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Genotype by Environment Interaction Effect on Lactation Pattern and Milk Production Traits in an Ethiopian Dairy Cattle Population

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ABSTRACT

The genotype by environment interaction (GEI) was evaluated for lactation milk yield (LY), initial milk yield (IY), peak milk yield (PY) and average milk yield per day (YD) in an Ethiopian multibreed dairy cattle population. Analyses used 4,488 lactation milk records from 1,320 cows collected at the Bako and Holetta research centers from 1979 to 2010. Breeds were Horro, Boran, Friesian crossbreds, Jersey crossbreds and Simmental crossbreds. The GEI for each trait was evaluated using estimates of cow breed group by environment (Bako and Holetta) interactions (univariate fixed models) and Spearman's rank correlations between sire-predicted values for the same trait measured in both environments (bivariate mixed models). Friesian crossbreds had higher ($P < 0.0001$) least squares mean (LSM) values for LY, IY, PY and YD than Simmental and Jersey crossbreds at Holetta, whereas Friesian and Simmental crossbreds had higher ($P < 0.0001$) LSM values for LY, PY and YD than Jersey crossbreds at Bako. Correlations between sire rankings at Bako and Holetta were 0.86 for LY and IY and 0.87 for YD indicating that substantial re-ranking occurred across locations. Thus, multiple-trait models with phenotypic information from Bako and Holetta would be needed to accurately select the most appropriate sires for each location.

Keywords: dairy cattle, genotype by environment interaction, multibreed

INTRODUCTION

Sustainable intensification of livestock production requires the appropriate use of genetic resources with an understanding of the limitations and opportunities of the production environment in which the animals will be maintained (Mathur and Horst, 1994). Tropical countries often rely on exotic germplasm for breeding purposes. Crossbreeding has been employed to combine high milk yield traits of *Bos taurus* breeds and adaptability traits of *Bos indicus* breeds (Koonawootrittriron *et al.*, 2002; Haile *et al.*, 2011; Gebreyohannes, *et al.*, 2013). However, climatic conditions, production systems and markets are frequently different from those where the animals were evaluated (Lin and Togashi, 2002). In countries like Ethiopia, with diverse agro-ecological conditions and livestock management practices, the performance of genotypes may differ substantially across the range of available environments. Differences between sires evaluated based on the genetic ability of their

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daughters to perform in different environments may be due to interactions between genotypes and environments (Boettcher *et al*., 2003).

Genotype × environment interaction (GEI) could be defined as a change in the relative performance of two or more genotypes measured in two or more environments. In general, GEI arises when the performance of the different genotypes is not equally influenced by the different environments (Falconer and Mackay, 1996). Studies (Merks, 1986; Cameron, 1993; Mathur and Horst, 1994; Calus, 2006) have defined genotype as breeds, lines, strains, families or sires, while environment has included factors such as time, location, nutrition, management and housing.

GEI may result in heterogeneity of genetic variances across environments, re-ranking of animals across environments and heterogeneity of correlations between two or more traits across environments (Merks, 1986; Calus, 2006). GEI that alters the ranking of series of genotypes between environments could considerably hamper selection. If GEI existed, the phenotypic expression of a trait in different environments would be determined by different sets of genes (Bertrand *et al*., 1987; Kolmodin and Bijma, 2004). In these cases, the breeding goal should account for both traits and the environments in which those traits would be expressed. Thus, the objective of this study was to evaluate the effect of genotype by environment interaction on the lactation pattern and milk production traits in Ethiopian dairy cattle from two geographical locations.

MATERIALS AND METHODS

Geographical locations and climatic conditions

Milk records of individual dairy cattle were obtained from research centers at Bako (1,672 records) and Holetta (2,816 records) in Ethiopia. The Bako Agricultural Research Center is located 250 km West of Addis Ababa at an altitude of 1,650 m above sea level (9º06' N and 37º09' E). The Center receives a mean annual rainfall of 1,200 mm in a bimodal distribution, 80% of which falls from May to September and the area had a mean relative humidity of 59% and monthly mean minimum and maximum temperatures of 13.5 and 27 ºC, respectively, with an average monthly temperature of 21°C (Gebreyohannes *et al*. 2003; Kumsa *et al*., 2006).

The Holetta Agricultural Research Center is located 45 km west of Addis Ababa at an altitude of 2,400 m above sea level (9º08' N and 38º05' E). It is situated in the central highlands of Ethiopia. It has an average annual rainfall of approximately 1,200 mm and the annual average temperature is 18 °C and the average monthly relative humidity is 60% (Demeke *et al*., 2004; Haile *et al*., 2011). Both Bako and Holetta receive a bimodal rainfall with a main rainy season ranging from May to September and a short rainy season from March to April. The season classification in both centers has varied in different studies with Demeke *et al*. (2004) classifying the year into three seasons based on the rainfall distribution as a main rainy season (June to September), a dry season (October to February) and a short rainy season (March to May). However, in the current study, four seasons were defined based on the rainfall distribution and availability of grasses in the grazing fields according to Kumsa *et al*. (2006). From June to August is the main rainy season where ample feed for the herd in the grazing paddocks is available as green grass. From September to November, grazing conditions deteriorate and rainfall decreases in both frequency and intensity and finally stops but the grazing conditions are supported by crop aftermath. From December to February (dry season) grazing paddocks are dry and animals need supplementary feed. Then from March to May (short rainy season) there are light showers in March which improve the grazing conditions and the availability of feed for the herds.

Herd feeding, management, breeding and health care

Herd feeding, management, breeding and health care have been in previous reports for Holetta (Demeke *et al*., 2004; Haile *et al*., 2011) and Bako (Gebreyohannes *et al*., 2003). The feeding system at Bako was mainly based on daily grazing natural pastures (*Cynodon* spp and *Hyparrhenia* spp*)* for approximately 9 hr (0800 to 1700 hours). Supplementation with hay (Rhodes grass (*Chloris gayana*) and natural pasture) or silage (Rhodes grass and maize (*Zea mays*) silage) at night was practiced depending on the grazing conditions. Concentrate supplement was fed only to milking cows at the time of milking and to pregnant cows during the last trimester of pregnancy. The concentrate mixture was composed of wheat bran (67%), '*noug'* (*Guizotia abyssinia*) seed cake (30%), bone meal (2%), salt and minerals (1%). Each kilogram of concentrate mixture provided 810.2 g of dry matter, 294.7 g of crude protein, 11.5 MJ of metabolizable energy and 717.5 g of digestible organic matter (Mesfin *et al*., 2003).

All animals were routinely monitored for any health problems and annually vaccinated against common diseases (such as, blackleg, anthrax, foot and mouth disease and contagious bovine pleuropneumonia) and sprayed against external parasites. Heifers were bred at age 2 yr or when they attained a body weight of 200 kg. Heat detection was done visually twice a day (between 0600 and 0800 hours and between 1700 and 1800 hours) by the inseminator and herdsmen during grazing time (0800 to 1700 hours) in the grazing paddocks. Cows that were bred and did not return to oestrous were checked for pregnancy after 2 mth. Pregnant cows were isolated from the rest of the herd during the last trimester of pregnancy and kept primarily indoors with limited grazing and exercise in nearby paddocks. After calving, the calf was separated from its dam and bucket fed colostrum and whole milk. Cows were hand milked twice a day (morning and evening). Breeding took place after a postpartum waiting period of 45 d (Gebreyohannes *et al*., 2003).

Cows in the herd at Holetta grazed on native pasture for approximately 8 hr during the day except during the main rainy season when animals were restricted from grazing. At night, all animals were housed and supplemented with natural pasture hay conserved from part of the grazing area. Except for the lactating cows, which were supplemented with approximately 3 to 4 kg of concentrate at each milking, no other animal received any regular concentrate supplement. Occasionally, during the long dry period and based on the condition of the animals, dry and young stock were supplemented with an unspecified amount of concentrate. All animals had free access to clean water (Demeke *et al*., 2004; Haile *et al*., 2011).

The breed groups represented at Bako and Holetta as sires and dams were: Horro (H), Boran (B), Friesian (F), Jersey (J), Simmental (S), (½ F × ½ H, ½ J × ½ H, ½ S × ½ H, ½ F × ½ B, ½ J × ½ B, ½ S × ½ B. Both centers used F, J and S semen supplied from the National Artificial Insemination Center (NAIC). Crossbred and local H and B bulls selected from available males in each center were used for natural service. Purebred sires (H, B, F, J and S) were mated to purebred indigenous dams (H and B) and to crossbred dams (½ F × ½ H, ½ J × ½ H, ½ S × ½ H, ½ F × ½ B, ½ J × ½ B, ½ S × ½ B). In addition, *inter se* matings existed between sires and dams of the six crossbred groups. Table 1 describes the mating design at both Holetta and Bako.

The semen was both imported and locally produced from purebred bulls by the NAIC. Mating took place throughout the year using both artificial insemination and natural service. The pedigree information of bulls and cows was checked to avoid mating between close relatives on both farms, but no selective mating based on performance information was practiced. The three exotic breeds were selected for the crossbreeding program because of their high milk yield (Friesian), high milk yield and milk fat percentage (Jersey;) and high milk and meat yield (Simmental) and the Boran and Horro breeds were chosen because they are both indigenous and widely distributed in southern and western Ethiopia, respectively (Gebreyohannes *et al.*, 2003; Demeke *et al.*, 2004).

Data and statistical analysis

The dataset consisted of lactation milk data from Horro, Boran, Friesian crossbreds, Jersey crossbreds and Simmental crossbreds collected from the Bako (from 1977 to 2010) and Holetta (from 1979 to 2010) research centers. The dataset was checked for connection among herd-year-season subclasses (contemporary groups) considering the presentation of sires using SAS (2003). Only herd-year-season subclasses with at least two sires, with one of them represented in two or more herd-year-season subclasses became part of the connected dataset for analysis as suggested by Koonawootrittriron *et al.* (2002).

The analysis used a total of 4,488 lactation records from 1,320 cows that were the progeny of 254 sires and 896 dams. There were 1,672 records of 460 cows born from 151 sires and 332 dams in the Bako dataset and 2,816 records of 860 cows born from 177 sires and 564 dams in the Holetta dataset. The two centers had 74 sires in common. The traits considered were actual lactation milk yield (LY; the sum of daily milk yield of the cow during the lactation period), initial milk yield (IY; the daily milk yield at the start of the lactation after the colostrum period of 5 d), peak milk yield (PY; the highest milk yield recorded during the lactation) and average milk yield per day (YD; average milk yield per day of lactation length). Data entry, sorting and preparation for the analysis were done using Microsoft Excel (Frye, 2007) and the Statistical Analysis System software package (SAS, 2003). Lactations shorter than 90 d were excluded from the analysis.

Table 1 Mating design at Bako and Holetta.

Sire breed group	Dam breed group	Progeny breed group
Horro (H)	Horro	Horro
Boran (B)	Boran	Boran
Friesian (F)	Horro	½ F × ½ H
Jersey (J)	Horro	½ J × ½ H
Simmental (S)	Horro	½ S × ½ H
Friesian	Boran	½ F × ½ B
Jersey	Boran	½ J × ½ B
Simmental	Boran	½ S × ½ B
½ F × ½ Horro	½ F × ½ H	½ F × ½ H
½ J × ½ Horro	½ J × ½ H	½ J × ½ H
½ S × ½ Horro	½ S × ½ H	½ S × ½ H
½ F × ½ Boran	½ F × ½ B	½ F × ½ B
½ J × ½ Boran	½ J × ½ B	½ J × ½ B
½ S × ½ Boran	½ S × ½ B	½ S × ½ B
Friesian	½ F × ½ H	¾ F × ¼ H
Jersey	½ J × ½ H	¾ J × ¼ H
Simmental	½ S × ½ H	¾ S × ¼ H
Friesian	½ F × ½ B	¾ F × ¼ B
Jersey	½ J × ½ B	¾ J × ¼ B
Simmental	½ S × ½ B	¾ S × ¼ B

The analysis of variance was first done to test the interaction between breed groups and environments using PROC GLM of SAS (2003) in terms of means. The model considered the fixed effects of calving year-season contemporary group, parity, environment (Bako and Holetta), breed group of cow and breed group of cow by environment interaction. The lactation length was included as a fixed covariate for the analysis of lactation milk yield. By combining the herds, calving years and seasons, 248 herd-year-season contemporary group subclasses were formed. There were seven parities (1 to 7 with the 7th parity including parities 7 and above), two environments (Bako and Holetta) and five cow breed groups (Horro, for pure Horro; Boran for pure Boran; Friesian crossbreds for Friesian crosses with Boran and Horro; Jersey crossbreds for Jersey crosses with Boran and Horro; and Simmental crossbreds for Simmental crosses with Boran and Horro). The statistical model used for the analysis had the general form shown in Equation 1:

$$y_{ijklm} = \mu + cg_i + P_j + Env_k + B_l + (B\times H)_{lk} + e_{ijklm} \quad (1)$$

where y_{ijklm} is the observation for m^{th} animal in i^{th} calving year-season contemporary group, j^{th} parity, k^{th} environment and l^{th} cow breed group subclass; cg_i is the i^{th} calving year-season contemporary group subclasses (i = 1 to 248); P_j is the j^{th} parity ($j = 1, 2, 3, 4, 5, 6$ and ≥ 7 parities); Env_k is the k^{th} environment (k = 1, 2; Bako and Holetta); B_1 is the l^{th} cow breed group (l = 1 to 5; Horro, Boran, Friesian crossbreds, Jersey crossbreds and Simmental crossbreds); $(B \times H)_{lk}$ is the interaction between the l^{th} cow breed group and k^{th} environment and e_{ijklm} is the residual error associated with y_{ijklm}.

Least squares means were estimated and they were compared among subclasses of fixed effects using Bonferroni *t*-tests (SAS, 2003).

Variance component estimation and prediction of estimated breeding value

Variance components were estimated using an average information restricted maximum likelihood (AI-REML) procedure of the ASREML software (Gilmour *et al.*, 2009). A bivariate sire model for repeated records that considered year-season subclasses, parity subclasses, H, B, F, J and S breed fraction of sire, H, B, F, J and S breed fraction of dam and the general heterozygosity of cow as fixed effects and the random effects of sire additive genetic, permanent environment of their daughters and residual were used to estimate the variance components and to predict breeding values. There were 137 year-season-of-calving subclasses and 7 parities. The general heterozygosity of cows involved in interbreed interactions between alleles of any two different breeds among the five breeds (H, B, F, J and S) present in the population was calculated using Equation 2:

$$H_g = 1 - \sum_{i=1}^{5} S_i \times D_i \quad (2)$$

where H_g is the general heterozygosity of a cow and S_i and D_i are the fractions of breed *i* in the sire and dam, respectively.

The random permanent environment effect was included in the model because of repeated records due to multiple parities. The expression of the same trait (LY, IY, PY and YD) in two environments was considered to be two different traits and the genetic correlation between them was estimated in the same way as for any two correlated traits. The model could be described in matrix notation by Equation 3:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix}\begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} + \begin{bmatrix} Q_1 & 0 \\ 0 & Q_2 \end{bmatrix}\begin{bmatrix} g_1 \\ g_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix}\begin{bmatrix} s_1 \\ s_2 \end{bmatrix} + \begin{bmatrix} W_1 & 0 \\ 0 & W_2 \end{bmatrix}\begin{bmatrix} pe_1 \\ pe_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} \quad (3)$$

where y_1 and y_2 are the vectors of observations (LY, IY, PY and YD) in environments 1 and 2, respectively; β_1 and β_2 are the vectors of the fixed effects of year-season of calving and parity subclasses and covariates (LL for the analysis of LY only); g_1 and g_2 are vectors of fixed sire breed, dam breed and general heterosis effects; s_1 and s_2 are the vectors of the random sire additive genetic effects; pe_1 and pe_2 are vectors of random permanent environmental effects due to repeated records; e_1 and e_2 are the vectors of random residual effects; X_1 and X_2 are known incidence matrices relating observations to fixed effects; Q_1 and Q_2 are matrices relating observations to sire breed effects (through sire breed fractions), dam breed effects (through dam breed fractions) and cow general heterosis effects (through cow general heterozygosities); W_1 and W_2 are known incidence matrices relating observations to random permanent environmental effects; and Z_1 and Z_2 are known incidence matrices relating observations to sires random effects in environments 1 and 2, respectively.

The model assumed the expected value of y to be Xβ + Qg. The vectors of sire additive genetic effects, permanent environment effects and residuals were assumed to have a normal distribution with a mean of zero. The variance-covariance matrix for the random effects was formulated as Equation 4:

$$\operatorname{var}\begin{bmatrix} s_1 \\ s_2 \\ pe_1 \\ pe_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\ \sigma^2_{s_1} & A\ \sigma_{s_{12}} & 0 & 0 & 0 & 0 \\ A\ \sigma_{s_{21}} & A\ \sigma^2_{s_2} & 0 & 0 & 0 & 0 \\ 0 & 0 & I_n\sigma^2_{pe_1} & 0 & 0 & 0 \\ 0 & 0 & 0 & I_n\sigma^2_{pe_2} & 0 & 0 \\ 0 & 0 & 0 & 0 & I_n\sigma^2_{e_1} & 0 \\ 0 & 0 & 0 & 0 & 0 & I_n\sigma^2_{e_2} \end{bmatrix} \qquad (4)$$

where σ^2_s, σ^2_{pe} and σ^2_e are sire additive genetic, permanent environment and residual variances, respectively; $\text{var}(y) = \sigma^2_s + \sigma^2_{pe} + \sigma^2_e$, $\sigma^2_s = 0.25\ \sigma^2_a$; matrix A is the numerator relationship matrix that includes all animals in the population; and matrix I_n is an identity matrix. The permanent environment and residual covariances between the environments 1 and 2 were assumed to be zero. The heritability for the trait in the ith environment was computed as $h^2_i = 4\sigma^2_{s_i} / \sigma^2_{p_i}$, where $\sigma^2_{s_i}$ and $\sigma^2_{p_i}$ are the sire additive genetic and phenotypic variances, respectively, for the trait in the ith environment (i =1 and 2). The genetic variance in the ith environment was $\sigma^2_{a_{ii}} = 4\sigma^2_{s_i}$ and the genetic standard deviation was for $\sigma_{a_{ii}}$ i = 1 and 2. The genetic covariance between environments 1 and 2 was $\sigma_{a_{12}} = 4\sigma_{s_{12}}$ and the genetic correlation between a trait evaluated in environments 1 and 2 was computed as $r_{g_{12}} = \sigma_{a_{12}} / (\sigma_{a_{11}} \cdot \sigma_{a_{22}})$.

Common sires in the two environments and their additive genetic relationships to other animals in the population permitted the computation of additive genetic correlations between traits measured at Holetta and Bako. The estimated breeding value (EBV) for sires was obtained using best linear unbiased prediction procedures and computed with ASREML (Gilmour *et al.*, 2009).

The EBV for a sire was calculated as the weighted sum of its additive breed group solution plus twice its additive genetic prediction as a deviation from its breed group. The EBV for each sire was computed as: $\hat{u} = Q_s g^o + 2\hat{s}$, where $\hat{u}$ is the EBV of an individual sire for a particular trait, g^o is a vector of generalized least squares solutions for differences between sire breeds H, F, J and S and B, Q_s is a vector of fractions of B, H, F, J and S breeds in an individual sire and $\hat{s}$ is the predicted value of the random sire additive genetic deviation from its breed group (Elzo and Famula, 1986; Arnold *et al*., 1992; Koonawootrittriron *et al*., 2002; Bryant *et al*., 2005). Sires were ranked within each environment based on their EBVs for each trait and then Spearman's rank correlations were estimated using PROC CORR of SAS (2003).

RESULTS AND DISCUSSION

Breed group by environment interaction

Lactation milk yield (LY), initial milk yield (IY), peak milk yield (PY) and average milk yield per day (YD) were significantly different (*P* < 0.0001) among herd-year-season contemporary group (CG), parity, environment, cow breed group and cow breed group × environment interaction (GEI) subclasses. The effect of lactation length on LY was significant (*P* < 0.0001). The herd at Holetta had higher least squares mean (LSM) values for LY (1,657.53 ± 27.18 versus 1,428.31 ± 25.83 kg), IY (6.76 ± 0.13 versus 4.52 ± 0.12

kg), PY (9.00 ± 0.13 versus 6.72 ± 0.12 kg) and YD (4.85 ± 0.08 versus 4.06 ± 0.08 kg) than the herd at Bako ($P < 0.0001$; Table 2).

The GEI showed that the Friesian crossbred cows at Holetta had higher ($P < 0.0001$) LSM values for LY (2,111.91 ± 16.88 kg), IY (9.26 ± 0.08 kg), PY (11.64 ± 0.08 kg) and YD (6.57 ± 0.05 kg) than Simmental and Jersey crossbreds cows at Holetta and Friesian, Jersey and Simmental crossbred cows at Bako. The LSM values for LY, IY, PY and YD from Jersey and Simmental crossbred cows at Holetta were similar ($P > 0.05$). The LSM values for LY, PY and YD from Simmental crossbred cows (1,725.06 ± 38.50 kg, 8.75 ± 0.18 kg and 5.29 ± 0.12 kg) and for Friesian crossbred cows (1,703.21 ± 25.06 kg, 8.64 ± 0.12 kg and 5.19 ± 0.08 kg) were higher ($P < 0.0001$) than the LSM values for LY, PY and

Table 2 Least square means ± standard errors for lactation pattern and milk production traits.

Factor	Trait			
	LY (kg)	IY (kg)	PY (kg)	YD (kg)
Breed group	$P = 0.0001$	$P = 0.0001$	$P = 0.0001$	$P = 0.0001$
Boran	1,167.64 ± 66.14^{c}	3.45 ± 0.30^{c}	5.30 ± 0.32^{d}	2.86 ± 0.20^{d}
Horro	1,189.28 ± 51.88^{c}	3.52 ± 0.24^{c}	5.42 ± 0.25^{d}	2.77 ± 0.16^{d}
Friesian XB	1,907.56 ± 15.14^{a}	7.64 ± 0.07^{a}	10.14 ± 0.07^{a}	5.88 ± 0.05^{a}
Jersey XB	1,684.09 ± 17.65^{b}	6.69 ± 0.08^{b}	8.92 ± 0.08^{c}	5.21 ± 0.05^{c}
Simmental XB	1,766.04 ± 26.60^{b}	6.90 ± 0.12^{b}	9.55 ± 0.13^{b}	5.55 ± 0.08^{b}
Parity	$P = 0.0001$	$P = 0.0001$	$P = 0.0001$	$P = 0.0001$
1	1,219.21 ± 25.30^{c}	3.65 ± 0.12^{d}	6.07 ± 0.12^{c}	3.48 ± 0.08^{c}
2	1,453.71 ± 25.58^{b}	5.15 ± 0.12^{c}	7.37 ± 0.12^{b}	4.18 ± 0.08^{b}
3	1,590.87 ± 27.06^{a}	5.88 ± 0.12^{b}	8.18 ± 0.13^{a}	4.61 ± 0.08^{a}
4	1,638.36 ± 28.75^{a}	6.15 ± 0.13^{ab}	8.43 ± 0.14^{a}	4.71 ± 0.09^{a}
5	1,667.29 ± 32.32^{a}	6.36 ± 0.15^{a}	8.63 ± 0.15^{a}	4.84 ± 0.10^{a}
6	1,604.07 ± 37.04^{a}	6.01 ± 0.17^{ab}	8.18 ± 0.18^{a}	4.65 ± 0.11^{a}
7	1,626.95 ± 34.75^{a}	6.27 ± 0.16^{ab}	8.19 ± 0.17^{a}	4.71 ± 0.11^{a}
Environment	$P = 0.0001$	$P = 0.0001$	$P = 0.0001$	$P = 0.0001$
Bako	1,428.31 ± 25.83^{b}	4.52 ± 0.12^{b}	6.72 ± 0.12^{b}	4.06 ± 0.08^{b}
Holetta	1,657.53 ± 27.18^{a}	6.76 ± 0.13^{a}	9.00 ± 0.13^{a}	4.85 ± 0.08^{a}
GEI	$P = 0.0001$	$P = 0.0001$	$P = 0.0001$	$P = 0.0001$
Bako–B	965.57 ± 106.38^{d}	2.17 ± 0.49^{e}	3.60 ± 0.51^{g}	2.34 ± 0.33^{e}
Bako–H	1,172.68 ± 33.97^{d}	2.87 ± 0.15^{e}	4.73 ± 0.16^{fg}	2.68 ± 0.10^{e}
Bako–FXB	1,703.21 ± 25.06^{b}	6.03 ± 0.12^{c}	8.64 ± 0.12^{c}	5.19 ± 0.08^{c}
Bako–JXB	1,575.06 ± 26.67^{c}	5.54 ± 0.12^{cd}	7.89 ± 0.13^{d}	4.81 ± 0.08^{d}
Bako–SXB	1,725.06 ± 38.50^{b}	6.00 ± 0.18^{c}	8.75 ± 0.18^{c}	5.29 ± 0.12^{bc}
Holetta–B	1,369.72 ± 76.75^{cd}	4.72 ± 0.35^{d}	6.99 ± 0.37^{de}	3.49 ± 0.24^{e}
Holetta–H	1,205.88 ± 96.65^{d}	4.17 ± 0.44^{de}	6.11 ± 0.46^{ef}	2.86 ± 0.30^{e}
Holetta–FXB	2,111.91 ± 16.88^{a}	9.26 ± 0.08^{a}	11.64 ± 0.08^{a}	6.57 ± 0.05^{a}
Holetta–JXB	1,793.11 ± 22.91^{b}	7.83 ± 0.11^{b}	9.96 ± 0.11^{b}	5.60 ± 0.07^{b}
Holetta–SXB	1,807.03 ± 34.17^{b}	7.79 ± 0.16^{b}	10.35 ± 0.16^{b}	5.72 ± 0.11^{b}

$^{a, b, c, d, e, f, g}$ Least square means within a column group with different superscript letters differ significantly ($P < 0.0001$).

GEI = genotype by environment interaction, B = Boran, H = Horro, FXB = Friesian crossbreds, JXB = Jersey crossbreds and SXB = Simmental crossbreds.

LY = lactation milk yield, IY = initial milk yield, PY = peak milk yield, YD = average milk yield per day.

YD from Jersey crossbred cows at Bako (Table 2). However, the LSM values for IY were not different ($P > 0.05$) among Friesian, Simmental and Jersey crossbred cows at Bako. The Boran cows were not different ($P > 0.05$) from Horro cows at both Holetta and Bako for all traits (LY, IY, PY and YD).

The significant effect of cow breed group on milk production traits observed in this study could have been due to the large genetic differences in milk yield among the additive genetic effects of introduced and indigenous animals as well as the nonadditive genetic effects generated by crossbreeding. Sires from temperate breeds have been used to improve the milk production of the tropical breeds in many countries (McDowell, 1985) due to the higher genetic ability of their daughters to produce milk. A similar situation existed here. Indigenous H and B cows had lower LY, IY, PY and YD compared to the Friesian, Jersey and Simmental crossbred cows.

The interaction between genotype (cow breed groups) and environment (Bako and Holetta) was significant for all traits ($P < 0.0001$; Table 2). According to Falconer and Mackay (1996), GEI arises when the performance of different genotypes is not equally influenced by different environments. In the present study, climatic conditions and the management of the herds differed at Bako and Holetta. These dissimilarities in climate, management and feeding likely contributed to breed group differences in performance at these two locations.

Variance components, genetic parameters and sire estimated breeding values

The variance components and genetic parameters were estimated for LY, IY, PY and YD. The sire additive genetic variance was larger for all traits, except for LY at Bako than at Holetta. Conversely, permanent environmental, residual and phenotypic variances for LY, IY, PY and YD were lower at Bako than at Holetta (Table 3). The heritability estimates (Table 4) for LY, IY, PY and YD were medium, ranging from 0.15 ± 0.06 (IY at Holetta) to 0.34 ± 0.13 (YD at Bako). The heritabilities at Holetta were somewhat lower than those at Bako for all traits. The lower heritabilities at Holetta than Bako were largely due to higher permanent environmental variances at Holetta than Bako (for example, 66,544.20 kg^2 vs. 125,166.00 kg^2 for LY; Table 3). The permanent environmental variance estimates suggested that the permanent environmental effects affected LY, IY, PY and

Table 3 Variance components for lactation pattern and milk production traits at Bako and Holetta.

	Trait			
	Lactation milk yield (kg^2)	Initial milk yield (kg^2)	Peak milk yield (kg^2)	Average milk yield per day (kg^2)
Bako				
σ^2_s	14,446.50	0.33	0.37	0.19
σ^2_{pe}	66,544.20	1.15	2.07	0.78
σ^2_e	118,158.00	3.36	2.98	1.28
σ^2_p	199,148.70	4.83	5.41	2.25
Holetta				
σ^2_s	18,681.10	0.24	0.33	0.17
σ^2_{pe}	125,166.00	1.95	2.30	1.10
σ^2_e	142,012.00	4.19	3.47	1.41
σ^2_p	285,859.10	6.38	6.11	2.68

σ^2_s = sire additive genetic variance, σ^2_{pe} = permanent environmental, σ^2_e = residual variance, σ^2_p = phenotypic variance.

YD to a higher degree at Holetta than Bako. The medium heritabilities obtained at Bako and Holetta suggested that genetic improvement for these traits could be achieved through the selection of sires at both locations.

The heritability estimates for LY at Bako and Holetta were lower than the value obtained using a single-trait repeatability animal model with a combined dataset from the same population (0.36 ± 0.04) according to Gebreyohannes *et al*. (2013). Despite the better environmental conditions at Holetta relative to Bako (reflected by the higher lactation milk yield at Holetta; Table 1), the heritability at Holetta was lower than at Bako suggesting that the higher level of production at Holetta was probably due to a larger extent to favourable environmental conditions than to genetic differences among sires. In agreement with these results, Sofla *et al*. (2011) reported heritability estimates for LY in Iranian Holstein in less favourable climates (dry desert, 0.28 ± 0.06; and semi-dry, 0.30 ± 0.07) that were similar to or higher than heritabilities in more favourable climates (Mediterranean, 0.24 ± 0.05; humid, 0.29 ± 0.06; and semi-humid, 0.26 ± 0.05). Similarly, Nauta *et al*. (2006) found lower heritabilities in conventional intensive production environments (0.48 ± 0.03) than in organic production environments (0.70 ± 0.08) in the Netherlands.

However, results from other studies differed. The estimate of heritability for LY in high input herds in Ireland was higher (0.43 ± 0.03) than in low input herds (0.29 ± 0.04) according to Cromie *et al*. (1998). Similarly, Castillo-Juarez *et al*. (2002) found higher heritability estimates in herds with high mature equivalent milk yield means (0.30) than herds with low mature equivalent milk yield means (0.22) in northeast USA using records from primiparous Holstein cows. The low and high milk yield environments had mature equivalent milk yield means of less than 9,307 and greater than or equal to 9,864 kg and standard deviations greater than or equal to 1,621 and less than or equal to 1,479 kg, respectively. The low milk yield environment reported by Castillo-Juarez *et al*. (2002) was substantially higher than the milk production levels at Holetta and Bako. GEI studies also found that less favourable environmental conditions across countries produced similar effects on the heritability for milk yield.

Ojango and Pollott (2002) investigated the relationship between breeding values of Holstein bulls for milk production used in the United Kingdom (UK) and Kenya. Milk yield was significantly higher in the UK than in Kenya, perhaps due to a combination of lower adaptability of Holstein cows and to lower feed intake under tropical Kenyan conditions. The heritability for first lactation 305 d milk yield was higher in the UK (0.45 ± 0.02) than in Kenya (0.26 ± 0.06) and the genetic correlation between these two countries

Table 4 Heritabilities, genetic correlations and Spearman's rank correlations for lactation pattern and milk production traits at Bako and Holetta.

Traits	Heritability		Genetic correlation[1]	Spearman's correlation
	Bako	Holetta		
Lactation milk yield (kg)	0.29 ± 0.12	0.26 ± 0.08	0.82 ± 0.32	0.86*
Initial milk yield (kg)	0.27 ± 0.11	0.15 ± 0.06	0.53 ± 0.39	0.87*
Peak milk yield (kg)	0.27 ± 0.01	0.22 ± 0.01	-	-
Average milk yield per day (kg)	0.34 ± 0.13	0.26 ± 0.08	0.61 ± 0.33	0.86*

Values are shown as least square mean ± standard error.

* $P < 0.0001$.

[1] = Genetic correlation for peak milk yield was inestimable.

was 0.49 ± 0.06. Milk yields for first-parity cows and the heritability value for milk yield in Kenya were comparable to those obtained at Bako and Holetta. The higher heritabilities estimated by Castillo-Juarez *et al*. (2002) in the USA, by Ojango and Pollott (2002) in the UK and by Nauta *et al*. (2006) in the Netherlands may have been due to a higher variability among animals and higher nutritional levels in these studies than in the two herds in the current study.

A high genetic correlation between a trait measured in two environments is an indication of the GEI interaction (Robertson, 1959; Falconer and Mackay, 1996). In the absence of GEI, the genetic correlation across environments is expected to be one. If the genetic correlation among environments is significantly less than one, then GEI needs to be considered in genetic-statistical models used for the genetic evaluation and selection of animals. Robertson (1959) suggested that to have biological and agricultural importance, the genetic correlation between two environments should be 0.8 or lower.

In the present study (Table 4), low genetic correlations between Bako and Holetta were obtained for LY (0.82 ± 0.32), IY (0.53 ± 0.39) and YD (0.61 ± 0.30) suggesting GEI between these two locations existed for these three traits. The genetic correlation between Bako and Holetta could not be estimated for PY. The estimate of the genetic correlation between Bako and Holetta for LY agreed with the genetic correlation (0.78) between two regions (Drier Overberg and South Cape region versus Subtropical Limpopo and Northern KwaZulu-Natal) obtained for a Jersey population in South Africa (Van Niekerk *et al*., 2006). Nauta *et al*. (2006) also estimated a similar genetic correlation for milk yield (0.80; $P < 0.01$) between a conventional production system and an organic production system suggesting the presence of GEI for milk yield between these two environments.

Similarly, genetic correlations for LY in Iranian Holstein were low (0.66 to 0.84) between a humid climate and three other climates (dry desert, semi-dry and Mediterranean) suggesting the presence of GEI. Boettcher *et al*. (2003) estimated a genetic correlation (0.93 ± 0.04) for milk yield in two herd management systems (intensive rotational grazing versus conventional involving stored feeds) in Canada suggesting minor GEI effects for milk yield. The lower genetic correlations for LY between Bako and Holetta suggested that environmental conditions (climate, feeding and management) in these two Ethiopian locations differed to a higher degree than the conditions in the two production systems in the Canadian study.

Differences in environmental conditions between Bako and Holetta were also reflected in the values of Spearman’s rank correlations (Table 4) between the sire EBVs from these two locations for LY (0.86), IY (0.86) and YD (0.87). These rank correlations associated with re-ranking of sires occurred for LY, IY and YD. Sire re-ranking between Bako and Holetta is illustrated with the group of sires within the top 20 based on their EBVs present at both locations. Of the top 20 sires with the highest EBVs for LY, IY and YD in each environment, 10 sires (50%) for LY and 9 sires (45%) for IY and YD were present at Bako and Holetta. Among the 10 sires in common for LY, 3 sires had higher ranking at Bako than Holetta, 4 sires had lower ranking at Bako than Holetta and 3 sires had the same ranking at both locations (Figure 1). Substantial sire re-ranking was also observed for IY (Figure 2) and YD (Figure 3). In addition, 6 of the top 10 sires for LY, 7 of the top 9 sires for IY and 8 of the top 9 sires for YD were Friesian. Thus, daughters of Friesian sires outperformed daughters of Jersey and Simmental sires for LY, IY and YD in this multibreed population.

Table 5 shows the means, SD and the minimum and maximum sire EBVs for LY, IY, PY and YD at Bako and Holetta. Means were higher, SD values were similar or higher and ranges wider at Bako than Holetta. These SD values and ranges reconfirm that the environment at

Holetta permitted a fuller expression of the genes affecting these dairy traits than the environment at Bako. The range of the sire EBVs for all traits showed a wide range of values among sires within and across breed groups at both locations. For example, the EBVs for LY ranged from -12.1 to 1,245.7 kg for Bako and -389.9 to 1,380.3 kg for Holetta. This range was wider than the range of values for Holstein cattle in Iraq (-394.00 to 475.00 kg) according to Ayied *et al.* (2011). This could have been due to genetic differences among breeds and sires within the breeds used in Ethiopia compared to the Holstein sires used in Iraq. The high variability in the sire EBVs observed at Bako and Holetta was likely due to the wide range of genetic merit of purebred and crossbred sires from the five local and temperate breeds utilized in this study (Boran, Horro, Friesian, Jersey, Simmental; Table 1). The wide range of sire EBVs suggests that there was little or no selection of sires in the two environments. This was expected because the primary objective of the crossbreeding program at Bako and Holetta was not the selection of animals, but the evaluation of different crossbred groups under two different environments. However, the wide range of sire EBVs found at Bako and

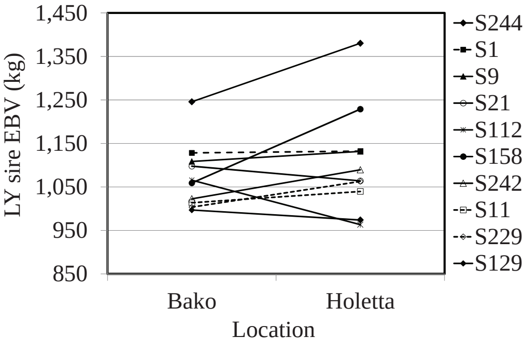

Figure 1 Estimated breeding value (EBV) of each of the top 10 sires for lactation milk yield (LY) at Bako and Holetta.

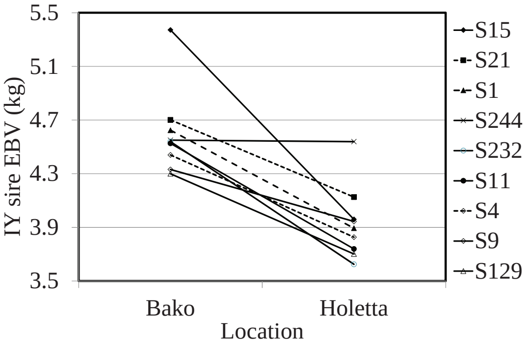

Figure 2 Estimated breeding value (EBV) of each of the top nine sires for initial milk yield (IY) at Bako and Holetta.

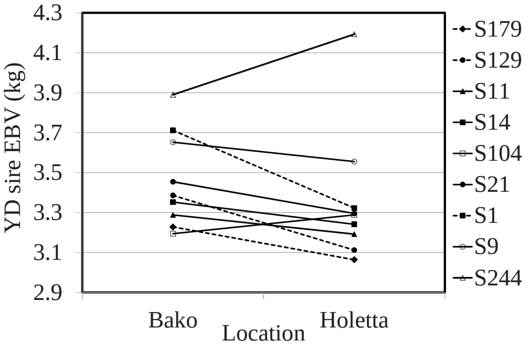

Figure 3 Estimated breeding value (EBV) of each of the top nine sires for average yield per day (YD) at Bako and Holetta.

Table 5 Mean, standard deviation, minimum and maximum of estimated breeding values for lactation pattern and milk production traits of sires used at Bako and Holetta.

Trait	N	Bako				Holetta			
		Mean	SD	Min	Max	Mean	SD	Min	Max
LY (kg)	254	673.6	278.7	-12.1	1,245.7	540.4	339.5	-389.9	1,380.3
IY (kg)	254	2.9	1.2	-0.3	5.4	2.0	1.2	-1.1	4.5
PY (kg)	254	4.1	1.6	-0.1	7.3	2.5	1.5	-0.9	6.0
YD (kg)	254	2.2	0.9	0.0	3.9	1.7	1.0	-1.0	4.2

LY = lactation milk yield; IY = initial milk yield; YD = average milk yield per day.
N = number of sires; SD= standard deviation; Min = minimum; Max = maximum.

Holetta suggests large genetic differences among them which could be advantageous if a selection program for dairy traits were to be implemented in these locations.

Estimates of genetic correlations for LY, IY and YD and changes in sire rankings between Bako and Holetta (Figures 1, 2 and 3) indicated that data and genetic predictions from only one location could not be used reliably to select sires for the other location. Thus, it would be advisable to use the phenotypic information from both locations (Bako and Holetta) and multiple-trait models to appropriately evaluate and select sires for each environment. Further, to help increase the accuracy of genetic predictions, genetic evaluation models that include two or more traits measured in both environments should be considered if sufficient data were available. For example, it is well known that IY and YD are highly correlated with LY within an environment (Tekerli *et al*., 2000; Seangjun *et al*., 2009). Considering the availability of LY, IY and YD data in this population, a genetic evaluation with these three traits could be a possibility provided that sufficient numbers of records were available at both locations to accurately estimate the genetic correlations between Bako and Holetta. Genetic correlations among LY, IY and YD within and across locations would be expected to increase the accuracy of sire genetic predictions within and across environments, thus increasing expected genetic trends in all environments.

CONCLUSION

Significant differences among breed group means at Bako and Holetta suggested that they expressed their milk yield production potential differently at these two locations. Genetic correlations between dairy traits measured at Bako and Holetta as well as Spearman’s rank correlations between sire predicted breeding values across locations suggested that genetic evaluation and the selection of sires would require information from both locations to accurately select the most appropriate sires for each location.

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