milk yield. The variance increased from the first lactation to the fourth under all production systems, indicating that variation in lactation milk yield due to environmental conditions is higher in the later lactations. Genetic group variance was, on average, highest in the low-production system and lowest in the high-production system. Genetic group variance is determined by breed representation. The low-production system had the most breeds and crosses compared with the other production systems, which could explain the higher genetic group variance. Moreover, smaller genetic group sizes, as a result of more breeds and crosses, also contributed to higher genetic group variation in the low-production systems. The high-production systems had mainly Friesians. Genetic groups under the low-production systems were higher in the later lactations, reflecting that breed differences are accentuated under the harsher conditions.

Traditionally, HYM and genetic groups are fitted as a fixed effects and therefore do not contribute to the denominator used in calculating heritability. In this study, HYM was fitted partly fixed (main effects) and partly as a random effect (the interaction). When herd sizes are variable and small, fitting the HYM interaction as a random effect helps recover genetic information confounded with herds, which would otherwise be
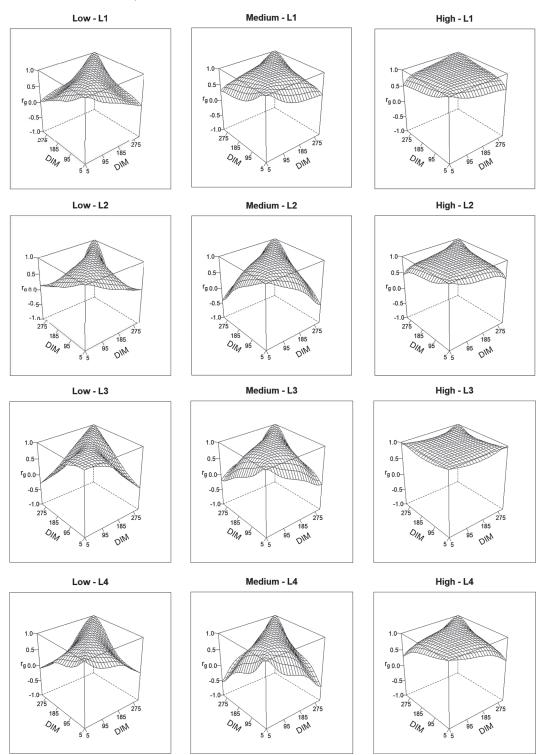
Figure 5. Genetic correlations (r_g) between milk yields in different DIM in 4 lactations (L1, L2, L3, and L4) for low-, medium-, and high-production systems.

swept away. Genetic group is also often fitted as a fixed effect; here they represent various breed crosses and are fitted as random because some groups have quite small group sizes. Although variation between genetic groups can be exploited in breeding programs and should be included in EBV, breed and breed-cross differences
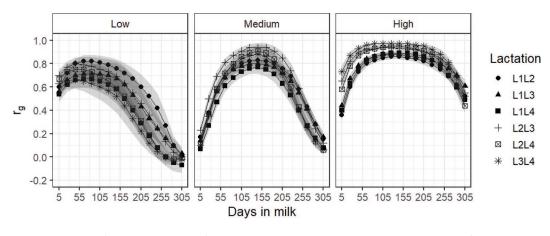
Figure 6. Genetic correlations (r_g, SE in gray bands) between test-day milk yield in the first 4 lactations (L1, L2, L3, and L4) under the low-, medium-, and high-production systems.

were not the focus of this study. Most often breeding programs are conducted within breed or with similar breed types, and so within-breed heritability is the relevant statistic for calculating selection response. The cubic spline represents the overall lactation curve and does not represent a random effect in the usual sense. This could be equivalently but less efficiently fitted as a fixed polynomial and therefore was also not included as part of the phenotypic variance to obtain heritability.

Comparing the heritability of test-day milk yield, higher heritabilities were estimated at the beginning of the lactation under the low-production system. Under the medium- and high-production systems, heritability was higher during mid-lactation. Previous studies have estimated higher heritability in mid-lactation (Ilatsia et al., 2007; Hammami et al., 2008). High heritability estimates were estimated in this study, similar to those reported by Cobuci et al. (2005) and Jamrozik and Schaeffer (1997). Muasya et al. (2014b) also reported heritability values similar to those estimated in the

third and fourth lactations under the low-production system. The high heritability estimated in this study could be partly due to the models used and data from the multiple-breed population. These heritability estimates, however, indicate that genetic gain can be achieved through selection for test-day milk yield under the 3 production systems. Age at first calving was more heritable in the low-production system than in the medium- and high-production systems. Muasya et al. (2014a) estimated heritabilities ranging from 0.16 to 0.27 for age at first calving, whereas a heritability of 0.38 was reported by (Ojango and Pollott, 2001) for the Holstein-Friesian population in Kenya. Heritability in the low-production system was associated with a high standard error due to fewer observations. Low heritability for age at first calving under the medium- and high-production systems indicates that, in these systems, the age at breeding is more influenced by farmers' breeding policy decisions and production environment. In low-production systems, the environment
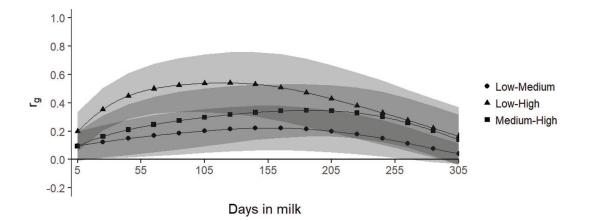

Figure 7. Genetic correlations (r_g, SE in gray bands) between the first-lactation test-day milk yields in low-, medium-, and high-production systems.
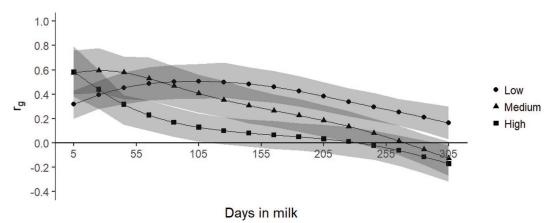
Figure 8. Genetic correlations (r_g, SE in gray bands) between first-lactation test-day milk yields and age at first calving under low-, medium-, and high-production systems.

is less favorable, and therefore, early breeding could be more influenced by genetics.

The variance components for 305-d milk yield and persistency increased with the level of production. Both traits are moderately or highly heritable, with high repeatability, which implies that these traits can be improved through selection. Yamazaki et al. (2014) reported heritability estimates ranging from 0.20 to 0.41 for 305-d milk yield in different lactations of Japanese Holstein. A high heritability (0.42) for 305-d milk yield was also reported for Danish Holsteins (Jakobsen et al., 2002) The heritability estimates for persistency in this study (0.16 to 0.48) are higher than what is mostly reported in literature: 0.16 for Danish Holsteins (Jakobsen et al., 2002), 0.10 for Girolando cows (Canaza-Cayo et al., 2015), and 0.15 for Holstein cows in Brazil (Padilha et al., 2019). This may be due to differences in populations and methods used to estimate the test-day variance components. The genetic correlation between 305-d milk yield and lactation persistency were positive and moderate to high (0.31 to 0.88). This indicates that genetic improvement of lactation persistency in this population would result in an increase in milk yield and vice versa. This provides an opportunity to select for persistency in a selection index with an aim to improve milk production. With many lactations going beyond 305 d, cows with high persistency may not need a yearly calving interval to be profitable (Cole and Null, 2009). A flatter lactation curve, without decreasing the total milk yield, may be more desirable.

Genetic Correlations

Between Test-Day Yields. Genetic correlations between test-day yields were higher between days adjacent to each other and then decreased as the distance in time between the test-days increased, similar to results reported in the literature (Figure 5). This pattern is intrinsic to the model used in this analysis, which borrows strength of the genetic and nongenetic animal effects from neighboring observations. Positive genetic correlations estimated between yields in different days within lactations indicate that genetic gain in the mid- and later lactation could be achieved by selecting for yield early in lactation. By contrast, negative genetic correlations could indicate that improvement of yield at the beginning of the lactation may result in reduced yield at the end of the lactation, reflecting lower persistency. This might also be an artifact of the polynomial functions and therefore suggest that early-lactation milk yield is not very predictive of total yield. Negative correlations were also reported by Rekaya et al. (1999), Kettunen et al. (2000), Bignardi et al. (2009), and Ojango et al. (2019). Test-day milk yield had a high genetic correlation around mid-lactation. To make more reliable genetic predictions, recording along the whole lactation is important for this population, because the heritability is high over the whole lactation trajectory.

Between Test-Day Milk Yields in Different Lactations. The genetic correlation between lactations was quite high (>0.9) in the middle of the lactation for all production systems but dropped sharply at the beginning and end of the lactation (Figure 6). This indicates that the mean component of the random regression is well estimated, but the slope and curvature components are much less consistent. The drop is more extreme for the medium and low environments, which have fewer data, and the peak occurs around d 75 for the low environment. Most of the correlations between lactations were not significantly different ($P \leq 0.05$). However, under the high-production system, the correlations among the second, third, and fourth lactations

were higher than between the first lactation and the later 3 lactations. A similar trend was observed under the medium production system at mid-lactation. Under the low production system, the first 3 lactations were more correlated among themselves than with lactation 4. Correlated response for higher milk yield in later lactations can, therefore, be achieved with higher accuracy when selection is done in the first lactation using EBV in the mid-lactation under the low production system and the second under medium and high production systems. Hammami et al. (2008) observed higher genetic correlations between lactation 1 and 2 and lowest correlations between lactation 1 and 3. Studies on differential expression of genetic effects in different lactations under different management or production systems could provide possible biological explanations of the genetic control of milk yield.

Between Test-Day Milk Yields in Different Production Systems. Genetic correlation estimates between test-day milk yield in different production systems (Figure 8) in Kenya ranged from 0.05 to 0.60, which is significantly lower than 0.80 (Robertson, 1959), suggesting the presence of genotype × production system interaction. This also implies that sires are re-ranked among the production systems defined in this study based on the herd mean production level. Sires that are best in the high-production system, therefore, may not perform best in the low- and medium-production systems for improvement of milk yield and lactation curve parameters. This study recommends that sires should be selected based on breeding values estimated within a production system. Alternatively, milk yield should be corrected for heterogeneous variance for genetic evaluation. A square root or log-transformation can be applied to the data set, or a reaction norm model with herd level or production level as a covariate can be used to account for the heterogeneity, leading to a simpler evaluation. Genetic correlations between production systems were not significantly different. This can be attributed to a high proportion of common sires. Hammami et al. (2009) estimated a higher genetic correlation (0.70) between high and low and between high and medium (0.78) in Holstein-Friesian herds in Tunisia, classified using herd-year of calving solutions. Raffrenato et al. (2003) estimated a genetic correlation of 0.63 between environments classified on within herd-year standard deviation for lactation milk yield in Italian Friesian and Brown Swiss cows. In Iran, Raffrenato et al. (2003) estimated genetic correlations ranging from 0.16 to 0.79 between milk yields from Holstein cows raised in moderate and warm climates. In these studies, the authors suggested re-ranking of sires due to the presence of genotype × environment interaction. The present study recommends a sire ge-

netic evaluation using a multivariate model within each production system, to allow selection of sire based on breeding values specific to each production system.

Between Milk Yield and Age at First Calving. The genetic correlations between test-day milk yield and age at first calving were not significantly different between production systems (Figure 8). Positive genetic correlations between age at first calving and test-day milk yield indicate that genetic improvement of milk yield, especially in the early stage of the lactation, would result in a delayed age at first calving. This could also imply that delaying first calving in a harsher environment results in cows with higher mature weight and better able to produce milk. A cow with higher mature weight would have a more persistent lactation under the low-production system. The negative genetic correlations estimated between age at first calving and milk yield at the end of the lactation under the medium- and high-production systems were not significantly different from zero. The lower correlations estimated in the high-production system indicate that the age at first calving has a minimal effect on milk yield in the later lactation period. In this context, studies on the genetic correlation of test-day milk yield and age at first calving are scarce. However, several studies have reported that breeding is a policy decision, where, for instance, dairy farmers may delay breeding of first-calf heifers in harsher environments (Berger et al., 1981). Positive correlation between 305-d milk yield and age at first calving have also been reported for cows in Kenya (Ojango and Pollott, 2001; Wahinya et al., 2018). Selection indexes, including fertility traits, therefore, would help to balance genetic improvement of milk yield and fertility, leading to a lower heifer rearing cost (Pirlo et al., 2000; Berry et al., 2003). Although low age at first calving is desirable under good conditions, too low an age could lead to reduced productive life (Ojango and Pollott, 2001; Menjo et al., 2009) as well as reduction in milk yield, resulting from underdevelopment of the mammary secretory tissue (Ettema and Santos, 2004; Mohd Nor et al., 2013).

CONCLUSIONS

This research showed that spline models can be combined with random regression to model test-day milk yield data from low-, medium-, and high-production systems and to estimate genetic parameters. The multivariate model considering test-day milk yield in different lactations as separate but correlated traits is recommended for genetic evaluation in this population. Variance components were heterogeneous between production systems and along the lactations. Test-day milk yield, lactation persistency, and age at first calv-

ing were heritable and, therefore, can be included in the breeding objective and improved through selection. Genetic correlations between test-day milk yield in different lactations were not unity, and therefore selection for higher milk yield in later lactations, using the first lactation, might be inefficient. In addition, genetic evaluation of multiple lactations, assuming a unity correlation between the lactations in this population, may result in biased evaluation. Genetic correlations between milk yield in low-, medium-, and high-production systems ranged between 0.04 and 0.54 along the different DIM, indicating that sires may rank differently across production systems. A genetic evaluation system, which accounts for genotype × environment interaction, is required for accurate prediction of performances across the 3 production systems. Using the output from the test-day random regression models, variance components and breeding values for 305-d milk yield and persistency can be predicted from the test-day model. A selection index including milk yield and age at first calving should be used to balance improvement in the 2 traits.

ACKNOWLEDGMENTS

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