EFFECTS OF GENOTYPE BY ENVIRONMENT INTERACTIONS ON MILK PRODUCTION BETWEEN HOLSTEIN-FRIESIANS IN KENYA AND THE UNITED KINGDOM

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SUMMARY

Countries that import semen and have no extensive bull evaluation facilities of their own are faced with the problem of choosing bulls from a world-wide gene pool that would be suitable to their selection objective and environment. Where environments differ greatly, effects of genotype by environment interaction on production need to be taken into account.

First lactation records of daughters of Holstein-Friesian sires in Kenya and in the United Kingdom were analyzed. One hundred and fifty of the sires used in Kenya had an estimated breeding value calculated in the United Kingdom. Genotype by environment interactions were investigated in two ways: by determining the genetic correlation between the two countries for milk yield using both an animal model and a sire model, and by assessing the correlation between sire proofs calculated in the two countries.

Milk yield in Kenya was lower than in the UK (4057kg vs 7024kg). The heritability estimate for first lactation milk yield was also lower in Kenya (0.26±0.06) than in the UK (0.45±0.02). Genetic correlations significantly less than one were obtained from the joint evaluation using an animal model and a sire model (0.49±0.06 and 0.58±0.1). The results implied that genotype by environment interactions affected production between the two countries. The product moment correlation between breeding values was 0.45, and there was a significant change in rank of certain sires based on estimated breeding value for milk yield between the two countries.

Importation of semen into Kenya has improved productivity; however, the effects of genotype by environment interactions impede genetic gain and contribute to a reduced net economic benefit from artificial insemination.

Keywords: Genotype by environment interactions, genetic correlation, milk production

INTRODUCTION

Importation of semen of "high genetic merit" bulls to help improve milk production in tropical environments continues to increase as restrictions on marketing across borders ease. In temperate environments, genetic changes in animals have resulted from intense selection for milk yield and composition. These changes have dictated that dairy cattle management practices be changed to meet the increased needs of the animals (Pearson *et al.*, 1990). Tropical countries that import semen are faced with the problem of choosing between sires from a world-wide gene pool to suit their selection objective and environment.

A better understanding and exploitation of genotype x environment interactions, which are commonly encountered in the tropics, would help in the genetic improvement of production and adaptation of livestock to different farming systems. Mean milk yield and its variance between environments helps predict the magnitude of genotype x environment interactions (Stanton *et al.*, 1991). The magnitude of the interaction needs to be determined in order for countries with less advanced animal evaluation programmes to effectively adopt progress achieved elsewhere and thus avoid duplication of selection programmes.

The objective of this study was to determine possible genotype x environment interactions between the performance of Holstein-Friesian cattle in Kenya (a tropical country) and the United Kingdom (a temperate country).

MATERIALS AND METHODS

Data

Data was collected from seven medium to large-scale farms registered by the Dairy Recording Services of Kenya (DRSK) that were identified as Holstein-Friesian breeders in Kenya. Characteristics

of the farms have been described previously (Ojango and Pollott, 2000). A total of 5355 individual lactation records of cows born from 1985 to 1997 were obtained. Data on performance of Holstein-Friesian cattle in the United Kingdom (UK) was obtained from the National Milk Records (NMR) company. Herds selected in the UK for this analysis were required to have daughters of sires that had been used in Kenya. The data set comprised records on performance of 2998 sires with daughters on 98 farms. In total, 57,141 milk production records for animals born from 1984 to 1997 were obtained. The data from both countries was edited to include only first to third parity yields of animals with known pedigrees. Only animals with first lactation yields from 1985 to 1997 were retained. For all the animals, there was a 305-day milk yield, and an actual end of lactation yield, indicating the number of days in milk. For the UK, sires were required to have at least 10 daughters in 5 herds, and herds were to have at least 100 animals. The recording system for the UK was such that even if an animal had a lactation extending beyond 305-days, its actual production at 305-days was recorded. If an animal had a lactation shorter than 305 days, that yield was taken as that animal's 305-day yield without any adjustment of the yield. The data from the farms in Kenya consisted of total milk yields from lactations of varying lengths. Records were adjusted to a 305-day yield using coefficients obtained from fitting the lactation curve of Wood (1967) to a sample of data. The final number of animals retained with summary statistics for milk production in the two countries is presented in Table 1.

Table 1. Mean levels of production from Holstein-Friesians in the UK and Kenya

	UK	Kenya
Number of records	43056	3185
	Mean ± SD	
Total milk yield (kg)	8236 ± 2232	4541 ± 1639
305-day milk yield (kg)	7674 ± 1820	4557 ± 1620
Lactation length (days)	334 ± 57	300 ± 54

Seasons for the UK data were classified into three according to specifications from the Animal Data Centre (ADC) (Mrode, 2000), whereas for the Kenyan data, two seasons were used based on the rainfall pattern in the country. This grouping of seasons was used in defining a herd-year-season effect.

Model for analysis of milk yield in the two countries

Sources of variation in milk production in the two countries were assessed using general linear model procedures of SAS (Statistical Analysis Systems Institute, 1997). The following model was fitted to 305-day milk data from each country:

$$Y_{ijkm} = \mu + H_{ij} + L_k + a_m + b_1(X_{ijkm} - \overline{X}) + b_2(X_{ijkm} - \overline{X})^2 + e_{ijkm} \qquad 1$$

where Y_{ijkm} is the observation on an animal; H_{ij} denotes the fixed effect of the jth HYS in the ith herd; L_k denotes the fixed effect of the kth lactation number; a_m denotes the random effect of the mth animal; X_{ijkm} denotes the age at calving pertaining to record Y_{ijkm}; $\overline{X}$ is the mean age, b_1 and b_2 are the linear and quadratic regression coefficients on age at calving, and e_{ijkm} is the random residual error. Animals were absorbed in the analysis in order to reduce the size of the matrix of fixed effects. The DFREML programmes of Meyer (1998) were used to obtain estimates of genetic parameters.

Joint evaluation of animals in Kenya and UK

From the data obtained from the NMR, there were 76 sires with daughters' records in both Kenya and the United Kingdom. First lactation cow production records from the two countries were thus combined and a joint evaluation of animals carried out. The structure of the data used for the joint analysis is presented in Table 2. Two different analyses were carried out, an animal model analysis to assess differences in productivity across the two environments, and an analysis using a sire model, to assess differences in the average performance of daughters of various sires in the two environments.

Table 1. Summary of data used in joint analysis of first lactation records from the UK and Kenya

Trait	UK (Mean ±SD)	Kenya (Mean ± SD)
305-Day Milk (kg)	7024±1809	4057±1366
No. of records	19617	1589
No. of sires with progeny records	1008	253
No. of grand-sires with progeny records	322	171
No. of Herd-Year-Seasons	2053	150

The following multiple trait animal model was used to estimate (co)variance components. All relationships among animals were included in the analysis through use of a pedigree matrix.

$$\begin{pmatrix} y_1 \\ y_2 \end{pmatrix} = \begin{pmatrix} X_1 & 0 \\ 0 & X_2 \end{pmatrix} \begin{pmatrix} \beta_1 \\ \beta_2 \end{pmatrix} + \begin{pmatrix} Z_1 & 0 \\ 0 & Z_2 \end{pmatrix} \begin{pmatrix} \mu_1 \\ \mu_2 \end{pmatrix} + \begin{pmatrix} e_1 \\ e_2 \end{pmatrix} \qquad 2$$

y_1 and y_2 are vectors of observations for milk yield in Kenya and the United Kingdom respectively; X_i and Z_i are known incidence matrices associated with vectors of fixed (β_i, herd-year-seasons) and random (μ_i, animal) effects respectively; e_i is the vector of residual effects.

The multivariate sire model used for a joint analysis of the average performance of daughters of a sire between the two countries was of the same form as the animal model, only in place of the animal, the sire was used. Also, the relationship matrix used included relationships among sires. Yields in the two different countries were considered as different traits.

Comparison of EBV for sires used in Kenya with EBV obtained by the Animal data centre UK

Of the three hundred and fifty four bulls that had been used in Kenya either as sires of cows or sires of bulls, one hundred and fifty had a breeding value calculated in the UK. The UK breeding values were obtained from the Animal Data Center UK and the EBV for milk in the UK was regressed on the EBV calculated from the Kenyan data. A product-moment correlation coefficient was estimated between breeding values in the two environments as:

$$\hat{r} = \frac{Cov(EBV_k, EBV_{uk})}{\sqrt{VarEBV_k * VarEBV_{uk}}} \qquad 3$$

Where $\hat{r}$ is the correlation coefficient, $VarEBV_k$ is the variance component for the EBV in Kenya, $VarEBV_{uk}$ is the variance component for the EBV in UK, and Cov (EBV_k, EBV_{uk}) is the covariance between the EBV calculated in the two countries.

RESULTS

Evaluation of milk yield

Results of the analysis of variance in 305-day milk yield for the data obtained from the NMR in the UK and from data collected on large scale farms in Kenya are presented in Table 3. All the effects fitted significantly affected 305-day milk production in both countries. The model fitted accounted for a high proportion of the phenotypic variation with an R^2 value of 88.9 for the UK and 86.4 for Kenya. The coefficient of variation (%CV) was 11.34 for the UK and 19.27 for Kenya.

Table 2. Summary of analysis of variance for factors affecting 305-Day milk yield in the UK and Kenya

Source of Variation	UK df	UK P	Kenya df	Kenya P
Herd-Year-Season	2226	***	147	***
Lactation Number (LNo)	2	***	2	***
Month of calving	11	***	--	--
Age at calving*LNo (Linear)	3	***	3	***
Age at calving*LNo (Quadratic)	3	***	3	***

Joint evaluation of animals in Kenya and UK

Estimates of (co)variance, heritability (h^2) and genetic correlation (r_g) for first lactation milk yields obtained from the bivariate animal model evaluation of animals in Kenya and the UK are presented in Table 4. The heritability of first lactation milk yield in Kenya was 42% lower than that in the UK. The genetic correlation between the two countries for the trait though positive, was less than unity (0.49), suggesting a genotype x environment interaction for milk yield.

From the analysis of first lactation production between the two countries using a sire model the genetic correlation between the two countries was 0.58±0.1. This value was as expected, higher than that obtained when an animal model was used because the link between the two countries was provided through sires. Sigurdsson *et al.* (1996) noted that when genetic links between populations were weakened, the genetic correlation between the countries would be underestimated. From their study, a better estimate of genetic correlation was obtainable based on a well-connected subset of data rather than from an entire dataset.

Table 3. Genetic parameter estimates from bivariate analysis of first lactation milk yield in the UK and Kenya

Country	Additive variance	Residual variance	Covariance	Heritability (h^2)	Genetic correlation (r_g)
Kenya	221797	639470	176589	0.26±0.06	0.49±0.06
UK	582537	723895		0.45±0.02	

The EBV calculated for sires based on their daughters' production in Kenya was plotted against the EBV calculated for the sire based on the daughters' production in the UK and a product-moment correlation coefficient of 0.446 was obtained between the two countries (Figure1). This result further showed that the ranking of sires across the two environments was not the same for all sires.

Results from a mixed model analysis of the estimated breeding values from the two countries with sires grouped according to their country of origin and year of birth only found a significant relationship between the breeding values in the two countries. The added effects of country of origin and period of birth improved the R^2 value slightly to 27.5%. However, their inclusion did not cause any significant change in the correlation between EBV in Kenya and the UK.

DISCUSSION

Milk production and genetic parameter estimates

Sources of variation in milk production in the UK were similar to those that cause variation in milk production in Kenya. It was interesting to note that although the official milk production in the UK is reported to be for 305-days, individual animal lactations are of variable lengths, with some extending well beyond 305-days (Table 1). Long lactation lengths in tropical environments are often a source of concern as they result in long calving intervals and fewer offspring within an animals lifetime.

Milk yield of Holstein cows in Kenya was significantly lower than that in the UK ($p < 0.01$). There are several possible causes of the lower yields achieved in tropical relative to more temperate environments. These include a lower feed intake in the tropical environments. Forages available in tropical environments also tend to have more cell wall constituents than forages in temperate environments and thus restrict feed intake (Preston, 1995). Adaptability in terms of the ability to cope with different animal disease challenges in tropical environments could also affect production. In addition to physical effects of each region, environmental effects include differences in economic constraints and agricultural policies and, hence the herd management practices implemented.

Holsteins raised in the tropical environment of South America have been reported to have lower milk yields than in the more temperate USA and Canada (Costa et al., 1998; Powell and Wiggans, 1991; Powell et al., 1990; Stanton et al., 1991). Powell et al. (1990) suggested that the genetic ability to convert pasture into milk may be a trait different from the ability to convert a high grain diet into milk. In a study on genotype x nutrition interactions for efficiency of milk production in the UK, Mayne and Gordon (1995) showed that under intensive feeding systems in the UK, higher animal performance was obtained with high genetic merit cows, whereas when the animals were offered a high forage diet (of low energy density), the animals were unable to express their full genetic potential for milk production. From the study it was concluded that higher milk production in high genetic merit cows was largely attributable to variation in partitioning of nutrients rather than to changes in food intake or digestive efficiency. Further research on genotype x nutrition interactions in tropical environments is necessary.

Genotype x environment interactions

The environment provided in Kenya, reduced the proportion of variation attributed to additive effects of genes, hence reduced the expression of genetic variance in milk production. Reduced variances result in a compression of differences in transmitting abilities among sires. Less selection response would therefore be expected in Kenya than in the UK if selection in Kenya was practiced based on EBV calculated for the UK.

The genetic correlation obtained between the two countries using both an animal model and a sire model was significantly less than unity. The low genetic correlation implied that a re-ranking of sires based on EBV calculated in the two countries would be expected as a result of genotype x environment interactions. The regression of EBV obtained from the ADC for sires in the UK on the EBV calculated for the sires in Kenya yielded a low correlation coefficient (0.44), and a re-ranking of sires between the two countries occurred. The results from the different analytical procedures indicated that genotype x environment interactions existed and hence affected performance of the Holstein-Friesian in Kenya relative to the UK. The presence of genotype x environment interaction reduces the potential benefits from strategies of improvement based entirely on imports of germplasm from animals with superior genetic merit for milk production.
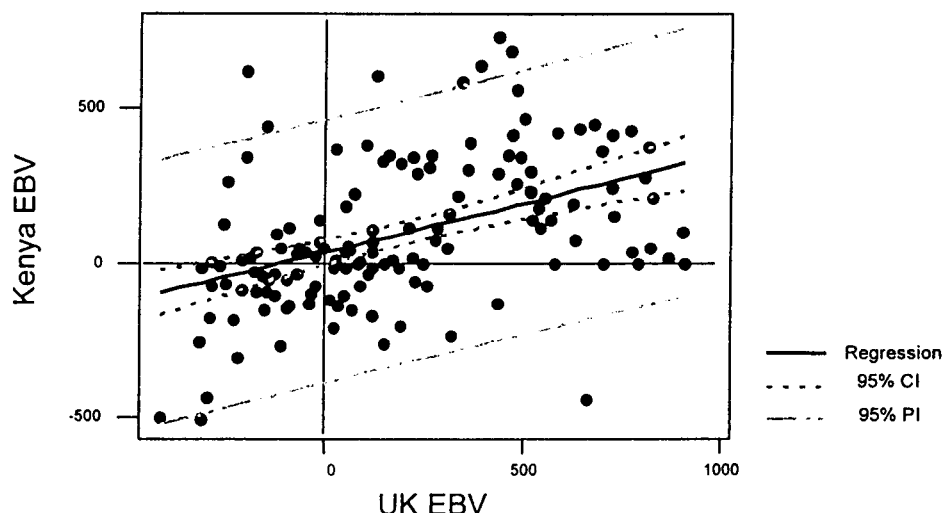
Figure 1 Product-Moment correlation between EBV calculated for Holstein-Friesians in Kenya, and EBV calculated by the Animal Data Centre in the UK

CI = Confidence interval
PI = Prediction interval
The regression equation for sire EBV in Kenya (y) on EBV in the UK (x) is:
$y = 36.3 + 0.315x$ $R^2 = 19.9\%$

CONCLUSIONS

Ignoring the genotype x environment interaction when selecting sires for use in Kenya could lead to random fluctuations in the genetic progress of milk production in the country. Due to the presence of genotype x environment interaction, wholesale importation of germplasm as a means of achieving sustainable genetic progress in more tropical environments is not a viable option. Selection of better performing dams within tropical environments to be used as dams of sires to be tested within the tropical environments should be encouraged.

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