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Estimation of Additive and Non-Additive Effects on Milk Production and Reproduction Traits in Crossbred Dairy Cattle at Holeta Agricultural Research Center, Ethiopia

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Abstract

This study aimed to assess the genetic effects of breed additive, heterosis, and recombination in indigenous Boran cattle and their crossbreeds with Holstein Friesian dairy cows at the Holeta Agricultural Research Center. A total of 14,028 performance records from pure Boran and crossbred dairy cattle were utilized in the study. To perform the estimations, crossbreeding parameters for milk production and reproductive traits were analyzed. The crossbreeding parameters—breed additive, heterosis, and recombination losses—were estimated using regression analysis with SAS software (2004). The analysis results showed that additive genetic effects were greater than heterosis effects across all milk production and reproductive traits. Compared to the indigenous Boran breed, the Holstein Friesian breed exhibited additive genetic effects of 3728 ± 139.4 kg for lactation milk yield (LMY), 10.89 ± 0.3 kg for daily milk yield (DMY), and 48.95 ± 14.8 days for lactation length (LL). Likewise, the direct heterosis effects observed in crossbred dairy cows were -81.65 ± 97.98 kg for lactation milk yield (LMY), 0.44 ±0.2 kg for daily milk yield (DMY), and -18.72 ± 10.38 days for lactation length (LL). Crossbreeding did not always have positive effects on milk production traits. In this study, unfavorable interactions of epistatic alleles (recombination loss) resulted in reductions of 1440.92 ± 152.25 kg in lactation milk yield (LMY), 2.55 ± 0.33 kg in daily milk yield (DMY), and 75.15 ± 16.13 days in lactation length (LL). The breed additive genetic effects of Holstein Friesian, compared to the Boran breed, for calving interval (CI), age at first calving (AFS), and age at first calving (AFC), were 21.51± 29.19 days, 2.29 ± 3.12 months, 2.23 ± 3.12 months, respectively. In the current study, the heterosis retention values for crossbred dairy cows were 5.33 ± 19.79 days for calving interval (CI), -8.79 ±2.7 months for age at first calving (AFS), and -8.84 ± 2.7 months for age at first calving (AFC). Friesian and Boran crossbred cows showed a reduction from Boran cows of approximately 81.01± 32.71days in calving interval (CI), 2.95 ± 3.15 months for age at first service (AFS), and 2.91± 3.15 months for age at first calving (AFC) due to favorable recombination effects.

1. INTRODUCTION

Crossbreeding refers to the mating of individuals from different breeds, lines, or populations. Its primary advantages include the benefits of heterosis and the additive genetic contributions from superior purebred animals (Wakchaure et al., 2015). There are two primary reasons for implementing crossbreeding in livestock. The first is to take advantage of the varying additive genetic levels among breeds to produce offspring with enhanced economic performance through new combinations of additive genetic traits. The use of differing additive genetic levels between breeds is known as “specific combining ability” (Falconer, 1996). Secondly, crossing pure lines breeds results in the expression of heterosis. Crossbred animals tend to be harder and more economically productive than their parent breeds (Mäki-Tanila, 2007). Crossbreeding is attractive to many livestock producers and has been advocated by Kalm (2002). Systematic crossbreeding can significantly enhance the economic efficiency of dairy production systems, as heterosis is present in many of the most economically valuable traits in dairy cattle (M. K. Sørensen et al., 2008). Crossbreeding can increase profitability for most dairy farmers when breeds with similar genetic merits are used. The heterosis achieved through crossbreeding serves

as an additional advantage beyond the genetic improvements gained through pure breeding. The extent of the bonus depends on both the number and the types of breeds used in the breeding program. The majority of studies indicate that F1 crosses between genetically unrelated breeds result in at least a 10% increase in overall economic gain per cow (McAllister et al., 1994).

Heterosis, first introduced by Shull in 1914 (Shull, 1948), refers to the improved performance of crossbred animals relative to the average performance of their purebred parent breeds. The enhanced performance results from changes in non-additive genetic effects, specifically dominance and epistasis. Dominance effects arise from interactions between genes at the same locus. Animals that possess a higher number of heterozygous loci generally perform better than those with a greater number of homozygous loci. Heterosis can be viewed as the opposite of inbreeding depression (Lynch and Walsh, 1998). Similar to inbreeding depression, heterosis is most evident in traits associated with fitness (Mäki-Tanila, 2007), such as fertility, ease of calving, and overall robustness. Generally, many traits that is crucial for profitability in dairy farming exhibit heterosis.

Epistatic effects arise from interactions between genes at different loci. While interactions between individual genes are the most significant, interactions involving gene pairs and those between single genes and gene pairs can also have an impact. The extent of heterosis in crossbred populations should not be estimated based only on F1 heterosis and the level of heterozygosity maintained. Various models have been suggested to estimate the effects of recombination resulting from additive × additive (A×A) interactions (Dickerson, 1973; Hill, 1982). Assuming the dominance model, which ignores epistatic effects, F1 heterosis is expected to represent the dominance effect. When two F1 individuals are crossed, the offspring (F2) typically express only half of the F1 heterosis.

Crossbreeding studies involving dairy cattle in over 25 tropical countries revealed that the Friesian breed generally showed greater additive genetic contributions to milk production traits than indigenous breeds like the Boran and Sahiwal (Cunningham, 1987). This may be due to the lower milk yield of indigenous tropical breeds in comparison to the Friesian. In the long-term crossbreeding experiment conducted at the Holeta dairy research farm, Boran and Holstein Friesian have been identified as suitable breeds for crossbreeding, with their offspring being considered for the development of a synthetic breed. Estimates of crossbreeding parameters for milk production and reproductive traits can assist breeders in developing optimal breeding strategies at the research farm. Therefore, the present study aimed to Estimate Crossbreed Parameters of Milk Production and Reproductive Traits from Crossbreeding between Holestein and Boran Breeds at Holeta Agricultural Research Center.

2. MATERIALS AND METHODS

2.1 Study Area

The study was conducted at Holeta Agricultural Research Center (HARC). Located in Ethiopia's central highlands, Holeta is situated approximately 40 kilometers west of Addis Ababa along the main road to

Ambo. The center's coordinates are 38.50° E longitude and 9.80° N latitude, at an elevation of 2,500 meters above sea level. The area receives an average annual rainfall of around 1,200 mm. The region's average yearly temperature is 18°C, with relative humidity averaging 60% throughout the year (Haile et al., 2011).

2.2. Overview of Dairy Cattle Research Farm

Holeta Research Center was established in 1966. The beginning, the beginning, preliminary characterization and milk production and reproductive performances of selected indigenous cattle breeds were evaluated at four experimental stations (Holeta, Horo, Melka-Werer and Adamitulu). As a result, these indigenous breeds produced an overall total lactation yield of 550 kg over a lactation period of 6 months. However, due to the lower milk yield of indigenous cows and high demand for milk and milk products associated with alarming human population growth, crossbreeding was proposed in 1972 by G. Winner FAO consultant.

The first preliminary results of the long-term dairy cattle crossbreeding experiments in Ethiopia were reported by Sendros, (1987), 20 years after the start of the experiment. The results indicated that first generation (F1) crossbred dairy cows in general produce three to five times more milk than indigenous cows. Kebede, (1992) conducted a comprehensive study and identified milk production as one of the breeding program's target goals, achieving significant success.

Currently, due to fluctuations in exotic gene inheritance among crossbreds produced as a result of crossing and lack of an appropriate breeding program, efforts are underway to develop a 75% synthetic/composite dairy breed at Holeta Agricultural Research Center (HARC).

2.3. Animal Management

The herds were managed according to their breed group, pregnancy stage, lactation period, sex, and age. The animals were provided with a shelter that had good ventilation and shades. The shelter had enough space where animals could feel free and comfortable. The animal management practices that were used are standard animal welfare practices. These practices included frequent shelter cleaning, provision of safe drinking water, and provision of a diet that could support animal growth and production adequately.

Consistent feeding and management protocols were applied to all animals within each specific category. Concentrate mixture composed of wheat bran (54%), noug (Guizocia abyssinica) cake (45%), and salt (1%) was supplemented based on their body weight, productivity and physiological status and genotype. Cows, heifers and calves are supplemented with a concentrate mixture at a rate of 4 kg, 1–1.5 and 0.25–1 kg per day/animal, respectively.

Calves were allowed to suckle their dam immediately after birth for four days to receive colostrum. Weighting and ear tagging applied within 24 hours after birth. After four days, the calves were transferred to a calf rearing pen and provided a dry diet and whole milk for 98 days through bucket feeding, except

the F1 calves which suckled their dams until weaning. Weaned calves were transferred to another pen and kept indoors up until 6 months of age.

Cows have been milked with a milking machine twice daily (early morning and evening). A selection process based on breeding value and phenotypic performance was used. All undesired male calves and unproductive animals were removed from the farm, except candidate bulls that were hired to produce semen. It was standard procedure to protect the herd from potential illness outbreaks. The HARC's animal health research division established a disease control calendar, which was followed in identifying and controlling seasonal outbreaks of key diseases of economic relevance.

2.4. Breeding Program

Breeding purebred Boran with Friesian, Jersey, and Simmental breeds has produced distinct genetic groups in the herd for many years. Unfortunately, crossbreeding efforts between Jersey and Simmental were halted. As a result, the study exclusively used HF X Boran crossbred data. Different genetic groups were produced using the HF X Boran mating system (50% F1, F2, and F3, with a few tries on high-grade 62.5%, 75%, and 87.5%). Holeta Agricultural Research Center (HARC) is now focusing more on the production of 50% F1, F2, F3, and 75% F1 and F2 crossbred dairy, while the 62.5% and 87.5% high-grade progeny developments were stopped. As a result, 50% and 75%of the generation were the focus of this research.

The 50% F1 crosses are produced by mating pure Boran dams with pure Friesian semen, while the 75% first generation is produced by backcrossing the 50% F1 with pure Friesian semen. In order to create a breed at 50% HF and 50% Boran and 75% HF and 25% Boran blood levels, the latter generations (F2 and F3) were created by *inter se* mating 50% male with 50% female and 75% male with 75% female. In order to provide the necessary generations, the Boran cattle used as a foundation stock for crossbreeding were transported from the Boran pastoralists in southern Ethiopia, which is where they originated. They were then rose on station and mated at random with NAIC Kality and WWS semen to produce required generations.

The farm used artificial insemination for mating throughout the year, bringing in pure Friesian semen from NAIC Kality, international sires, or locally recruited crossbred bulls. When animals became repeat breeders with AI, natural service was occasionally employed. For on-station breeding operations, bulls born on the farm were chosen for breeding based on dam milk performance and physical conformation for semen collection in NAIC. Care was given during bull selection for NAIC to prevent genetic relationships. The research station has just begun selecting bulls based on their breeding value. As a new operation at the Holetta Agricultural Research Center (HARC), cross-breeding Borena cows with exotic Frisian bulls utilizing worldwide sire (WWS) imported semen by ALPPIS was started in 2010 with the goal of improving milk output, selection, and quality. Teaser bulls were raised with cows for daily heat detection in addition to herdsmen. Qualified technicians used artificial insemination to couple cows that were found to be in heat. After 45 days of service, cows that had not been observed in heat for more than 45 days were diagnosed as pregnant. 50% F1 Friesian X Borena and 75% crossbred cows and bulls

were used in the on-station selection effort, which was most likely initiated in 2005. Selection produced enough information to preserve the best genotype for future crossbred dairy cow production.

2.5. Data source and data collection

The study utilized data collected over a 30-year period, from 1995 to 2024, at the Holetta Agricultural Research Center (HARC). Overall, 14,028 pure Borena and crossbred dairy cattle performance records were used for this study (Table 1).

Table.1.Number of records used for crossbreeding parameter analysis.

Genotypes	Milk production Traits			Reproduction Traits			
	LMY	DMY	LL	CI	AFS	AFC	Total
Pure Boran	240	240	132	205	44	51	912
50% F1	1665	1665	1665	1329	828	828	7980
50% F2	236	236	236	156	158	158	1180
50% F3	142	142	142	84	131	131	772
75% F1	436	436	436	304	515	515	2642
75% F2	85	85	85	35	126	126	542
Total	2804	2804	2696	2113	1802	1809	14,028

2.6. Traits to be studied

The traits analyzed in this study were classified into two groups: productive and reproductive traits. Productive traits comprised lactation milk yield (LMY), daily milk yield (DMY), and lactation length (LL). Reproductive traits include age at first service (AFS), age at first calving (AFC), and calving interval (CI).

2.7. Statistical analysis

The regression analysis was performed using the Generalized Linear Model (GLM) procedure in SAS version 9.0 (2004) was used to analyze the productive (LMY, DMY, and LL) and reproductive (AFS, AFC, and CI) performance traits on crossbreeding parameters. Crossbreeding effects were decomposed into breed additive effects, heterosis, and recombination loss coefficients. These components were fitted as covariates in the model to estimate the breed additive (gi), heterosis (hij), and recombination loss (rij) coefficients, following the methodologies outlined by Dickerson *et al*. (1964) and Akbaş *et al*. (1993). The genetic model used for estimation of crossbreeding parameters is indicted as follows;

$Y = X_1b_1 + X_2b_2 + \beta\alpha$. Where;

Y, is a vector of observations for the traits of interest.

b_1, is a vector of fixed effects other than genotype.

b_2, genetic effect (breed additive difference, heterosis and recombination coefficients)

B is the matrix of expected genetic contribution (breed additive, heterosis and recombination loss)

α is a vector of the estimated corresponding parameters including overall mean

X_1, matrices relating records to fixed effects.

X_2 is a matrix of coefficients relating fixed breed additive, heterosis and recombination effects to the individual trait record.

The equation uses to calculate breed additive (g^i), heterosis (h_{ij}) and recombination loss (r_{ij}) effects will as follows:

Breed additive (g^i) = ½ ($\alpha i^s + \alpha i^d$),

Heterosis (h_{ij}) = $\alpha i^s \alpha j^d + \alpha j^s \alpha i^d$ and

Recombination loss (rij) = $4_{gi\ gj} - h_{ij}$ (Wolf et al., 1995 cited by Demeke et al., 2004b) where $\alpha i^s$and αi^d denote the gene proportion of breed i in the sire and dam of the cow, respectively

Table.2.The proportions of Holstein Friesian genes, individual and maternal heterosis and individual recombination coefficients used in prediction of performance of different genetic group

Breed and Genetic group (sire x dam)	Genetic coefficient		
	gI	h^I	rI
Pure Borena	0	0	0
50% F1 (HF*Bo)	0.5	1	0.5
F2 (HF*Bo) *(HF*Bo)	0.5	0.5	0.5
F3 (((HF*Bo)*(HF*BO))*((HF*Bo)*(HF*BO)))	0.5	0.5	0.5
75% F1 HF * (HF*Bo)	0.75	0.5	0.25
F2 ((HF * (HF*Bo) * (HF * (HF*Bo))	0.75	0.375	0.375

g^I; individual additive genetic, h^I ; individual heterosis, r^I individual recombination effect Bo; Borena, HF; Holstein Friesian.

3. RESULTS

Additive and non-additive genetic contributions to traits related to milk production.

Table 3 presents the estimates of individual additive effects, individual heterosis, and individual recombination effects for milk production traits in Friesian, and their crossbreeds examined in this study.

3.1. Additive genetic effects of milk production traits

The additive genetic difference of the Holstein Friesian breed, relative to the Boran breed, was significantly positive ($P < 0.001$) for lactation milk yield and daily milk yield, but not significant for lactation length. In the current study, the pure Holstein Friesian breed contributed 3728 ± 139.39 kg to lactation milk yield (LMY), 10.89 ± 0.30kg to daily milk yield (DMY), and non-significant 48.95 ± 14.77 days to lactation length (LL) through additive genetic effects. It was attributed to the genetic disparity between the two breeds, with the Boran showing lower values for LMY and DMY, while the Holstein Friesian demonstrated superior milk production performance. This indicates that no selection or genetic improvement programs have been implemented for Boran dams throughout the years of crossbreeding at the research station. In contrast, the pure Holstein Friesian breed has undergone multiple generations of selection aimed at enhancing milk production.

3.2. Impact of heterosis on milk production traits

The estimated direct heterosis in Boran and Holstein Friesian crossbred dairy cows varied, showing positive and non-significant values ($P > 0.05$) for both lactation length (LL) and daily milk yield (DMY). However, for traits of lactation milk yield, it was negative and non-significant value.

3.3. Recombination genetic effects of milk production traits

In the current study, the estimated recombination effects for milk production traits in Boran and Holstein Friesian crossbreds were significantly negative ($p < 0.0001$) and higher than heterosis effects. The estimated recombination losses were − 1440.92 ± 152.3kg for lactation milk yield (LMY), -2.55 ± 0.33 kg for daily milk yield (DMY), and − 75.15 ± 16.13days for lactation length (LL). This means that approximately 1440.92 ± 152.3kg of lactation milk yield (LMY), 2.55 ± 0.33 kg of daily milk yield (DMY), and 75.15 ± 16.13 days of lactation length (LL) were lost due to unfavorable interactions between epistatic alleles.

Table.3.Estimates of Crossbreeding Parameters and their Standard Errors for Milk Production Traits

Crossbreeding parameters	LMY	DMY	LL
Breed additive genetic	3728 ± 139.39***	10.89 ± 0.3***	48.95 ± 14.77^{ns}
Individual heterosis	-81.65 ± 97.98^{ns}	0.44 ± 0.21^{ns}	-18.72 ± 10.38^{ns}
Individual recombination	-1440.92 ± 152.25***	-2.55 ± 0.33***	– 75.15 ± 16.13***
LMY=lactation milk yield, DMY=daily milk yield, LL=lactation length ns: non-significant; ** significant; *** highly significant			

3.4. Additive and Non-Additive Genetic Influences on Reproductive Traits

Table 4 provides a summary of the estimated individual additive effects, individual heterosis, and individual recombination effects for reproductive traits observed in this study.

3.4.1. Additive Genetic Influence on Reproductive Traits

The additive effect of individuals had no significant negative impact on age at first service (AFS), age at first calving (AFC), and calving interval (CI) traits. The genetic estimate for individual heterosis in the current study was a small significant negative and desirable for AFC and a non-significant negative effect for AFS.

The recombination effect in the current study was non-significant and positive for AFS, AFC and CI traits. Friesian crosses with Boran about 2.95 ± 3.15 months and 2.91 ± 3.15 months delay in AFS and AFC, which could be attributed to the recombination loss.

Table.4.Estimates of crossbreeding parameters and their standard errors for reproductive traits

Crossbreeding parameters	CI	AFS	AFC
Breed additive genetic	-21.51 ± 29.19^{ns}	-2.29 ± 3.12^{ns}	-2.23 ± 3.12 ^{ns}
Individual heterosis	5.33 ± 19.79^{ns}	-8. 79 ± 2.69^{ns}	-8. 84 ± 2.71*
Individual recombination	81.01 ± 32.71^{ns}	2.95 ± 3.15^{ns}	2.91 ± 3.15 ^{ns}
CI=calving interval AFS = age at first service AFC = age at first calving ns: non-significant;*: slightly significant			

4. DISCUSSION AND CONCLUSIONS

The main objective of the current study was to explore the genetic factors associated with milk and reproductive traits in crossbred dairy cows, particularly breed additive effects, heterosis, and recombination loss of Holstein Friesian x Boran crossbred cows at Holeta agricultural research center

4.1. Additive Genetic Effects

The additive genetic effects showed a significant contribution from Holstein Friesian compared to Boran cattle, especially in the milk yield attributes. This is supported by the results obtained for the additive contribution of the breeds, where the lactation milk yield (LMY) was approximately 3,728 ± 139.39 kg, and the daily milk yield (DMY) was approximately 10.89 ± 0.30 kg, indicating the superior contribution of Holstein Friesian compared to Boran in milk production, as supported by other authors (Getahun *et al*., 2018; Tadesse et al., 2019). The non-significant contribution to lactation length (LL) implies that the contribution of the additive effects is related to the quantity of milk produced and not the length of lactation.

The low contribution of Boran cattle in terms of additives points to their adaptability to their environments. It also points to their low genetic potential for milk production. The failure of the indigenous breed to undergo selection could have contributed to its low contribution in terms of additives. These points to the need for breed improvement in the indigenous breed.

4.2. Heterosis Effects

The heterosis effects for milk production traits were mostly negative or nonsignificant. This means that the heterosis effects for the traits were low or unfavorable. The heterosis effect for lactation milk yield was − 81.65 ± 97.98 kg. This no significant result could be attributed to the diminishing heterosis in the later generations as noted in other studies (Tadesse et al., 2019). This could be due to the reduction in heterozygosity and the disruption of favorable gene combinations in the later generations as noted in other studies (Lynch & Walsh, 1998).

The effects of heterosis in reproductive traits were found to be minimum, but non-significant, showing only a slight negative estimate for age at first calving. These results indicate that the effect of heterosis may be negligible in reproductive performance, or these environmental factors and management practices may be more important for reproductive traits. However, the possibility of heterosis having an impact on production traits needs to be further investigated, especially through optimized parental selection for maximum heterotic effects.

4.3. Recombination Losses

One of the major findings of this study was the substantial negative impacts of recombination losses on milk production traits. The losses in lactation milk yield amounted to about 1,440.92 ± 152.25 kg, DMY was about 2.55 ± 0.33 kg, and lactation length was about 75.15 ± 16.13 days. These findings support earlier research that highlighted the impacts of recombination as a major factor affecting the reduction of heterosis through disruptions in epistatic gene combinations.

The magnitude of recombination loss indicates that the current breed combinations or strategies employed are suboptimal for sustaining heterotic advantages. There is also a difference in selection history, as Holstein Friesian has been subjected to rigorous selective breeding compared to Boran, which

has not been subjected to any significant selection pressure. Therefore, it is necessary to adopt strategic breeding programs, which could include genomic selection or marker-assisted selection, to sustain heterotic advantages.

4.4. Implications for Breeding Strategies

The dominance of additive effects in milk production traits points to the effectiveness of selection within breeds to improve productivity. Similarly, the low and often negative effects of heterosis point to the need to select parents properly to achieve the benefits of heterosis, while the large recombination losses point to the need to develop strategies to conserve heterozygosity and epistatic effects.

In addition, the findings promote the integration of genetic improvement programs with better management practices such as nutrition, health, and reproductive management to maximize the benefits of genetic improvement. The development of a formal breeding program focusing on within-breed selection and crossbreeding is also a key aspect in the enhancement of productivity.

In conclusion, the study confirms that additive effects are the main factors in the improvement of milk production in Holstein Friesian Boran crossbreds. The heterosis effect, although positive in the F1 generation of crossbreds, tends to decrease in the subsequent generations due to recombination losses. The presence of significant negative recombination effects further reduces the genetic potential of crossbreds. It is recommended that for the optimization of the genetic potential of crossbreds, molecular technology be employed along with selection in indigenous breeds and good husbandry practices. It is recommended that genomic technology be employed in the future for better insight into the genetic potential of certain traits and for developing precision breeding technology for dairy development in the tropics.

Declarations

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Authors’ contributions

AA contributed to design of the study, data analysis and interpretation, drafting and revising the manuscript. HW contributed to conception and design of the study, data collection, data analysis and interpretation and drafting the manuscript. ZW contributed to drafting and revising the manuscript.

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Availability of data and materials

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Declarations

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This study did not require official or institutional ethical approval.

Consent for publication

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Competing interests

The authors declare that they have no competing interests.

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