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# Genetics of milk yield and fertility traits in Holstein-Friesian cattle on large-scale Kenyan farms<sup>1</sup>

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**ABSTRACT:** Purebred Holstein-Friesian cows are the main exotic breed used for milk production on large, medium, and small farms in Kenya. A study was undertaken on seven large-scale farms to investigate the genetic trends for milk production and fertility traits between 1986 and 1997 and the genetic relationships between the traits. This involved 3,185 records from 1,614 cows, the daughters of 253 sires. There was a positive trend in breeding value for 305-d milk yield of 12.9 kg/yr and a drop in calving interval of 0.9 d/yr over the 11-yr period. Bulls from the United States (U.S.) had an average total milk yield breeding value 230 kg higher than the mean of all bulls used; Canada (+121 kg), Holland (+15 kg), the United Kingdom (U.K., 0 kg), and Kenya (-71 kg) were the other major suppliers of bulls.

Average breeding values of bulls for calving interval by country of origin were -1.31 (Canada), -1.27 (Holland), -0.83 (U.S.), -0.63 (Kenya), and 0.68 d (U.K.). The genetic parameters for 305-d milk yield were 0.29 (heritability), 0.05 (permanent environment effect as proportion of phenotypic variance) resulting in an estimated repeatability of 0.34. Using complete lactation data rather than 305-d milk yield resulted in similar estimates of the genetic parameters. However, when lactation length was used as a covariate heritability was reduced to 0.25 and the permanent environment effect proportion increased to 0.09. There was little genetic control of either lactation length (heritability, 0.09) or calving interval (heritability, 0.05); however, there were strong genetic correlations between first lactation milk yield, calving interval, and age at first calving.

Key Words: Breeds, Genetic Parameters, Heritability, Repeatability

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## Introduction

Holstein-Friesian cattle comprise a high proportion of the exotic dairy animals raised in Kenya. The country's total dairy population is approximately 3.0 million cows (Peeler and Omore, 1997). Large- and medium-scale farms rear approximately 24% of the dairy cows in the country and produce the majority of milk sold in main urban centers. Since 1992, there has been an increase in the use of Holstein bulls from several countries to upgrade the Kenyan Holstein-Friesian population. As a consequence, and because of improved management of animals, milk production from farms

> 20 ha has increased from a mean of 3,577 kg/cow in 1985 (Rege, 1991) to 5,056 kg/cow in 1997 (Ojango, 2000). In the same period, the mean calving interval decreased from 412 d in 1985 (Rege, 1991) to 406 d (Ojango, 2000).

Estimates of genetic parameters and breeding values, using animal models, for dairy traits from tropical cattle are rare. A recent review of cattle genetic parameters from tropical regions by Lobo et al. (2000) reported only 15 out of 490 studies (1970 to 1997) that had used animal models. Of the 10 reports from Kenya, only three were on European breeds, and these used half-sib models to estimate variance components. Estimates of heritability for milk yield from European breeds kept in the tropics were lower than those from similar breeds kept in temperate countries. Lobo et al. (2000) also supported the conclusion of Madalena (1994) that different methods of correcting for lactation length should be compared using the same data set.

The primary objectives of this study were to calculate breeding values for production and fertility traits, to estimate genetic trends over recent years, and to estimate genetic and phenotypic relationships between reproductive traits and milk production of Hol-

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stein-Friesian cattle in Kenya. The secondary objective was to examine different methods of adjusting for variable lactation length as they affect estimates of genetic parameters for milk yield.

## Materials and Methods

### *Data Source, Environment, and Cattle Management*

Data were obtained from seven large-scale farms registered by the Dairy Recording Services of Kenya and identified as Holstein-Friesian breeders of Kenya. The farms were selected based on their maintaining complete pedigree records for all animals from before 1980 to the present. The farms were located in the Rift Valley and central provinces of the country, which are classified as having medium to high potential for agricultural production. The management system of the farms has been described previously (Ojango, 2000). Briefly, animals were grouped and managed according to their age into three basic classes: calves, weaners, and mature stock. From the age of 14 mo, female animals coming into estrus regularly were served. Most of the farms tried to have all heifers served by 18 mo of age. A strict disease control regimen was maintained. Pasture and fodder crops were grown on all the farms. Calving occurred throughout the year, but a slightly higher number of animals were planned to calve toward the end of the year when demand for milk increases due to drier weather conditions.

Seasons in the country are generally classified into the green season, when soil moisture from rainfall is sufficient to sustain growth of pastures, and the dry season, when the moisture content of the soil is too low to sustain growing pastures (Stotz, 1983). Monthly rainfall totals over 12 yr (1985 to 1997) were used to determine the rainfall pattern of the different regions and to define the green and dry seasons.

### *Data Preparation*

On the farms, records for individual animals were kept on animal cards arranged in order according to the year in which the animal was born. All information about the animal, including whether it had been sold or had died, was written on the card. Daily milk yields were recorded in a milk record book. When the cow ceased lactating a total lactation yield was obtained by summing all the daily records. Total yield and lactation lengths were then recorded on the individual animal card.

Only total lactation information from the farms was entered onto a computer, yielding 5,355 individual lactation records. Records of animals without birth or calving information and those that originated from a different herd were discarded. Records of animals that had been sold before having completed at least 150 d of the first lactation were also discarded. Use of later lactation records would bias estimates of genetic pa-

rameters if a first lactation record was not available. Hence, an animal was required to have a first lactation record in the current herd for records from subsequent lactations to be retained for the analysis. After editing, 3,185 records remained from 1,614 cows, the daughters of 253 bulls. The data covered animals born over 12 yr, from 1985 to 1997. Individual animals had to have an identification number, sire and dam identification, birth date, and calving dates. Pedigree records for individual animals were checked with records from the Kenya Stud Book, which issues certificates of registration showing the date of birth and the sire, dam, and grandparents of an animal. Cow birth dates were compared with dam calving dates for verification. Performance in the first three parities was used for the analysis of production traits.

### *Adjustment of Milk Yields to 305 days*

The data consisted of total milk yields from lactations of varying lengths. Some animals had been sold before completing a lactation, some animals died in the middle of a lactation, and, for some animals, the lactation was still in progress. Animals that were still lactating and had not calved within a year of the previous calving were continuously milked, resulting in lactations well over 305 d in length. The lack of weekly individual yields for animals reared on the various farms prompted the need to adjust lactation milk yields to a 305-d length. In most countries, the test interval method has been the standard method of calculating 305-d lactation yields. Test-day yields are taken at approximately 30-d intervals throughout the lactation and special adjustments are made for first and last test day yields to give an unbiased 305-d milk yield (Jamrozik and Schaeffer, 1997).

To derive typical lactation curves, by lactation number, for adjustment of total milk yield to 305 d, the average daily milk yield for each week of 253 cows calving between July 1995 and July 1997 was calculated on one of the farms in the study. Only records of animals in their first through third parities were considered. The records were grouped according to the year and month of calving, forming 26 monthly groups. Least squares methods for unbalanced data were used to examine how cow, month of calving, and week of lactation influenced average daily milk yield during a lactation. Least squares means of daily milk yield in the different lactations were plotted for lactations one to three by week of lactation. To obtain coefficients for the lactation curves the incomplete gamma function (Wood, 1967) was applied to the data within lactation number.

Total lactation milk yields of animals that extended beyond 305 d were thus adjusted to a 305-d record using the appropriate age-based lactation curve, derived using the incomplete gamma function as described above. Lactation length ranged from 161 to 499 d. Records of animals still being milked when data

for the study were collected were adjusted to a 305-d length, if the lactation had been in progress for a minimum of 180 d.

### *Relationships Among Animals*

A pedigree file containing all animals with all known relationships going back for two generations was constructed. Parentage and original herd-book numbers were obtained from the Kenya Stud Book. Pedigrees of sires used from different countries were constructed with assistance of the Animal Data Centre of the United Kingdom. The resulting file was used in construction of the numerator relationship matrix. The degree of connectivity was evident from the numbers of sires used between farms. Of the 253 bulls used as sires of animals with milk records on all the farms, 38% had daughters on more than one farm, and 62% were used exclusively on individual farms. Two sires had daughters on all farms. Fifty-six percent of the 247 bulls used as maternal grandsires were used exclusively on individual farms and 44% were used by at least one other farm. However, 67% of the sires of sires were represented on more than one farm. A summary of the final data used in the analysis is presented in Table 1.

### *Analytical Procedure*

A derivative-free restricted maximum likelihood procedure (**DFREML**; Meyer, 1989) was used to estimate variance components for various measures of milk yield, lactation length, age at first calving, and calving interval. For traits for which more than one lactation record from each cow was analyzed, a repeatability animal model was used to account for permanent environmental effects common to the repeated records on the same animal.

The model for analysis of milk production traits included the fixed effects of herd-year-season, lactation number, and linear and quadratic effects of age at calving (mo) within a lactation (see Ojango, 2000). The model also included a random additive genetic and a permanent environmental effect for each animal. It was assumed that the covariances between additive, permanent environmental, and residual effects were zero and that levels of each were independently distributed with variance  $\sigma_a^2$  for animals,  $\sigma_{pe}^2$  for permanent environmental effects, and  $\sigma_e^2$  for residuals. Approximate sampling errors of estimates were calculated as outlined by Smith and Graser (1986).

Mixed-model equations in the analyses were solved iteratively. The Simplex procedure was used to locate the maximum of the log-likelihood function. Analyses were terminated when the change in the variance of function values ( $-2 \log$  likelihood) fell below  $10^{-5}$ . Restarts were performed for all analyses, using the final results of the previous analysis, in order to locate the global maximum for the log likelihoods.

Bivariate analyses were carried out for milk yield in the first lactation, calving interval, and age at first calving for all cows having complete records for these three traits. To obtain starting values for the bivariate analysis, univariate analyses were carried out on each trait. From the bivariate analysis, the genetic and environmental correlations between traits were calculated. The standard error for the genetic correlation was calculated as described by Falconer (1989).

Best linear unbiased prediction of estimated breeding values were obtained by back-solution using the DFREML program for all animals in the pedigree file. Breeding values are presented as deviations from a mean of zero in the base population.

## **Results**

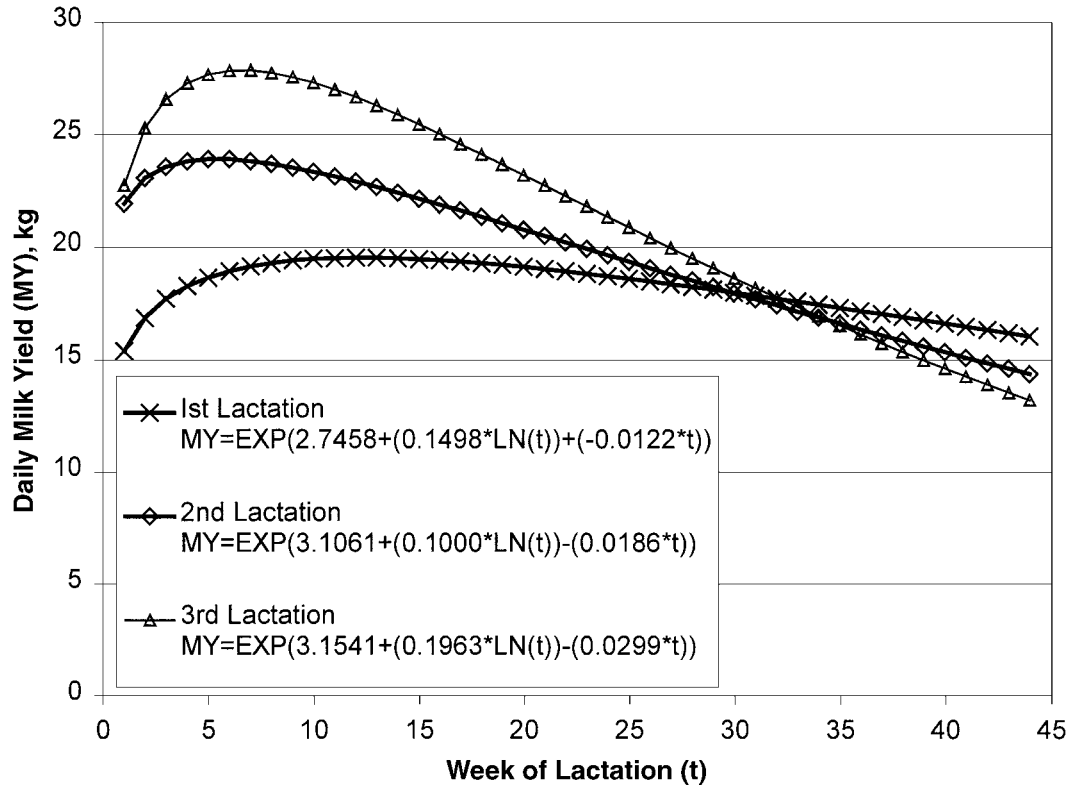
### *Adjustment of Total Milk Yield to 305 days*

Fitting the incomplete gamma function (Wood, 1967) to the weekly least squares means by lactation number resulted in the curves shown in Figure 1. The effect of using these curves to adjust lactation records greater than 305 d in length to their 305-d equivalent is shown in Table 1. Means for total milk yield before and after adjustment to 305 d were similar because records longer than 305 d were reduced and milk yields from lactations still in progress, and greater than 180 d in length, were increased to 305-d equivalents. The net effect was little difference in the means.

### *Milk Yield*

Heritability estimates for various traits are presented in Table 2. The heritability estimate for milk yield, considering lactation length as a covariate, was moderate ( $0.25 \pm 0.04$ ) and less than the estimate for total milk yield ignoring lactation length ( $0.30 \pm 0.04$ ). Overall phenotypic variation for milk yield was also reduced when lactation length was included as a covariate in the model. Madalena (1988) noted that using lactation length as a covariate in analyses of milk yield tended to reduce differences between animals, making low-producing animals seem to produce more milk. Including lactation length as a covariate for milk yield also caused a greater proportion of the overall phenotypic variation to be apportioned to permanent environmental effects of the cow.

Heritability for 305-d adjusted milk yield was similar ( $0.29 \pm 0.04$ ) to that for total milk yield with lactation length as a covariate. Total phenotypic variation for 305-d adjusted milk yield was also higher than for yield with lactation length as a covariate. Variation due to permanent environmental effects of the cow was, however, less for the 305-d adjusted yield than for total milk yield with lactation length as a covariate. Repeatability estimates for both measures of milk yield were similar (0.34, Table 2).



**Figure 1.** Lactation curves for first to third lactations derived by fitting the incomplete gamma function to average daily milk yield per week of lactation.

### Lactation Length

With lactation length considered to be a genetically controlled trait, a low heritability estimate of  $0.09 \pm 0.03$  (Table 2) was found. The proportion of phenotypic variation in lactation length due to permanent environmental effects of the animal ( $c^2$ ) was also low (0.03). Repeatability of lactation length was 0.11. These results imply that variation in lactation length is more a result of variation in management and feeding in the given environment of a particular lactation rather than of factors associated with the cow.

**Table 1.** Characteristics of the data structure and means and standard deviations for production and fertility traits

| Data structure              | Number |       |  |
|-----------------------------|--------|-------|--|
| Records                     | 3,185  |       |  |
| Cows                        | 1,614  |       |  |
| Sires with progeny          | 253    |       |  |
| Herd-year-season subclasses | 159    |       |  |
| Traits                      | Mean   | SD    |  |
| Total milk yield, kg        | 4,541  | 1,639 |  |
| 305-d milk yield, kg        | 4,557  | 1,620 |  |
| Calving interval, d         | 406    | 79    |  |
| Age at first calving, mo    | 31     | 3.8   |  |
| Lactation length, d         | 300    | 54    |  |

### Calving Interval

A heritability estimate of  $0.05 \pm 0.02$  was obtained for calving interval (Table 2). The estimate was within limits of estimates for reproductive traits reported by other authors (Dematawewa and Berger, 1998; Hayes et al., 1992; Marti and Funk, 1994). The proportion of phenotypic variation due to the common environmental effects of the cow was also low ( $0.01 \pm 0.03$ ). Thus, the repeatability of calving interval was low (0.06) and the major influences on it were due to temporary and environmental factors.

### Relationship Between Milk Yield and Fertility Measures

Performance of animals in first parity was used to assess relationships between milk yield and calving interval and between milk yield and age at first calving. Parameter estimates from these analyses are presented in Table 3. The heritability estimate obtained for 305-d milk yield in the first lactation was slightly less than that obtained for 305-d milk yield considering production in the first three parities ( $0.26 \pm 0.06$  vs  $0.29 \pm 0.04$ ). The heritability estimate obtained for calving interval following the first parity varied slightly from that obtained for intervals following the first three parities ( $0.06 \pm 0.02$  vs  $0.05 \pm 0.02$ ).

The phenotypic correlation between first lactation 305-d milk yield and calving interval between first and

**Table 2.** Estimates of additive variance ( $\sigma^2_a$ ), variance due to permanent effects of cow ( $\sigma^2_{pe}$ ), phenotypic variance ( $\sigma^2_p$ ), heritability ( $h^2$ ), relative permanent environmental variance ( $c^2$ ), and repeatability

| Parameter       | Trait <sup>a</sup> |             |              |              |              |
|-----------------|--------------------|-------------|--------------|--------------|--------------|
|                 | TLMY-LL, kg        | TLMY, kg    | 305-d MY, kg | LL, d        | CI, d        |
| $\sigma^2_a$    | 216,593            | 392,295     | 360,274      | 249          | 272          |
| $\sigma^2_{pe}$ | 79,868             | 61,991      | 62,590       | 71           | 72           |
| $\sigma^2_p$    | 865,741            | 1,298,784   | 1,232,113    | 2853         | 5676         |
| $h^2$           | 0.25 ± 0.04        | 0.30 ± 0.04 | 0.29 ± 0.04  | 0.087 ± 0.03 | 0.047 ± 0.02 |
| $c^2$           | 0.09 ± 0.04        | 0.05 ± 0.04 | 0.05 ± 0.04  | 0.025 ± 0.03 | 0.013 ± 0.03 |
| Repeatability   | 0.34               | 0.35        | 0.34         | 0.11         | 0.06         |

<sup>a</sup>Abbreviations: total lactation milk yield with lactation length as a covariate (TMY-LL); unadjusted total lactation milk yield (TLMY); total lactation milk yield to 305 d (305-d MY); lactation length (LL); calving interval (CI).

second parity was 0.37 (Table 3). However, the genetic correlation between the two traits was negative ( $-0.64$ ). Because phenotypic correlation is a function of both genetic and environmental covariances, the negative genetic and positive phenotypic correlation between the two traits implies a positive environmental correlation. Thus, within the given environment, animals that produced higher milk yields in their first lactation would tend to have a longer first calving interval. However, animals with a higher breeding value for total milk yield would tend to have a breeding value for a shorter calving interval.

A heritability estimate of  $0.38 \pm 0.09$  was obtained for age at first calving. Age at first calving is economically important because it determines when an animal begins its productive life and hence could influence the lifetime productivity of an animal. The phenotypic correlation between age at first calving and milk yield was small and negative ( $-0.2$ , Table 3). However, the genetic correlation between the traits was moderate and positive ( $0.54$ ). To assess the possible influence of age at first calving on milk yield, least squares means for milk yield in the first lactation alone and in the first three lactations combined were plotted against various ages at first calving (Figure 2). The regression equation showed a slight decline in yield as age at first calving increased when considering milk yield in the first lactation alone. When the average milk yield in the first three parities was considered, there was a

slight increase in yield as age at first calving increased.

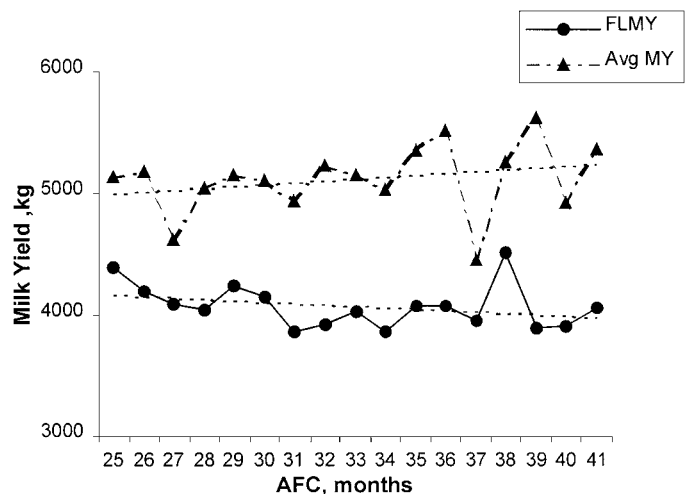
#### Trends in Estimated Breeding Values for Various Traits

Mean breeding values by year of birth were plotted against time as an indication of genetic trend in milk production and calving interval (Figures 3 and 4).

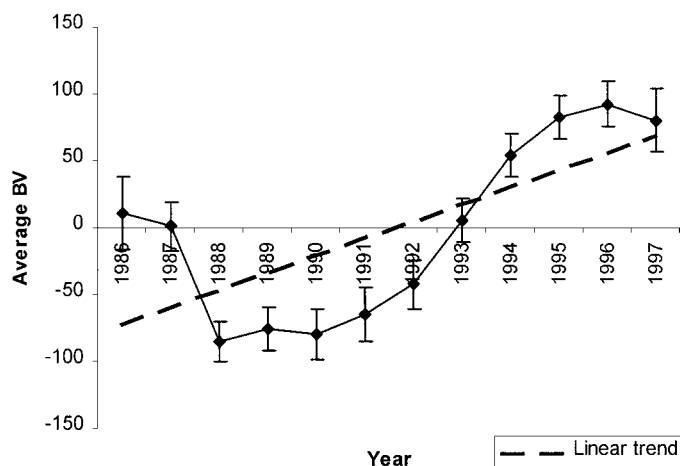
There was a positive trend in breeding value for milk yield over time on all farms. The regression coefficient indicates an overall rate of increase in milk production of 12.9 kg/yr. However, the initial trend from 1986 to 1988 was negative. Improvement in milk production was accompanied by a reduction in calving interval, showing that higher yields per animal were due to factors other than an increase in the lactation length.

**Table 3.** Estimates of genetic correlations (above diagonal), phenotypic correlations (below diagonal), and heritabilities (on diagonal) for 305-d first-lactation milk yield (FLMY), calving interval in the first parity ( $CI_1$ ), and age at first calving (AFC)

| Trait      | FLMY        | $CI_1$           | AFC             |
|------------|-------------|------------------|-----------------|
| FLMY, kg   | 0.26 ± 0.06 | $-0.64 \pm 0.11$ | $0.54 \pm 0.12$ |
| $CI_1$ , d | 0.37        | $0.06 \pm 0.02$  | $0.89 \pm 0.13$ |
| AFC, mo    | $-0.20$     | 0.02             | $0.38 \pm 0.09$ |



**Figure 2.** Least squares means for milk yield in first three parities (AvgMY) and in the first lactation (FLMY) for different ages at first calving (AFC). Regression equations: Average milk yield in lactations 1 through 3 (AvgMY) on AFC ( $x$ ):  $y = 4,988 + 14.95 x$ ;  $R^2 = 0.687$ ; first lactation milk yield (FLMY) on AFC ( $x$ ):  $y = 4,173 - 10.8 x$ ;  $R^2 = 0.899$



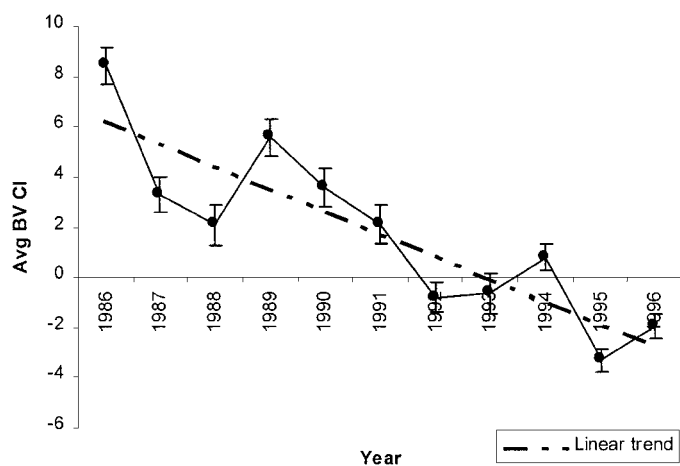
**Figure 3.** Trend in estimated breeding value (BV) for 305-d milk yield (kg). Regression equation for BV MY (y) on year of calving (x):  $y = -85.62 + 12.9x$ ;  $R^2 = 0.47$ .

The genetic trend in calving interval was negative, indicating a reduction in calving interval over time (Figure 4). The regression of breeding value for calving interval on year was  $-0.9$  d/yr.

#### Summary of Sire Breeding Values

The Holstein-Friesian breed in Kenya is said to be a heterogeneous mixture because the sires originated from several different countries (Rege, 1991). To investigate the variation in performance due to origin of the bulls, the average breeding values for 305-d milk production and calving interval for sires that were from various countries were calculated from the data (Table 4).

Only 28.5% of all the sires or grandsires of cows were born within the country. Of the other 69.5% the



**Figure 4.** Trend in estimated breeding value (BV) for calving interval (d). Regression equation for BV calving interval (y) on year of calving (x):  $y = 7.15 - 0.90x$ ;  $R^2 = 0.76$ .

highest proportion (18.6%) were from the United States; 17.5% originated from the United Kingdom and 11.3% from Canada. The standard deviations for the estimated breeding values were highly variable. The average breeding values of sires from the various countries do not show a well-defined selection criterion. However, the small number of sires originating in Israel seemed to have the highest mean breeding value for milk production in Kenya. Animals from the United States and Australia also had high breeding values.

## Discussion

### Genetic Trends Over Time

The overall trend in productivity of the Holstein-Friesian in Kenya has been positive (Ojango, 2000). This has been achieved partly through improved management and nutrition and through the quality of sires selected from various countries over time. In this study we investigated the genetic component of that trend. Figure 3 shows that after an initial decrease in mean breeding value for milk yield there has been a steady increase for cows born between 1988 and 1996, with a small decline in 1997. Over the 11-yr period the average increase in mean breeding value was 12 kg/yr. Figure 4 shows that this increase was accompanied by a decrease in mean breeding value for calving interval at the rate of 0.9 d/yr.

### Effect of Country of Origin of Bulls

Since the period under study represented between two and three cow generations, most of the genetic change found in this Kenyan population was due to the different AI sires used in the population. Table 4 shows the estimated breeding values for sires born in the major semen exporting countries. Bulls from Israel had the highest mean breeding value for milk yield, but this mean was based only on four animals. Of the countries with more than 20 bulls, those bulls originating in the United States had the highest mean breeding value (231 kg) for 305-d milk yield, followed by bulls from Canada (121 kg), Holland (15 kg), the United Kingdom (0 kg), and Kenya (-71 kg).

The pattern of mean breeding values for calving interval by country was somewhat different from that for milk yield. Bulls from Canada (-1.31 d) and Holland (-1.27 d) had the lowest mean EBV for calving interval, followed by bulls from the United States (-0.83 d) and Kenya (-0.63 d). Bulls from the United Kingdom had a higher breeding value for calving interval (0.68 d).

### Milk Production

Heritability estimates obtained for either adjusted or unadjusted milk yield in this study using an animal model for analyses were less than estimates obtained

**Table 4.** Average breeding values of (grand)sires used in Kenya by country of origin estimated from productive daughters between 1986 and 1997

| Country of origin | 305-d Milk yield, kg | Calving interval, d | Number of (grand)sires |
|-------------------|----------------------|---------------------|------------------------|
| Australia         | 229 ± 28.2           | -0.33 ± 0.59        | 5                      |
| Canada            | 120 ± 37.6           | -1.31 ± 0.45        | 40                     |
| Germany           | 117 ± 64.9           | 1.71 ± 2.06         | 13                     |
| Holland           | 15 ± 39.6            | -1.27 ± 0.66        | 38                     |
| Israel            | 409 ± 56             | 3.9 ± 1.95          | 4                      |
| Italy             | 107 ± 67.5           | -0.39 ± 0.41        | 4                      |
| Kenya             | -70 ± 26.8           | -0.63 ± 0.56        | 101                    |
| New Zealand       | -66 ± 35             | -0.44 ± 0.58        | 4                      |
| South Africa      | 68 ± 97              | -1.80 ± 1.54        | 8                      |
| United Kingdom    | 0.02 ± 26            | 0.68 ± 0.63         | 62                     |
| United States     | 231 ± 32.8           | -0.83 ± 0.34        | 66                     |
| Zimbabwe          | 275 ± 142            | -1.19 ± 8.3         | 2                      |
| Others            | -15 ± 47.2           | 0.38 ± 1.2          | 7                      |

from a previous study of the population in which a sire model was used for analyses (0.29 vs 0.32; Rege, 1991). The heritability estimate for milk yield adjusted to a standard 305-d length using the formula of Wood (1967) was greater than that for total lactation milk yield with lactation length fitted as a covariate (0.29 vs 0.25). Use of the shape of the lactation curve to adjust yields to a fixed lactation length rather than assuming an average change per day over the entire lactation more faithfully describes lactation in the given environment. Correction of total milk yield for lactation length also may remove some of the additive variance (Madalena, 1994) and thus reduce the heritability.

Studies in temperate environments estimating the heritability for 305-d milk yield have reported values of 0.36 (Cue et al., 1987) from Canada and 0.28 (De Jager and Kennedy, 1987) from first-lactation data of North American Holsteins. Teepker and Swalve (1988), using black and white sires from northern Germany, obtained heritability estimates for lactations one, two, and three of 0.25, 0.20, and 0.22 respectively. Dematawewa and Berger (1998) reported a heritability of 0.20 in U.S. Holsteins. Majjala and Hanna (1974) and Pearson et al. (1990) summarized estimates for milk traits from several studies. From their reviews heritability estimates for milk yield averaged 0.26 (up to 1974) and 0.31 (since 1974).

In a review of genetic parameters for cattle in the tropics, Lobo et al. (2000) reported least squares mean heritabilities of 0.34 (total milk yield) and 0.22 (305-d milk yield) for European breeds. Our results confirm their conclusion that European breeds kept in the tropics have a slightly lower heritability for milk yield than those in temperate countries.

### Calving Interval

The heritability estimate obtained in this study for calving interval was greater than has previously been reported for Holstein-Friesians in Kenya (0.05 vs 0.01, Rege, 1991). The repeatability estimate for calving interval

was, however, less than that obtained in the study by Rege (1991) (0.06 vs 0.253). The low repeatability estimate obtained in this study is an indication that calving interval is more influenced by effects due to temporary environmental variation. It would thus be possible to reduce calving interval through improvement in management of reproduction. The heritability estimate obtained in this study was comparable to estimates obtained from studies on reproductive performance of Holstein-Friesian cattle in other countries (Berger et al., 1981; Marti and Funk, 1994; Dematawewa and Berger, 1998). Other studies on fertility traits have analyzed days nonpregnant, which is similar to calving interval considering the relatively small variation in gestation length (Hansen et al., 1983b; Seykora and McDonald, 1983). In those studies, heritability estimates of 0.05 and 0.03 were obtained for days nonpregnant.

The weighted mean heritability for calving interval for tropical cattle herds, reported by Lobo et al. (2000), was 0.11. They found no difference between European and local breeds for this trait.

### Relationship Between Fertility and Production

A negative estimate of the genetic correlation was obtained between calving interval and milk yield in the first lactation. The negative genetic correlation implies that genes that positively affect milk production are likely to reduce calving interval. However, the phenotypic correlation between milk yield and calving interval was positive, implying that animals that produce more milk have longer calving intervals. This antagonistic relationship between production and fertility was, therefore, due to environmental rather than genetic factors. Several authors have reported antagonistic relationships between production and fertility traits in animals that have been selected for high milk yield (Oltenacu et al., 1991; Campos et al., 1994; Ouweltjes et al., 1996). In those studies, higher-yielding animals were associated with more days nonpregnant and hence longer calving intervals. Some studies

have reported no correlation between yield and fertility (Raheja et al., 1989; Weller, 1989).

Increasing the calving interval is undesirable, particularly in a production system in which there is a high demand for pregnant or lactating heifers, as in Kenya. This can occur if higher-yielding animals produce fewer replacements, due to a negative phenotypic correlation between calving interval and milk production. Also, a negative energy balance during early lactation in high-producing cows could affect the onset of estrus and hence result in longer calving intervals. Management has an important influence on the relationship between energy balance and milk yield. Further efforts need to be made in controlling the production environment to avoid slowing the rate of genetic gain in milk production due to an antagonistic relationship with fertility.

Age at first calving was used as a measure of heifer fertility in the Kenyan environment. A high heritability estimate (0.38) was obtained for this trait. This high estimate indicates that there is potential for improvement of this trait in Kenya through selection. A positive genetic correlation between age at first calving and milk yield in the first lactation was obtained. This implies animals with genetic potential for high milk production would tend to be older at first calving.

Age at first calving is a trait influenced by the breeding practices of producers. When calving is aimed for specific seasons, less variation in age at first calving can be expected. Published estimates of the heritability of age at first calving in Holsteins range from 0.05 (Seykora and McDonald, 1983) to 0.22 (Allaire and Lin, 1980). However, in the former study, herd-year-month of birth was used as a fixed effect, rather than herd-year-season of calving, which was used in the study by Allaire and Lin (1980). Seykora and McDonald (1983) and Hansen et al. (1983a) obtained negative (favorable) genetic correlations between yield and age at first calving. Grosshans et al. (1997) reported positive genetic and phenotypic correlations between age at first calving and milk production traits of dairy cows in New Zealand. Their result, obtained under conditions whereby seasonal breeding was practiced, indicated that heifers born early in the calving season produced more milk than those born later. Hodel et al. (1995) found that among first lactation cows, those with an age at first calving of more than 32 mo had poorer fertility than cows that calved at an earlier age. Early breeding of animals also had negative consequences such as calving difficulties, lower milk production, and poorer general body condition and hence was not advocated.

### Implications

Genetic parameter estimates for milk yield and calving interval obtained for the Kenyan Holstein population are comparable to those obtained in other regions. Earlier age at first calving was associated with higher

first lactation performance but a lower average milk yield over the first three lactations. Management of reproductive performance was adversely affected by higher milk yield. Higher-yielding animals require more attention to ensure that they calve regularly. Careful attention should be given to the selection of sires originating from various countries to avoid drastic fluctuations in cow productivity resulting from failure to identify specific selection criteria.

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