



Effects of breed exoticness, agro-ecological zone and their interaction on production and fertility traits of multibreed dairy cattle in Kenya

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Executive summary

The aim of this study was to evaluate the effect of degree of exoticness, agro-ecological zone, and their interaction on production and fertility traits in multibreed dairy cattle. Milk yield (MY) records ($n = 62,321$) together with fertility trait records on age at first calving (AFC) ($n = 1,490$) and calving interval (CI) ($n = 2,640$) from a total of 1,490 dairy cows performing in semi-arid arable (SAA), semi-arid pasture-based (SAP) and semi-humid (SH) agro-ecological zones of Kenya were analysed. Animals were grouped into two degree of exoticness classes based on the proportion of exotic blood in their breed composition. These classes were, Exotic Class 1 (EC1) ($\leq 50\%$ exotic, $n = 481$) and EC2 ($> 50\%$ exotic, $n = 1,009$). To achieve the objectives of this study, a multiple linear regression model was fitted for AFC and a mixed-repeatability model for CI and daily MY. Overall, EC2 cows had significantly lower AFC than EC1 cows (32.4 ± 0.2 vs. 34.0 ± 0.2 months, $P < 0.001$) while EC1 cows had a shorter CI than EC2 cows (452 ± 6 vs. 466 ± 7 days, $P < 0.05$). No significant difference was observed in MY between the two breed groups at the population level. Across environments, the comparison showed that EC1 had a larger AFC of 36.7 ± 0.4 months in SAP agro-ecological zone compared to 31.0 ± 0.6 months in the SH environment. For EC2, however, it was in SAA agro-ecological zone where cows had higher AFC compared to the SH environment (34.7 ± 0.2 vs. 28.9 ± 0.3). Milk yield was highest in SH and lowest in SAP environment for both breed groups. Although the SH agro-ecological zone seemed to favour the onset of puberty and high milk yield, this environment had a significantly longer CI for both breed groups (478 ± 9 days for EC1 and 484 ± 7 for EC2). Genotype by environment interaction was significant for AFC and MY ($P < 0.01$). These findings have demonstrated that biophysical variation in different agro-ecological zones affects production and fertility traits in multibreed dairy cattle differently and hence, it is an important factor to consider when designing genetic improvement programs.

1 Introduction

Sub-Saharan Africa (SSA) host about 14.3% of the world's human population. However, it only produces around 3.4% of global cow milk (FAOSTAT 2021). The demand for milk and dairy products in this region is increasing by more than 2% per annum (Alexandratos and Bruinsma 2012) due to population growth, income growth and increasing urbanization (Steinfeld et al. 2006; Thornton 2010). There is therefore a need for dairy production in this region to significantly increase in order to match the anticipated increased demand. Although considerable growth in this sector has been witnessed in recent years, the demand for dairy products still outweighs the production level (Marshall et al. 2019; Ojango et al. 2019). The observed low production levels can be attributed to several factors including inadequate quantity and quality of feeds, poor housing, parasite and disease pressure, unfavourable climatic conditions, and poor breeding strategies specifically undue preference for exotic cattle breeds regardless of the prevailing local conditions, the low production potential of local breeds, and unsystematic crossbreeding (Galukande et al. 2013; Mwai et al. 2015; Ojango et al. 2016; Chagunda et al. 2018).

The performance of dairy cattle does not depend only on their genetic merit but also on the production environment related factors such as health, feeding and management practices (Marshall et al. 2019; Mekonnen et al. 2020). These two important clusters of factors have often been considered separately in many genetic evaluations, in which the effect of genotype by environment (GxE) interactions were neglected (Huquet et al. 2012). Most genetic improvement strategies in Africa are more inclined towards increased milk yield than other functional traits related to the environment (Wilson 2018). As a result, it has been difficult to realize full milk production potential of the improved cows in different environments, hence failing to achieve the overall desired goal of increasing production and productivity. Even within tropical African regions, there are significant variations in climatic conditions and production systems that affect dairy cattle performance.

As Renaudeau et al. (2012) reported, different cattle genotypes perform differently in different systems. In Kenya, there are 7 different agro-ecological zones (Sombroek et al. 1982), mostly reflecting different climatic conditions, within which varied production systems are practised. As a result, the performance of different dairy cattle genotypes is expected to differ from one environment and production systems to another. Therefore, a better understanding of genotype by environment interaction is needed to appropriately match breed types to the various production systems and environments. This will ultimately ensure improved animal welfare, as well as enhanced productivity (Chagunda et al. 2018).

Large- and medium-scale dairy systems offer a great opportunity to investigate the production levels of different cattle genotypes as the genotypes are reared in the same production environment under similar management practices. Even though smallholder farmers produce bulk of the milk for the Kenyan needs, to date, their breeding decisions are largely influenced by the large- and medium-scale dairy systems. Large- and medium-scale commercial dairy systems serve as a source of replacement animals for smallholder dairy farmers. The selection and improvement of dairy cattle in Kenya is mainly undertaken by large- and medium-scale dairy herds (Kahi et al. 2004; Makoni et al. 2013; Ojango et al. 2016) signifying their importance in the dairy value chain. Thus, enhancing the production potential of dairy cattle in large- and medium-scale farmers would to a significant extent, improve dairy production at the smallholder level.

The majority of dairy cattle in SSA are crosses of highly adapted zebu breeds and high production potential exotic breeds such as Ayrshire, Guernsey, Holstein Friesian, and Jersey. And indeed, crossbreeding has shown some performance improvement in SSA (Werf van der and Marshall 2003; Galukande et al. 2013). Nonetheless, the right proportion of exotic breeds that would result in optimum profits is not very well known for different production environments and agro-ecological zones. To provide farmers with advice on how to optimize dairy productivity in different agro-ecological zones in Kenya through use of crossbreds, a better understanding of the magnitudes and directions of genotype by environment interaction effects on different traits is critically needed. Of all the traits, fertility and milk production are important components that determine the profitability of a dairy farm and influence herd replacement and culling. In this study, we aimed at examining the effect of breed class and environment on the production (daily milk yield) and fertility (age at first calving and calving interval) traits of multibreed dairy cattle performing in three different agro-ecological zones of Kenya. We also assessed the existence of genotype by environment interaction for these three traits.

2 Materials and methods

2.1 Agro-ecological zones and climatic conditions

Data were collected from three large-scale farms in three subcounties in Kenya, namely Kilome, Naivasha and Malindi, representing three agro-ecological zones of Kenya. Kilome lies in the northern part of Makueni at an altitude of 1,800–2,100 metre above sea level (masl) in the upper midland–sunflower maize (semi-arid arable) agro-ecological zone. Naivasha is in Nakuru county and lies approximately 90 km northwest of Nairobi at an altitude of 1,829–2,330 masl. The region falls within agro-ecological zone UM 5 (upper midland–livestock) and is defined as semi-arid pasture-based (SAP). Malindi is in Kilifi county and is located about 120 km north of Mombasa with a usually hot and humid climate all year round. It falls under the coastal lowland (CL 4) semi-humid (SH) agro-ecological zone.

The semi-arid arable (SAA) agro-ecological zone receives annual average rainfall ranging between 800–950 mm. It has a bimodal rainfall pattern with the long rains occurring from March to April and the short rains from November to December. The mean daily temperature ranges between 20.2 to 24.6°C. The 66% reliability of rainfall is surpassed normally in 10 out of 15 years, falling during the agro-humid period which allows growing of most cultivated crops. The 60% length of the growing period is surpassed normally in 6 out of 10 years. In semi-arid arable zone, the 66% reliability of main rain is 200–280 mm while that of short rain is 200–250 mm. The rainfall reliability is 60%, while the length of growing period ranges from 70–85 days for both rainy seasons (Jaetzold et al. 2006). Early maturing crops such as maize that can benefit from the short humid period are normally cultivated in this zone. The rainfall is somehow sufficient for the regeneration of annual/perennial pasture and browse material to support livestock production (Jaetzold et al. 2006; Makueni County 2013).

The semi-arid pasture-based (SAP) zone has an annual mean temperature ranging between 18.3 and 19.6°C and an annual average rainfall of 650–750 mm. The zone receives bimodal rainfall with a main rainy season ranging from March to June and a short rainy season from October to December. The 66% reliability of the main rainy season is only 230–260 mm. There are 60% chances that only 75 to 85 days in the main rainy season can reliably support the crop growth in this zone. For the short rainy season though, there is no guaranteed reliable agro-humid period to support crop production. Droughts are sometimes experienced in this agro-ecological zone, of which the frequency and severity has been on the rise in recent times due to climate change. Since the water in this zone is not sufficient to support sustainable crop production, farmers mainly practice livestock production (Jaetzold et al. 2010b).

The mean daily temperature of the semi-humid (SH) agro-ecological zone ranges from 25.2°C to 27.0°C. The zone has two rainy seasons with the long rain occurring between April to June and short rains between October to December. The average rainfall ranges from 850 mm to 1,100 mm. The 66% reliability of the long rain season is 320–600 mm while that of the short rain season is 50–130 mm. Sixty per cent dependability of crop growing period are 135 to 155 days and less than 40 days in the long and short rain seasons, respectively. Mixed farming is the main source of livelihood although more than half of the region in this zone is under ranching. The region depends mostly on the long rain although farmers attempt crop production

during the short rain season. The rainfall received is adequate for regeneration of annual/perennial pasture and browse material adequate to support livestock until the next rain season (Malindi District 2008; Jaetzold et al. 2010a).

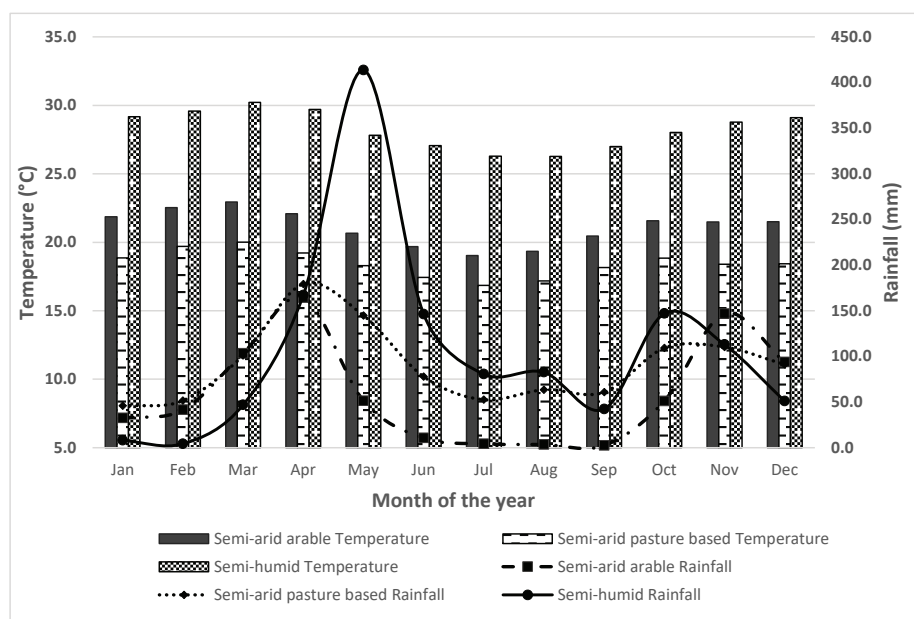
In this analysis, four seasons were defined for each zone based on climatic data extracted from aWhere (www.awhere.com) and recent classification of climatic seasons in the literature (Jaetzold et al. 2006; Malindi District 2008; Jaetzold et al. 2010b; Makueni County 2013). The rainfall pattern that normally influences feed and water availability was used in this classification. The long rain and short rain periods were considered green seasons 1 and 2, respectively. The dry period before the long rain was considered as dry season 1 and that before the short rains as dry season 2. The classification of the seasons for each agro-ecological zones, with rainfall and temperature patterns are presented in Table 1 and Figure 1 below.

Table 1. Classification of climatic seasons across the three agro-ecological zones under study

Agro-ecological zone	Seasons defined by months of the year			
	DS1	GS1	DS2	GS2
Semi-arid arable (SAA)	January to February	March to April	May to October	November to December
Semi-arid pasture (SAP)	January to February	March to June	July to September	October to December
Semi-humid (SH)	December to March	April to June	July to September	October to November

DS: Dry season; GS: Green season.

Figure 1. Rainfall pattern of the study sites based on global climate data extracted from aWhere online climate website.



2.2 Herd management and crossbreeding strategies

At the Naivasha farm, calves are separated from their dams within 12 hours after birth, and thereafter bucket fed on colostrum for the first 4 days of life and on fresh milk for about 9 weeks. The calves are gradually weaned onto concentrates and hay from 5 weeks of age and are fully weaned from whole milk by 9 weeks of age. After this they are reared on natural pastures except under drought conditions when they receive lucerne hay as supplements. Bulls and heifers are migrated to separate farms where they are grazed on natural pastures with no supplementary feeding for their remaining rearing period. They, however, have access to a balanced mineral salt lick. Lactating cows are grazed on the best pastures through rotational grazing with the cows rarely staying longer than a week in one paddock. The cows are milked twice daily in a modern milking parlour. Water is made available to all animal groups *ad libitum*. All animals are treated for endoparasites and dipped at least once

weekly to control ectoparasites. Routine vaccination is done against foot and mouth disease (FMD), rinderpest, blackquarter, anthrax, Rift Valley fever (RVF), and brucellosis.

In Malindi, the calves are removed from their dams within one hour after birth and bucket fed twice per day with colostrum for the first three days and milk up to 4 months of age. Additionally, calves receive calf early weaner pellets and total mixed rationed (TMR) silage *ad libitum* as a dairy meal replacement. The pellets and TMR are gradually replaced with sifted chicken litter/maize bran mixture and normal silage (made from standing hay or maize stover), respectively. Heifers are fully zero-grazed until 15 months where they join the adult herd. The heifers (>15 months old and older) are grazed on natural pasture and paddocked together as a single herd. Lactating cows are zero-grazed and additionally provided with TMR *ad libitum*. Milking cows are hand milked twice or three times a day depending on the milk market situation. Water is available to all the animals *ad libitum*. Ticks and flies are controlled by pour-on 1 to 2 weeks apart depending on the tick and biting fly challenge. No deworming is done for any age group. Vaccination against FMD, lumpy skin disease (LSD), RVF, brucellosis, rabies, anthrax, blackquarter and bovine viral diarrhoea (BVD) is done routinely.

For the dairy farm in Kilome, the calves are separated from their dams at 5 days of age and tube-fed on fresh milk twice a day until they are 2 months old. They are then weaned from dairy meal to hay, concentrates (wheat bran and maize germ) and mineral salt licks that are provided *ad libitum*. At the age of 9 months, they are moved into the grazing herd where they feed on natural pastures supplemented with mineral licks. Bulls and heifers are fed on natural pastures with mineral lick given as supplements. The lactating herd is grazed on natural pastures except during milking time when they are provided with a mixture of seed cake, wheat bran and maize germ. Milking is done by hand twice a day. During the dry season when there is little standing hay and no preserved hay, the animals are fed on silage supplements. Water is available to all animal groups *ad libitum*. The animals are drenched regularly until they are 9 months old after which it is stopped, and the animals are then treated only when there is an infection. Ectoparasites are controlled in all animal groups by dipping on weekly basis. Vaccination is done routinely against LSD, FMD, RVF, brucellosis, anthrax, blackquarter and BVD.

The breeding strategy deployed at the Naivasha and Kilome herds was the same except for the zebu breeds used to cross with the exotic dairy breeds. In Naivasha, Sahiwal is used whereas in Kilome improved Boran is used. In both farms, the exotic dairy cow herd comprises pure Friesian females that are kept for breeding. They apply both rotational and grading up crossbreeding strategies where the respective indigenous cows are crossed with exotic bulls and vice versa. The subsequent generations are back-crossed with either pure indigenous or exotic breeds to get the different breed proportions in the population. Mating is done through AI except in a few cases where the indigenous bulls and their crosses are used to naturally mate the female herds. The main exotic breed used is Friesian, but Jersey and Ayrshire bulls are also occasionally used. A few selected indigenous and crossbred bulls are used to serve pure exotic and crossbred females.

The most preferred breed proportion in the farm in Kilome is 75% Friesian and 25% Boran. In Naivasha, 50% Friesian and 50% Sahiwal is the most predominant. The herd located in the semi-humid zone (Malindi) is made up of a stable intermating population of composite cattle originating from crossbred parents. The farm produces synthetic crossbreds of different breed levels, comprising between 25 to 50% Gir blood in its breed composition. The remaining 50 to 75% breed proportion is divided between taurine and indicine breeds as evenly as possible with every single breed contributing less than 25%. Mating is done naturally or through AI.

2.3 Data

The data used in this study included bimonthly milk yield and calving records of multibreed cows born between January 2000 to December 2017. The data was assessed for quality and cows with missing dates of birth were excluded from the analysis. Contemporary grouping of the animals was done by linking the year and season of either birth, calving, or milking depending on the trait, and groups having less than 5 records were excluded from the analysis. Besides, performance records for parity 7 and above were not representative enough and were removed from the analysis.

Breed proportions of the cows were generated from the information provided by the farmers and used to group the animals into two breed classes (which is referred to in this analysis as genotypes), based on the proportion of exotic dairy breeds. The exotic dairy breeds included Holstein Friesian, Jersey, Guernsey, Ayrshire, Brown Swiss, Fleckvieh, Milking Shorthorn, Meuse Rhine Issel, Scandinavian Redwood and Montbéliarde. Non-exotic or zebu dairy breeds in this population included Sahiwal, Boran and Gir. Exotic class 1 (EC1) was made up of animals having 0–50% exotic breed proportion ($n = 481$) while exotic class 2 (EC2) had animals with more than 50% proportion of exotic dairy breed proportion ($n = 1,009$). The performance of cows belonging to the two exotic blood groups was evaluated for age at first calving (AFC, $n = 1,490$), calving intervals (CI, $n = 2,640$) and milk yield (MY, $n = 62,321$).

2.4 Statistical models

To determine the effects of environment and genotype and the interaction effects between these factors on the age at first calving, calving interval, and daily milk yield, the different animal models were fitted for the traits. Analysis of variance was performed prior to fitting animal models to determine the significant factors of variation. For AFC, a multiple linear regression model with the herd, exotic class, exotic class by environment interaction, and a contemporary group of the combination of year and season of birth of the cow was used as explanatory variables.

$$Y_{ijkl} = U + YSB_i + EC_j + Env_k + EC_j * Env_k + e_{ijkl} \quad (1)$$

where Y_{ijkl} is the AFC observation of the l th animal, YSB_i is the i th year-season of birth ($i = 1-72$), EC_j is j th exotic class ($j = 1-2$), Env_k is the k th environment ($k = 1-3$), $EC_j * Env_k$ is the interaction between j th exotic class and k th environment and e_{ijkl} is the residual error.

For calving interval, a mixed-effect repeatability model with fixed effects of exotic class, combination of year and season of calving, herd, exotic class by environment interaction, parity, and age nested within parity, and a random effect of animal was fitted as shown below.

$$Y_{ijklmno} = U + YSC_i + EC_j + Env_k + EC_j * Env_k + Parity_l + "Age_m(Parity_l)" + Animal_n + e_{ijklmno} \quad (2)$$

where $Y_{ijklmno}$ is the calving interval observation of the o th cow, YSC_i is the i th year-season of previous calving ($i = 1-66$), EC_j is j th exotic class ($j = 1-2$), Env_k is the k th environment ($k = 1-3$), $EC_j * Env_k$ is the interaction between j th exotic class and k th environment parity _{l} is the l th parity ($l = 2-6$), "Age _{m} (Parity _{l})" is the m th age ($m = 31-133$) nested within the l th parity, $Animal_n$ is the n th animal ($n = 1-1,000$), and $e_{ijklmno}$ is the residual error associated with $Y_{ijklmno}$.

A similar repeatability model was fitted for MY with fixed effects of herd, exotic class, the interaction of exotic class and location, year season of calving and testing, parity, age nested within parity and days in milk nested with parity. The random effects consisted of animal and year and season of milking effects. The model fitted for milk yield was as follows:

$$Y_{ijklmnopq} = U + YSC_i + EC_j + Env_k + EC_j * Env_k + Parity_l + YST_m + Age_n(Parity_l) + dim_o(Parity_l) + Animal_p + e_{ijklmnopq} \quad (3)$$

where $Y_{ijklmnopq}$ is the daily record (milk yield in kilogram) of the p th cow, YSC_i is the i th year-season of calving ($i = 1-70$), EC_j is j th exotic class ($j = 1-2$), Env_k is the k th environment ($k = 1-3$), $EC_j * Env_k$ is the interaction between j th exotic class and k th environment, parity _{l} is the l th parity ($l = 1-6$), YST_m is the m th year-season of calving ($m = 1-70$), $Age_n(Parity_l)$ is the n th age in months ($n = 19-142$) nested within the l th parity, $dimo(Parity_l)$ is the o th days in milk ($o = 1-400$) nested within l th parity, $animal_p$ is the p th animal effect ($p = 1-1,281$) and $e_{ijklmnopq}$ is the residual error.

Least-square means (LSM) of the genotype classes for AFC, CI and MY were calculated and contrasted across the 3 different environments. The data was analysed using the R statistical software version 4.0.5 (R Core Team 2021).

3 Results

3.1 Summary of the performance traits

Descriptive statistics for AFC, CI and daily MY are shown in Table 2. The coefficient of variation (CV) was 15.6% for AFC, 21.1% for CI and 38.19% for MY. The large CV for MY shows that milk yield varied widely within and across these herds. Results from the analysis of variance (ANOVA) showed that contemporary group and environmental effects were important sources of variation ($P < 0.001$) for all the traits analysed. The effect of exotic breeds was significantly different ($P < 0.01$) for AFC and CI but not for daily milk yield. The interaction between exotic breed class and herd location or environment was significant for all traits except calving interval. Parity was also a significant source of variation in milk yield but not in calving interval.

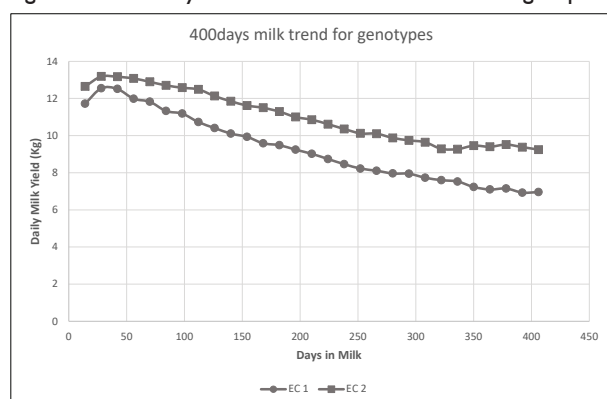
Table 2. Descriptive statistics showing the number of observations (n), mean, standard deviation (SD), and coefficient of variation (CV) for age at first calving (AFC), calving interval (CI) and daily milk yield (MY)

Trait	n	Mean	SD	Range	CV %
AFC (months)	1,490	34	5.3	27	15.60
CI (days)	2,640	436.8	92	510	21.10
MY (kg)	62,321	10.98	4.26	22.9	38.19

3.2 Effect of genotype on productivity traits

Milk production trend in the first 400 days in milk for the two genotype groups has been shown in Figure 2. The animals in both groups peaked at about one month post-parturition and the EC2 (> 50% proportion of taurine genetics) class had slightly higher milk production than EC1 (0–50% proportion of taurine genetics). Table 3 presents the least-square means for AFC, CI and MY by the exotic class group. Although the EC2 group seemed to produce higher milk yield than EC1 cows, no significant difference was observed in total milk yield between the two breed groups at a population level. The heifers with more than 50% exotic genetics calved significantly earlier (1.6 ± 0.3 months) than those with less than 50% exotic genetics ($P < 0.001$). For calving interval, it was however the EC1 cows that had 14.6 ± 6 days shorter compared to EC2 cows ($P < 0.05$).

Figure 2. A 400-day lactation curve for the two breed groups of cows under study.



EC1 and EC2 represent exotic class 1 and exotic class 2, respectively.

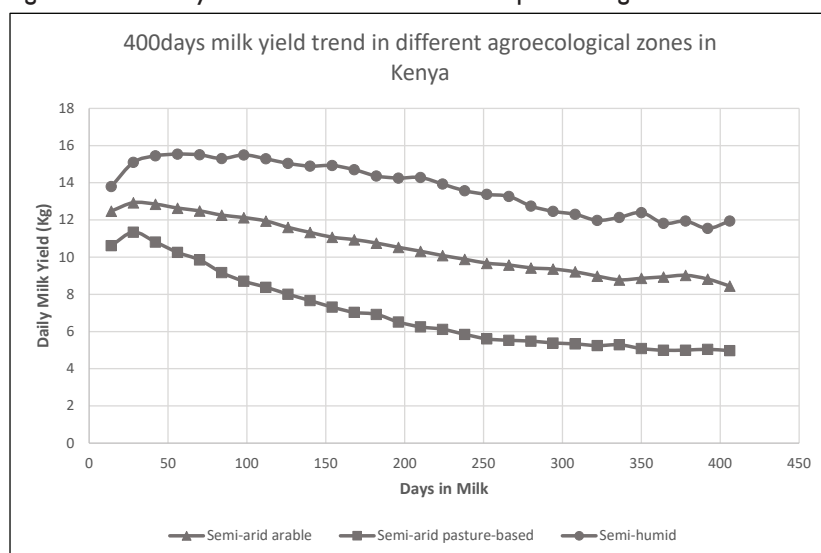
Table 3. Least square means (LSM) (standard error) for age at first calving (AFC), calving interval (CI) and milk yield (MY) at each factor across agro-ecological zones and breed exoticness levels

Variable and level	AFC		CI		MY	
	n	LSM (SE)	n	LSM (SE)	n	LSM (SE)
% exoticness						
EC1 (0–50%)	481	34.0 (0.2)	896	452 (6)	19,316	11.3 (0.14)
EC2 (> 50%)	1,009	32.4 (0.2)	1,744	466 (7)	43,005	11.3 (0.13)
Agro-ecological zone						
Semi-arid arable	966	34.5 (0.2)	2,013	434 (6)	43,126	11.0 (0.12)
Semi-arid pasture-based	210	35.2 (0.4)	293	463 (9)	9,502	7.9 (0.19)
Semi-humid	314	30.0 (0.3)	334	481 (7)	9,693	14.9 (0.17)

3.3 Effect of agro-ecological zone on productivity traits

Lactation curve for the herds at three agro-ecological zones followed a normal pattern under medium- and large-scale farming conditions in Kenya (Ojango and Pollott 2001; Wasike et al. 2011). The lactations peaked within the 60 days of lactation (Figure 3). Animals at semi-humid zone had generally the highest milk production and peaked at around 60 days while those in semi-arid zones peaked earlier at 30 days. Overall, compared to those in semi-arid zones, animals in the semi-humid region had significantly shorter age at first calving (30.0 ± 0.3 vs. 34.5 ± 0.2 and 35.2 ± 0.4 months for SAA and SAP, respectively, $P < 0.001$) and higher average daily milk yield (14.9 ± 0.17 vs. 11.0 ± 0.12 and 7.9 ± 0.17 kg for SAA and SAP, respectively, $P < 0.001$). Nonetheless, the animals in semi-arid regions had significantly shorter calving intervals than those in the semi-humid region (29 and 19 days shorter than SH for SAP and SAA, respectively, $P < 0.001$). The performance of animals in semi-arid areas was relatively similar in age at first calving (34.5 ± 0.2 vs. 35.2 ± 0.4 months). However, a significant difference ($P < 0.05$) was observed in calving intervals and daily milk yields between these two herds in semi-arid zones. Animals in the SAA zone had a higher average daily milk yield (3.12 kg/litres more) and a lower calving interval (29 days less) than those raised in the SAP zone.

Figure 3. A 400-day lactation curves for the herds performing in three different agro-ecological zones.



3.4 Genotype by environment interactions

The performance of the two breed groups across agro-ecological zones is presented in Table 4. Within breed group comparison showed that EC1 had a particularly older AFC of 36.7 ± 0.4 months in the SAP agro-ecological zone compared to 31.0 ± 0.6 in the SH environment. This means that puberty was delayed in the SAP agro-ecological zone. However, for the EC2 cows, it was in the SAA agro-ecological zone where cows were oldest at first calving compared to the SH environment (34.7 ± 0.2 vs. 28.9 ± 0.3). For both breed groups, milk yield was highest in the SH zone than in semi-arid zones. Although the SH agro-ecological zone seemed to favour the onset of puberty and high daily milk yield, cow raised in SH had the longest CI for both breed groups (478 ± 9 days for EC1 and 484 ± 7 for EC2).

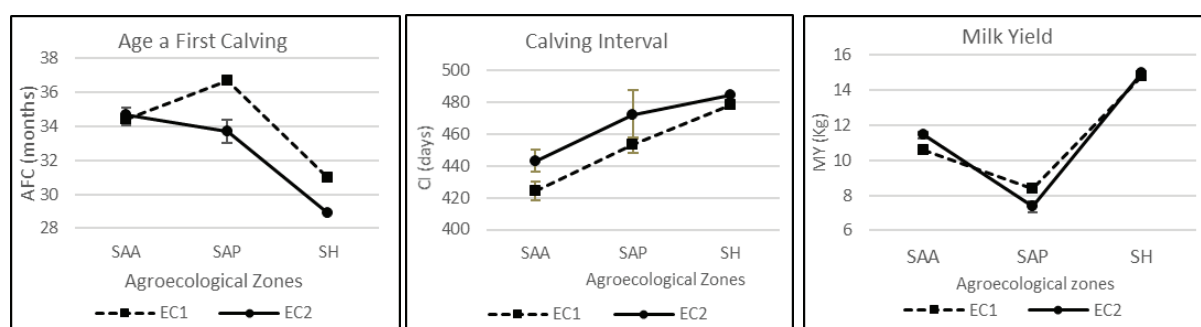
The genotype by environment interaction was significant for AFC in a scaling manner and in a reranking manner for MY (Figure 4, $P < 0.001$). The EC2 heifers raised in SH and SAP zones were younger ($P < 0.05$) at first calving compared to EC1 heifers. However, in the SAA zone, the performance of the two classes of animals for AFC were quite similar. The EC1 and EC2 had nearly similar average daily milk production in the SH zone (14.82 ± 0.27 vs. 14.99 ± 0.15 , $P > 0.05$). A significant variation in daily milk production was observed in the semi-arid zones between the two breed groups. In SAA zone, the average daily milk yield of hybrids with more than 50% exotic genes was significantly higher ($P < 0.001$) than that of cows with less than 50% exotic genetics by 0.89 ± 0.17 kg. In SAP zone, the EC1 cows produced 1.05 ± 0.32 kg more milk than the EC2 cows. There was no genotype by environment interaction for calving interval.

Table 4. Least square means (SE) for age at first calving (AFC), calving interval (CI) and daily milk production (MY) of exotic classes (EC1 and EC2) across the 3 agro-ecological zones

Performance trait	EC1 (0–50%)	EC2 (> 50%)	Pairwise comparison (EC2–EC1)	Significance level
AFC (months)				
Semi-arid arable	34.4 (0.3)	34.7 (0.2)	0.3 (0.3)	
Semi-arid pasture-based	36.7 (0.4)	33.7 (0.7)	3.0 (0.7)	***
Semi-humid	31.0 (0.6)	28.9 (0.3)	2.1 (0.6)	*
CI (days)				
Semi-arid arable	424 (6)	443 (5)	19 (0.4)	***
Semi-arid pasture-based	453 (7)	472 (15)	18 (15)	
Semi-humid	478 (9)	484 (7)	7 (9)	
MY (kg)				
Semi-arid arable	10.55 (0.17)	11.45 (0.11)	0.89 (0.17)	***
Semi-arid pasture-based	8.4 (0.18)	7.35 (0.30)	–1.05 (0.32)	***
Semi-humid	14.82 (0.27)	14.99 (0.15)	0.17 (0.28)	

***, **, *, and ‘.’ indicate significant differences at $P < 0.001$, 0.01, 0.05, and 0.1, respectively. EC1 and EC2 represent exotic class 1 and exotic class 2, respectively.

Figure 4. Genotype by environment interaction for age at first calving, calving interval and milk yield.



EC1 and EC2 represent exotic class 1 and exotic class 2, respectively.

4 Discussion

In this study we found that heifers with less exotic blood had delayed onset of sexual maturity. Lukuyu et al. (2016) found that body linear measurements for cows in Kenya increased with increasing percentage of exoticness. Hence, the delayed onset of sexual maturity in less exotic blood heifers could be attributed to their lower growth rates as compared to those with a higher proportion of exotic blood (Le Cozler et al. 2008; Krpálková et al. 2014; Duplessis et al. 2015). A higher proportion of breed exoticness was positively associated with longer calving intervals. Other studies have also reported a reduction in reproductive performance of crossbred cows (i.e. longer calving intervals) as the proportion of exotic taurine blood increases above 50% (Asimwe and Kifaro 2007; Madani et al. 2008; Bahmani et al. 2011).

Longer calving intervals observed in high grade crossbred cows could be due to inadequate nutrition that lowered the pregnancy and first service conception rates as earlier reported (Randel 1990). Additionally, it could be linked to high metabolism and reduction in the circulating concentration of Estradiol-17 β . The concentration of circulating Estradiol-17 β is positively correlated to different aspects of reproductive physiology such as oestrus and ovulation (Barnes et al. 1980; Lopez et al. 2004). High genetic merit cows readily mobilize their body energy reserves to maintain their milk production profile when their energy requirements exceed the energy supply leading to a negative energy balance (Gallo et al. 1996). Estradiol-17 β , a steroid hormone, is one of the components that are broken down during the process of body reserves metabolism (Lopez et al. 2004). In this population, Holstein Friesian was the most used exotic breed for crossbreeding, and as previously documented, the higher the proportion of Holstein blood in crossbred cattle, the higher the tendency to metabolize body reserves (Koenen et al. 2001). Furthermore, the deterioration in fertility of high grade crossbred cows as degree of taurine exoticness increases could be due to the associated lowered adaptation or resilience that follows as a result of decrease in heterozygosity and genes of indicine origin in such crosses (Bahmani et al. 2011).

Although we did not find a significant difference in milk yield production between the two breed groups at population level, a study of a large-scale dairy herd in the central highlands of Ethiopia found that 62.5% and >75% HF crossbred dairy cattle significantly produced higher daily milk yield than 50% crossbred cows (Shibru et al. 2019). Similarly, Haile et al. 2009 observed higher lactation milk yield for higher (75% and 87.5%) exotic crossbred than low (50%) exotic crossbred in experimental dairy cattle herds of Ethiopian Boran Holstein crossbreds. Ojango et al. (2014, 2019) also found that high grade crossbred (61–87.5% and >87.5% dairy genes) gave higher yields than lower grade cows especially in high input systems. In these studies, dairy animals were categorized into 4 or 5 groups based on their proportion of exotic genes. In this study, however, there was not sufficient representation for grouping the animals into more classes, and as a result, a broader classification of two exotic classes was opted for.

Performance of the animals differed for the studied traits across the three agro-ecological zones. Animals performing in semi-arid environments had lower milk production, longer age at first calving, and shorter calving intervals than those in the semi-humid environment. These differences can be partly attributed to the differences in climatic conditions across the environments. Since semi-arid environments are characterized by high temperatures and poorer natural feed resources, metabolic and physiological adjustments to alleviate the effects of thermal stress might have negatively affected the milk production, growth potential, and health of cows with higher taurine blood (Henry et al. 2012; Renaudeau et al. 2012; Ekine-Dzivenu et al. 2020).

This might have led to the low milk production and late onset of puberty in the semi-arid environments observed in our study. Besides, semi-arid areas are subjected to low rainfall and frequent droughts which cause shortages in feed and water quality and quantity available to the animals, hence making them prone to new diseases, low milk production and slow growth rates (Nardone et al. 2010; Thornton 2010; Mpofu et al. 2017; Rojas-Downing et al. 2017). Longer calving intervals observed in cows performing in the semi-humid region could be partly due to the deliberate breeding decisions taken by the farmer that made sure cows calved at a specific time. The priority of the farmer is to ensure that cows are in their peak milk production during hottest and driest months when the demand for milk is high and market is readily available. Alternatively, since the animals from semi-humid zone produced higher milk yield than those in semi-arid regions, longer calving intervals could be associated with more loss of body condition in the early postpartum period to maintain milk production needs (Leroy et al. 2008a; Leroy et al. 2008b; Roche et al. 2009). This has the effect of extending the duration before the first postpartum oestrus is displayed (Broster and Broster 1998; Butler 2003) leading to longer days open.

Overall, the variation in production and reproduction performance across the environments could have resulted from differences in approach and breeds used in crossbreeding as well as level of herd management (Gebreyohannes et al. 2014). Milk production potential differs in different exotic and zebu cattle breeds with Holstein Friesian known to have the highest genetic merit for milk production (Walsh et al. 2008). Consequently, hybrid of different types of breeds are expected to perform differently. Moreover, the farms in the two semi-arid zones apply upgrading and rotational crossbreeding which has been indicated to give variable results from generation to generation (Cunningham 1981; McDowell 1985; Rege 1998). The herd in semi-humid region is maintained through formation of synthetic cattle lines that have been reported to benefit from hybrid vigour and lead to long lasting improvement of milk production (Galukande et al. 2013). The level of herd management differed across herds and an earlier study found that the performance of dairy cows responded positively to the farm's level of investment in the form of composition of the herd, available feeds and health interventions (DeLay et al. 2020).

The interaction between the genotype and environment arises when the performance of different genotypes is not equally influenced by different environments or when the same genotype develops different phenotypes in different environments (Falconer and Mackay 1996). The scaling effect of genotype by environment interaction is seen when genotypes show significant changes in the magnitude of effect across different environments but do not rerank. The reranking effect exists when genotypes show significant changes in effect across different environments and rank differently. In this study, AFC showed a scaling effect while milk yield showed a reranking effect of $G \times E$. The scaling $G \times E$ interactions effect in the age at first calving is of less worry because the best selected individuals in one environment would still perform the best in other environments. Preadjustment in the data (Wiggans and VanRaden 1991) or correction in the evaluation model (Meuwissen et al. 1996) can take this type of $G \times E$ into account with no consequence on selection decisions. However, with the reranking $G \times E$ interaction effect seen in daily milk yield, superior individuals in one environment would be inferior in the other environments. In this case, the breeding strategy needs to involve the selection of a specific genotype for each environment. This strategy would achieve optimum milk production for each environment and help maintain genetic diversity even though it is expensive and time-consuming.

Based on the results of our study, crossbred cows with more than 50% exoticness might be more suited for higher profitability in semi-humid agro-ecological zone. This is because, although they displayed similar performance on daily milk yield and calving intervals as those with less than 50% taurine genetics, they had a significantly shorter age at first calving. Calving at an early age has economic benefits to a dairy farmer because it results in a longer productive life and more lifetime milk production of a dairy cow (Gupta et al. 2016). In semi-arid arable agro-ecological zone, cows with lower proportion of taurine genes had shorter calving intervals whereas those with higher proportion had superior milk production ability. In semi-arid pasture-based zone, cows with higher proportion of *Bos taurus* genes calved at an earlier age while those with lower proportion of taurine genetics produced more milk. In these two semi-arid areas, a trade-off between milk production and fertility, and the long-term profitability associated with these traits should dictate the breed group of cows to be reared. An evaluation of potential lifetime gains/losses associated with these traits need to be done to empirically demonstrate the potential profitability differences and to solidify the results of the current study.

5 Conclusion

These findings demonstrated that production and fertility traits in multibreed dairy cattle, which crucially influences herd replacement, are significantly affected by the biophysical variation in different agro-ecological zones. This differential performance should be considered when designing genetic improvement programs in SSA. The results of this study are useful for farmers and breeders in determining the exotic proportion of crossbred cows which suits different agro-ecologies for improved performance and profitability. Nonetheless, the use of the right genotypes should not be deemed as a replacement for better management practices if considerable improvements are to be realized. To fully understand the extent of $G \times E$ interaction for these traits, the analysis should be done not only at the phenotypic level as in this study, but also at the genotypic level. Traits such as milk components that were not included in this study might have also obscured the potential overall $G \times E$ effects. Thus, there is a need for a more comprehensive study in the near future, when more data becomes available.

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