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Estimates of breed additive, heterosis and epistasis genetic effects on milk production and reproductive traits from indigenous Borena and crosses with Holstein Friesian dairy cows at Holetta dairy research farm, Ethiopia

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Abstract The aim of this study was to evaluate the breed additive, heterosis and recombination genetic effects on indigenous Borena and its crosses with Holstien Friesian dairy cows at Holetta dairy research farm. Overall, 19,454 pure Borena and crossbred dairy cattle performance records were used for the study. Crossbreeding parameter analysis on milk production and reproductive traits were applied for estimation. The regression analysis of SAS (2004) software was used to estimate the crossbreeding parameters (breed additive, heterosis and recombination losses). Results of this analysis revealed that additive effects were larger than heterosis effect for all milk production and reproductive traits. The breed additive genetic effects of Holstein Friesian breed relative to local Borena breed were 2674 kg, 7.1 kg and 142 days for lactation milk yield (LMY), daily milk yield (DMY) and lactation length (LL) traits, respectively. Similarly, the direct heterosis effects of crossbred dairy cows for LMY and DMY were 423kg and 1.25kg, respectively. Crossbreeding did not always positive effects on milk production traits. In the present study, 1902.3 ± 200kg of LMY, 4.2 ± 0.5kg of DMY and 91 ± 20.8 days of LL were lost due unfavorable epistatic allele's interaction (recombination loss). The breed additive genetic effects of Holstein Friesian as deviated from Borena breed for age at first service (AFS), age at first calving (AFC), calving interval (CI), days open (DO) and number of service per conception (NSC) were 373.9 ± 114.8 days, 337.1 ± 112.6 days, 105.7 ± 54.2 days, 98.5 ± 54.2 days and 0.05 ± 0.4 days, respectively. The heterosis retention of crossbred dairy cows for AFS, AFC, DO, and NSC in the present study were -117.6 ± 61.3 days, -207.9 ± 59.8 days, -4.9 ± 27.6 days and -0.2 ± 0.2 days, respectively. However, Friesian with Borena crosses were about 129.2 ± 97 days and 70.5 ± 95.2 days delayed AFS and AFC due to the recombination losses. This study recommended that improvement of management level (feed, health, etc.), and selection on Borena and their crosses should be implemented to favor the genetic base of crossbreeding parameters (additive and non-additive genetic effects.

Keywords: additive genetic effect, crossbreeding parameter, hybrid vigor, recombination loss

1. Introduction

The genetic basis for crossbreeding is broadly classified into two components; additive and non-additive (Swan and Kinghorn 1992). Crossbreeding as a mating system optimizes the additive genetic and non-additive (heterotic) breed effects of *Bos taurus* and *Bos indicus* cattle in sustainable breeding systems and it also allows considerable flexibility in matching complementary breed types to local environmental resources and constraints (Gregory and Cundiff 1980).

The additive component is the average merit of the parental lines or breeds, with simple weighting according to the level of gene representation of each parental breed in the crossbred genotype (Swan and Kinghorn 1992). This additive component can be divided into individual and maternal additive genetic effects. The individual additive genetic effect is the contribution to offspring phenotype attributable to its own set of genes. Maternal additive genetic effects are defined as any contribution or influence on the offspring's phenotype attributable to its own dam (Maurer and Gregory 1990). Maternal effects can be classified into prenatal (e.g. the cytoplasm of the egg and uterine environment) and postnatal (for example, milk production, method of rearing and/or mothering ability).

Heterosis (hybrid vigor) is a measure of the difference between the average performance of a crosses and the average of the parents. Significant heterosis values are usually obtained under optimum conditions by combining indigenous and exotic

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breeds. It is widely used in the world in order to enhance the production of milk and meat, particularly under commercial farms (Cunningham 1982). The genetic basis of heterosis requires the expression of non-additive action, including dominance (interactions between alleles within-locus) and epistasis (interaction among allele's between-loci) (Cunningham 1982). Earlier, the study by Rich and Bell (1980) explained that crossbreeding theory is largely (though not exclusively) based on the arrangement of favorable dominance effects in each generation. In this regard, heterosis alone will not guarantee success in a crossbreeding program. Because these dominance effects are not cumulative from one generation to the next, though they can be enhanced by appropriate selection. From a genetic point of view, heterosis quantifies the amount of non-additive genetic effects that deviate from the additive component. Heterosis in crossbred animals may contain a dominance effect and negative component caused by the breakdown of favorable interactions between loci that have been built up-on through both natural and artificial selections. Dominance genetic effect results from the action of pairs of alleles at a locus for a trait (Mrode and Thompson 2005). Therefore, the benefit of crossbreeding is exploiting heterosis in a structured way because heterosis is a bonus that dairy producers can expect in addition to the positive effects of the individual additive gene. However, heterosis is minimal in dairy cattle crossbreeding compared to other domestic species. The effect of heterosis is known to be generally higher for traits with low heritability, such as reproductive traits (Arthur et al 1999).

Crossbreeding can also cause risks of negative (unfavorable) effects and one of them is recombination loss (epistasis). Epistasis refers to the interactions among additive and dominance effects between loci (Kinghorn and Vercoe 1989 and Mrode and Thompson 2005). Koch et al (1985) defined epistasis (recombination effect) as the deviation due to change in non-allelic gene interaction effects in second filial generation (F_2) individuals relative to those of the first filial generation (F_1) from gamete recombination between the chromosomes of parent breed.

Cunningham and Syrstad (1987) reviewed reports on dairy cattle crossbreeding in more than 25 countries across the tropics and showed the breed additive contributions of Friesian breed for milk production traits are generally high compared to another indigenous breed like Boran, and Sahiwal. This might be a result of the lower milk production of the indigenous tropical breeds compared to Friesian. In the long-term crossbreeding experiment at Holetta dairy research farm, Borena and Holstein Friesian have been referred to as ideal breeds for crossbreeding and their progenies are available for synthetic breed development. Knowledge of the kind and amount of the additive and non-additive genetic effects in the existing crossbred dairy cows can be used to the breeder to design optimum breeding plans at the research farm. Therefore, the present study was aimed to evaluate the long-term crossbreeding (breed additive, heterosis and epistasis) genetic effects between the two breeds and their progenies. Long-term data were available for these estimates.

2. Materials and Methods

2.1. Study location

Data were collected from indigenous Borena and crossbred dairy cows recorded spread over 42 years (1974-2017) maintained at Holetta dairy cattle research farm, located 29 km away from the capital, Addis Ababa, in the western direction. Getahun et al (2019) described the detailed geographical location and environmental condition of the study area. Overall, 19,454 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.

Traits	Number of observations in each breed (genotype)						Total
	Borena	50%			75 %		
		F_1	F_2	F_3	1st generation	2nd generation	
Lactation milk yield	482	1598	234	139	299	43	2795
Daily milk yield	478	1543	234	139	236	34	2664
Lactation length	478	1543	234	139	236	34	2664
Age at first service	54	461	89	60	143	26	833
Age at first calving	59	470	89	60	143	26	847
Calving interval	1147	1295	162	89	167	22	2882
Days open	1124	1271	161	87	163	22	2828
Service per conception	1410	1762	258	150	313	48	3941
Total	5232	9943	1461	863	1700	255	19454

F_1, F_2 and F_3 named for 50% crosses, which means 1st, 2nd and 3rd filial generations, respectively.

2.2. Breeding program

The 50% F_1 generations (Borana x Holstein Friesian) were produced by the mating of pure Borana dam and pure Friesian sire. On the other hand, 50% F_1 is backcrossed with pure Holstein Friesian (HF) semen to produce the 75% first generations. The later generations, F_2 (F_1 male x F_1 female), F_3 (F_2 male x F_2 female) and 75% second generations were produced by *inter se* mating of 50% male with 50% female and 75% male with 75% female to produce synthetic breed at 50% HF and 50% Borana and 75% HF and 25% Borana blood levels (Figures 1A, 1B, 1C, and 1D).

Figure 1 Sample photos of indigenous Borena and crossbred with different genotype at Holetta dairy research farm. **A:** indigenous Borena breed. **B:** 75% crossbred dairy cows. **C:** crossbred calves (mixed genotype). **D:** 50% crossbred dairy cows.

2.3. Statistical analysis

The regression analysis of generalized linear model (GLM) procedure of SAS 2004 version 9.0 was used to analyze crossbreeding effects on milk production (LMY, DMY and LL) and reproductive (AFS, AFC, CI, DO and NSC) traits. The genetic model used for estimation of crossbreeding parameters are indicated as follows;

$Y = X_1b_1 + X_2b_2 + e$. where:

Y, is a vector of observations for the target trait.
b_1, is a vector of fixed effects other than genotype (year, season, parity), which were significant.
b_2, coefficients of genetic effect (breed additive, heterosis and recombination coefficients).
X_1, matrices relating records to fixed effects.
X_2 is a matrix of coefficients relating to breed additive, heterosis and recombination effects to the individual trait record.
e, vector of random residual effect.

Table 2 indicated the genotypes and their expected individual breed additive, heterosis and recombination coefficients used for estimation of crossbreeding parameters.

The expected breed additive, heterosis and recombination coefficients were fitted as covariates to calculate the breed additive (g_i), heterosis (h_{ij}) and recombination loss (r_{ij}) (Dickerson 1973; Akbas et al 1993; Wolf et al 1995). The same method was used in the present study. The equation used to calculate coefficients of breed additive (g_i), heterosis (h_{ij}), and recombination loss (r_{ij}) effects were 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 (r_{ij}) = 4 $g_i\,g_j$ - h_{ij} where α_i^s and α_i^d denote the gene proportion of breed i in the sire and dam of the cow, respectively (Wolf et al 1995).

Based on the above formula, the breed additive, heterosis and recombination loss coefficients of genes from indigenous Borena and Holstein Friesian in the crossbreeding experiment were calculated as follows:

$g^I = 1/2\,(g^sF + g^dF)$
$h^I = (g^sB \times g^dF) + (g^sF \times g^dB)$
$r^I = 4gBgF - h^I$

where, g^I, individual breed additive effect of Friesian as deviated from Borena breed; g^sF, proportion of gene from Friesian sire; g^dF, proportion of gene from Friesian dam; h^I, individual heterosis; g^sB, proportion of gene from Borena sire; g^dB, proportion of gene from Borena dam; r^I, individual recombination loss; gB, proportion of Borena gene; gF, proportion of Friesian gene.

No separate estimation was applied for each cross. Rather, heterosis and recombination for all crosses were fitted as a single parameter.

Table 2 Genetic coefficients (breed additive, heterosis and recombination loss) for each genotype.

Breed and Genotype (sire * dam)		Genetic coefficients		
		g^I	h^I	r^I
Pure Borena		0	0	0
50 %	F_1 (HF*Bo)	0.5	1	0
	F_2 (HF*Bo) *(HF*Bo)	0.5	0.5	0.5
	F_3 (((HF*Bo)*(HF*BO))*((HF*Bo)*(HF*BO)))	0.5	0.5	0.5
75 %	First generations HF * (HF*Bo)	0.75	0.5	0.25
	Second generations ((HF * (HF*Bo) * (HF * (HF*Bo))	0.75	0.375	0.375

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

3. Results and discussion

3.1 Additive and non-additive genetic effects of milk production traits

Estimates of individual additive, individual heterosis and individual recombination effects of milk production traits for Borena, Friesian and its crosses in the present study are presented in table 3.

3.1.1 Additive genetic effects of milk production traits

The individual breed additive difference of Holstein Friesian as deviated from Borena breed was positive and highly significant (p<0.001). The pure Holstein Friesian breed additive contributions in the present study was 2674 kg for LMY, 7.1 kg for DMY and 142 days for LL. This was attributed by the genetic difference between the two breed for the three milk production traits i.e., lower LMY, DMY and LL of Borena and higher milk production performances of Holstein Friesian. This showed that no selection and improvement program were made on the Borena dams over years of crossbreeding in the research station. On the other hand, the pure Holstein Friesian breed has been selected for many generations to boost milk production. The present result was comparable with breed additive difference of 2774kg LMY, 7.1 kg DMY and 152 days LL reported by (Demeke et al 2004a) in the Friesian breed relative to Borena. However, this result was higher than the significant Friesian additive breed contribution of 2055kg LMY, 5.9 kg DMY and 108 days LL reported by (Haile et al 2009a). Earlier study carried out by Million and Tadelle (2003) the additive contribution of Friesian deviated from the Arsi breed was significant and positive values of 3.63 kg of milk yield per day for lactation length. Recently a similar crossbreeding estimate was done by Tadesse et al (2015) and found significantly positive additive effect but lower value for the three productive traits compared to the present study. Beyene (1992) reported an average genetic difference of 2472 ± 398 kg and 2659 ± 324 kg of first lactation milk yield between Friesian and Borena in the wet and dry regions of Ethiopia, respectively. The author also reported the additive genetic effect of milk production was higher in the dry region (Melka Worrer and Adami Tulu) than in the wet region (Holetta and Bako).

3.1.2 Heterosis effects of milk production traits

The estimated direct Heterosis for Borena and Holstein Friesian crossbred dairy cows was different. For LMY and DMY, it was significant and positive (P<0.001) but for LL trait, it was a non-significant negative value (table 3). This indicated that crossbreeding Holstein Friesian with Borena resulted in a desirable individual heterosis effect on LMY and DMY. The present

423 kg of LMY individual heterosis contribution was in agreement with Demeke et al (2004a) who found 454 kg. However, the present heterosis result of the three milk production traits were lower than the finding of (Haile et al 2009a and Tadesse et al 2015). A significantly desirable heterosis contribution of Holstein Friesian and Arsi breed gene for milk yield per lactation length (1.08 kg) and for milk yield per calving interval were reported by (Million and Tadelle 2003). The non-significant negative heterosis effect for LL trait observed in the present study might be due to reduction of heterosis in the F_2, F_3 and backcrosses or management change of the farm. Syrstad (1989) concluded that most of the decline in productivity from the F_1, to F_2 generations was due to loss of heterozygosity, i.e. dominance effects were the most important contributor to heterosis, with perhaps a small negative effect of recombination on milk yield but not fertility traits.

3.1.3 Epistasis genetic effects of milk production traits

The recombination effect estimates of Borena and Holstein Friesian crosses for milk production traits in the present study were significantly (p<0.0001) negative and higher than heterosis effects with estimated values of -1902.3 kg, -4.2 ± 0.5 kg and -91 ± 20.8 days for LMY, DMY and LL. In other words, the 1902.3 ± 200 kg of LMY, 4.2 ± 0.5 kg of DMY and 91 ± 20.8 days of LL were lost due unfavorable epistatic allele's interaction. Sheridan (1981) pointed out that recombination effect has been found most notably for milk production in the tropic. The result was in line with the finding of Demeke et al (2004a) except for LL who reported a positive recombination loss. The negative recombination estimate for milk production traits in the crosses of Friesian with Borena were expected. The Friesian breed has been selected for generations to increase milk yield per cow. On the other hand, the indigenous Borena has not been selected for several generations. Thus, by crossing the selected Friesian with the unselected Borena, favorable epistatic interactions between genes in different loci may have evolved, and these interactions may have been lost due to recombination. This shows that no optimal use of breed combination was presented in our research farm. Recently estimated a significant recombination loss of -586.44 ± 162.02 kg for LMY and non-significant negative (-0.61 ± 0.4 and -25.47 ± 17.5) for DMY and LL were reported by (Tadesse et al 2015).

Table 3 Crossbreeding parameter estimates and their standard error for milk production traits.

Traits	Estimates ± SE			
	Borena mean	Direct Additive	Direct Heterosis	Direct Recombination
LMY (kg)	421.5 ± 110.2	2674.05 ± 252.8***	423.9 ± 128.7**	-1902.3 ± 200***
DMY (kg)	4.1 ± 0.3	7.1 ± 0.6***	1.25 ± 0.3***	-4.2 ± 0.5***
LL (days)	180.4 ± 11.3	88.4 ± 26.6**	-0.1 ± 9.3^{ns}	-91 ± 20.8***

ns: non-significant; ** significant ; *** highly significant; SE, standard error.

3.2 Additive and non-additive genetic effects of reproductive traits

Estimates of individual additive, individual heterosis and individual recombination effects for reproductive traits in the present study are summarized in table 4.

3.2.1 Additive genetic effects of reproductive traits

The individual additive genetic contribution of Friesian as relative to indigenous Borena breed for the improvement of reproductive performances of the progeny was only negative and significant (P<0.01) for AFS and AFC and non-significant negative effect for CI, DO and NSC, which might be indicated that small additive effect of Holstein Friesian breed for CI, DO and NSC traits. In the present study, Holstein Friesian heifers are served 373.9 ± 114.8 days and calved 337.1 ± 112.6 days earlier than Borena. When *Bos taurus* dairy breeds are crossed with tropical indigenous breeds, the crossbreds exhibit a reduction in AFS and AFC as a result of the additive genetic contributions of dairy breeds or heterosis or both (Cunningham and Syrstad 1987; Demeke et al 2004b; Haile et al 2009b). In contrast to this, (Beyene 1992; Demeke et al 2004b; Haile et al 2009b) reported non-significant additive differences for CI, DO and NSC between Holstein Friesian dairy breed and indigenous tropical cattle in the tropical environment of Ethiopia. However, it was surprising that Tadesse et al (2015) reported significant positive estimates of 55.01 ± 54.5, 40.51 ± 54.3 and 385.30 ± 208.9 days for CI, DO and AFC traits, respectively with higher standard errors.

3.2.2 Heterosis effect of reproductive traits

The estimated direct heterosis in the present study was desirable and significantly negative for AFC and non-significant negative effect for AFS, DO and NSC. However, CI was positive and non-significant. Demeke et al (2004b) reported a significant estimates (-3.5 months, -50 days, -23 days and -0.24 days) for AFC, CI, DO and NSC traits, respectively. Regardless of its actual values, the significant heterosis estimate particularly AFC and non-significant values of the majority of reproductive traits were also consistent with (Beyene 1992; Haile et al 2009b; Tadesse et al 2015). However, the positive non-significant estimate of calving interval in the present study did not agree with Tadesse et al (2015) who found highly significant negative (p<0.05) with an estimated value of -70.14 days.

3.2.3 Epistasis genetic effects of reproductive traits

The results of recombination effects for reproductive traits in the present study was non-significant positive for AFS and AFC and, significant negative for CI and DO traits. In this study, the results indicated that for Friesian with Borena crosses about 129.2 ± 97 days and 70.5 ± 95.2 days delayed in AFS and AFC due to recombination losses. The significant positive AFC and the non-significant negative values of CI, DO and NSC estimate in the present study was agreed with the finding of (Demeke et al 2004b). However, inconsistent with the finding of Tadesse et al (2015) who reported a significant and negative estimate (-8.51 ± 33.88 and -62.60 ± 138.41) for days open and age at first calving with higher standard errors. Different authors pointed out that recombination loss is difficult to estimate even though it reduces the level of heterosis (Cassell & McAllister, 2009) and is often ignored when designing crossbreeding programs (Swan and Kinghorn 1992).

Table 4 Crossbreeding parameter estimates and their standard error for reproductive traits

Traits	Estimates ± SE			
	Borena mean	Additive effects	Heterosis effects	Recombination effects
AFS (in days)	947.4 ± 50.5	-373.9 ± 114.8**	-117.6 ± 61.3ns	129.2 ± 97.2^{ns}
AFC (in days)	1315.5 ± 48.5	-337.1 ± 112.6**	-207.9 ± 59.8**	70.5 ± 95.2^{ns}
CI (in days)	450.8 ± 14.3	-105.7 ± 54.2^{ns}	2 ± 27.5^{ns}	-113.6 ± 43*
DO (in days)	176.3 ± 14.5	-98.5 ± 54.2^{ns}	-4.9 ± 27.6^{ns}	-122.3 ± 43.6**
NSC (in days)	2 ± 0.1	-0.05 ± 0.4^{ns}	-0.2 ± 0.2^{ns}	-0.3 ± 0.3^{ns}

ns: non-significant; ** significant ; *** highly significant; SE, standard error.

4. Conclusions

The extent of individual additive, heterosis and recombination effects were varied among traits in this study. The coefficient for the additive effects was larger than coefficient for heterosis effect for milk production and reproductive performance traits indicating that major portion of successes were resulted from additive genetic variation for these traits. The estimated additive and heterosis effect of milk production and reproductive traits were gone in the right direction which means have shown positive values for milk yield and negative values for reproductive traits. Significant recombination losses have appeared in all milk production traits, which means unfavorable. The recombination effect for reproductive traits was significant negative for CI and DO traits and non-significant positive values for AFS and AFC. In general, the present study showed that

1. Borena breed has a lower additive genetic contribution for milk production and reproductive potential compared to Holstein Friesian breed.
2. Regardless of small or large values, positive heterosis effects were obtained in the crossbred cow's for milk production and reproductive traits.
3. Favorable genes were lost during gamete recombination because of the lack of selection of the indigenous Borena breed and crossed with the selected Friesian.

Therefore, our study recommended that improvement of management level (feed, health, etc.) and selection on Borena and their crosses should be implemented to favor the genetic base of crossbreeding parameters (additive and non-additive genetic effects) and optimal use of breed combination in our breeding program.

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Conflict of Interest

The authors declare no conflicts of interest.

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