



Estimation of (co)variance components, genetic parameters, and genetic trends of growth traits in community-based breeding programs of Bonga sheep



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ABSTRACT

Community-based sheep breeding programs (**CBBPs**) have been adopted strategically to improve Bonga sheep, the most popular sheep breed in Ethiopia. The present study was undertaken to estimate genetic parameters and genetic trends for growth traits and inbreeding levels in each Bonga sheep CBBP. Data pertaining to growth traits, spanning a period of seven years (2012–2017), were collected from 14 Bonga sheep CBBPs. Data were analyzed using the General Linear Model procedure of SAS to study the performance of the breed over the years. The genetic parameters were estimated by univariate and multivariate animal model using restricted maximum likelihood method of WOMBAT software. The genetic trends were estimated by the regression of the average breeding values of the animals on the year of birth. The overall least square means \pm SE of BW (kg) were 3.10 ± 0.010 , 16.1 ± 0.07 , 24.7 ± 0.20 , 30.4 ± 0.40 and 34.0 ± 0.84 for birth weight (**BWT**), weaning weight (**WWT**), six-month weight (**SMWT**), nine-month weight (**NMWT**) and yearling weight (**YWT**), respectively. Direct heritability estimates from selected models were 0.56 ± 0.030 , 0.36 ± 0.030 , 0.22 ± 0.040 , 0.17 ± 0.070 and 0.13 ± 0.150 for BWT, WWT, SMWT, NMWT and YWT, respectively. Six-month weight was the selection trait and presented positive trends for 10 CBBPs, and negative trends for four CBBPs. Moderate to high heritability estimates and positive genetic trends indicated scope for further improvement of BW. Additionally, the positive and high correlation between BW traits indicated that selection for just one trait would also improve the other traits through correlated responses.

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Implications

The aim of this paper was to expand community-based breeding program breed improvement strategy to further improve genetic gains in Bonga sheep. Nongenetic factors (birth type, sex, dam parity, community-based sheep breeding program cooperatives and year of birth) should also be considered during breeding value estimation. Both direct and maternal additive genetic effects should be considered during selection of sires at their six-month weight. The moderate to high estimated heritability for most of the growth traits, and positive genetic trends, indicated scope for further improvement of these traits. The positive and medium correlation between body weights guaranteed early age selection.

Introduction

Sheep breeds in Ethiopia make an immense contribution in terms of cash income through production of meat, milk, skin and manure. Sheep in Ethiopia are considered as social prestige (Nigussie et al., 2013) and are used as a source of foreign exchange (Berhan and Arendonk, 2006). The Bonga sheep breed is characterized by a long and wide fat tail with a tapering and twisted end. Both sexes are polled, having a short and smooth hairy coat of various colors, with light red predominating. The breed is also known for its docile temperament, good fattening potential, fast growth rate and prolificacy (Duguma, 2010).

Community-based breeding program (**CBBP**) was implemented to improve the productivity of indigenous breeds (Haile et al., 2019a). The program was started in Ethiopia in 2009, involving four sheep breeds (Bonga, Afar, Horro and Menz) (Haile et al.,

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2019a). Out of the initial four breeds, Bonga sheep CBBP was the most successful and has been expanded to 14 CBBPs (Haile et al., 2019a). The breeding objective traits, identified by the community for Bonga sheep, were growth rate, tail type, absence of horn, twinning rate, mothering ability and coat color (Mirkena et al., 2012).

Knowledge of genetic parameters for BW traits at various ages is important to determine breeding strategies. Information about the associations between traits is required when making selections based on one growth trait in order to guarantee improvements across other traits as well (Behzadi et al., 2007). The main purpose of any breeding program was maximum exploitation of genetic variation for different traits (Mohammadi and Abdollahi-arpanahi, 2015). Comparing different methods of selection and management requires estimations of genetic, phenotypic and environmental trends. Nongenetic factors *viz* sex, birth type, dam party and birth season of lambing influence growth traits. Random factors, including direct genetic effect, maternal genetic effect and environmental factors, also affect both lambs and their dams (Behzadi et al., 2007). The performance of the Bonga sheep breed in the 14 CBBPs has not been studied; therefore, the current study was taken up with the objective of estimating genetic parameters, genetic trends and inbreeding levels in each CBBP for optimization of the programs.

Material and methods

Description of the study area

The study was conducted in four districts, namely Adiyu, Gesha, Shishonde and Tello, of Kaffa zone of Southern Nation Nationalities and People Region, Ethiopia. The production system of the area is mixed crop-livestock farming system. The major rainy season in the study area extends from May to October and a dry season lasts from October to April (Mirkena et al., 2012). The altitude range of the study area is 1 600–3 348 meters above sea level and the minimum and maximum temperature was 14 and 32 °C respectively with an average of 24 °C. Similarly, the coordinates for the study area are 7°34'N latitude and 37°6'E longitude and 467 km away from the capital city, Addis Ababa.

Breeding program and animal management

Among the 14 CBBPs, five (Abeta, Buta, Dacha, Dirbedo and Shosha) were established in 2012 while the remaining were created in 2014. As the breed is not a seasonal breed, lambing is observed all year round. The animals were tagged for identification with a plastic ear tag before the lambs were weaned. The ear tags contained information on the code of the CBBP cooperative, the identification number (ID) of the lamb and its year of birth. The data recorded for each lamb included their sex, birth weight (BWT), weaning weight (WWT), six-month weight (SMWT), nine-month weight (NMWT), yearling weight (YWT), coat color, animal ID, sire ID, dam ID, birth date (date, month and year), birth type, parity, cooperative name and owners name.

Selection of male lambs was carried out separately within each CBBP, and in two stages: screening of heavy weaners at weaning (3 months), followed by selection at 6 months (postweaning) by using their estimated breeding values (EBVs). When Bonga CBBP started, selection was carried out at 6 months and, fast growing lambs were sold before they reached the selection age of 6 months. The two-stage selection was therefore implemented to select best breeding rams. Lambs with undesirable traits like horns, a short tail and black coat were culled regardless of their EBVs. Selection for the maternal line was not implemented in Bonga CBBP due to the limited flock size per household.

Flocks were kept in animal houses during the night and mid-day. The houses were made of bamboo walls corrugated with any locally available roofing materials. The major feed resources in the study areas were pasture, crop residues and kitchen leftovers, in that order of importance.

Data collection

BW data used for this study were BWT, WWT, SMWT, NMWT and YWT. Fixed effects included in genetic analysis were those significant in phenotypic analysis. Age corrected BW formulas were in kg:

$$\text{Adjusted WWT} = \frac{90(W2 - W1)}{D} + W1$$

$$\text{Adjusted SMWT} = \frac{180(W3 - W1)}{D} + W1$$

$$\text{Adjusted NMWT} = \frac{270(W4 - W1)}{D} + W1$$

$$\text{Adjusted YWT} = \frac{365(W5 - W1)}{D} + W1$$

where

W1 = BWT, W2, W3, W4 and W5 = weight at 3, 6, 9 and 12 months

D = number of days between weighing date and date of birth.

Additionally, average daily gains (ADGs) from birth to adjusted WWT (ADG1), from weaning to 6 months (ADG2), from 6 months to 9 months (ADG3) and from 9 months to YWT (ADG4) were also calculated.

$$\text{ADG1 (g)} = \frac{(W2 - W1)}{D} \times 1000$$

$$\text{ADG2 (g)} = \frac{(W3 - W2)}{D} \times 1000$$

$$\text{ADG3 (g)} = \frac{(W4 - W3)}{D} \times 1000$$

$$\text{ADG4 (g)} = \frac{(W5 - W4)}{D} \times 1000$$

A suspended weighing scale (50 kg capacity) with an accuracy of 100 g was used to record BW. The number of sires and dams for the studied data was 968 and 6 647, respectively (Table 1). Thus, on average based on BWT data, there were 16.7 and 2.4 pro-

Table 1
Pedigree structure of Bonga sheep included in the study.

Item	Numbers
No. of animals	22 352
No. of records	16 116
No. of sires	968
No. of dams	6 647
No. of animals with unknown sire	11 095
No. of animals with unknown dam	6 580
No. of animals with both parent unknown	6 335
No. of animals with known paternal grandsire	5 774
No. of animals with known paternal grand dam	8 162
No. of animals with known maternal grand sire	963
No. of animals with known maternal grand dam	1 594

genies per sire and dam, respectively. The detailed data structure and number of records for the pooled data of studied traits are indicated in Table 1.

Data analysis

Phenotypic performance analysis

To reduce bias, weights measured at different ages were adjusted using the formula of Inyangala et al. (1992). The data were analyzed by SAS (2012) using its General Linear Model function to assess the fixed effects of nongenetic viz; year of birth (7 levels: 2012–2018), lamb sex (2 levels), type of birth (3 levels: single, twin, triple and above), season of birth (2 levels: wet and dry), dam parity (7 levels: parity 1–6 and 7 and above) and CBBP cooperative (14 levels) on different growth traits. The statistical significance of various fixed effects in the least square model was determined by the 'F' test. For significant effects, the differences between pairs of levels of effects of nongenetic factors were tested by the modified Tukey-Kramer method in SAS.

Genetic component analysis

(Co)variance components, genetic parameters and EBVs were estimated by restricted maximum likelihood fitting an animal model using WOMBAT software (Meyer, 2007) (Supplementary Material S1). The statistical models used were as follows:

$$\text{Model 1: } y = \mathbf{X}_b + \mathbf{Z}_1 a + e$$

$$\text{Model 2: } y = \mathbf{X}_b + \mathbf{Z}_1 a + \mathbf{Z}_2 m + e$$

$$\text{Model 3: } y = \mathbf{X}_b + \mathbf{Z}_1 a + \mathbf{Z}_2 m + e \text{ with } \text{Cov}(a,m) = 0$$

$$\text{Model 4: } y = \mathbf{X}_b + \mathbf{Z}_1 a + \mathbf{Z}_2 m + e \text{ with } \text{Cov}(a,m) = A\sigma_{am}$$

$$\text{Model 5: } y = \mathbf{X}_b + \mathbf{Z}_1 a + \mathbf{Z}_2 m + \mathbf{Z}_3 c + e \text{ with } \text{Cov}(a,m) = 0$$

$$\text{Model 6: } y = \mathbf{X}_b + \mathbf{Z}_1 a + \mathbf{Z}_2 m + \mathbf{Z}_3 c + e \text{ with } \text{Cov}(a,m) = A\sigma_{am}$$

where y is $n \times 1$ vector of observations for each trait, b is a vector of fixed effects (birth year, dam parity, season, sex, CBBP cooperative and birth type), a , m , c and e are vectors of random effects for direct additive genetic effect, maternal additive genetic effect, permanent environmental effect of dam and residual effects, respectively. The incidence matrices of fixed effects were \mathbf{X} , and \mathbf{Z}_1 , \mathbf{Z}_2 and \mathbf{Z}_3 for direct additive genetic effect, maternal genetic effect and permanent environmental effect of the dam. The numerator relationship matrix between animals was A , and σ_{am} was covariance between direct and maternal genetic effects.

According to El Fadili et al. (2000), the (co)variance structure of the random effects in the analysis was as follows:

$$V_{(a)} = A\sigma_a^2, V_{(m)} = A\sigma_m^2, V_{(c)} = I_d\sigma_c^2, V_{(e)} = I_n\sigma_e^2, \text{Cov}_{(a,m)} = A\sigma_{am}$$

where σ_a^2 , σ_m^2 , σ_c^2 , σ_{am} and σ_e^2 are direct additive genetic variance, maternal additive genetic variance, maternal permanent environmental variance, direct-maternal genetic covariance and residual variance, respectively. I_d and I_n are identity matrices of an order equal to the number of dams and the number of lambs, respectively.

Estimates of additive direct (h_a^2) and additive maternal (h_m^2) heritability and ratio of maternal permanent environmental variance with phenotypic variance (c^2) were calculated as a ratio of estimates of additive direct (σ_a^2), additive maternal (σ_m^2) and maternal permanent environmental (σ_c^2) variances to the phenotypic variance (σ_p^2), respectively. Total heritability (h_t^2) was calculated as under Willham (1972):

$$h_t^2 = (\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am}) / \sigma_p^2$$

The genetic correlations between direct and maternal genetic effect (r_{am}) were estimated as the ratio of the estimates of σ_{am} to the product of the square roots of the estimates of σ_a^2 and σ_m^2 .

The multivariate animal model was used to estimate correlation among traits (Supplementary Material S2). The genetic correlation (r_g) between traits was estimated as the ratio of the estimates of the genetic covariance between the traits one and two to the product of the square roots of the estimates of genetic variance for trait one and genetic variance for trait two. Genetic trends were estimated by the regression of the breeding values on the birth year (Kariuki et al., 2010). Genetic gain was calculated as the difference between the EBVs from the last and first year of the program (Amarilho-silveira et al., 2018). Estimation of breeding values and inbreeding levels was estimated for each CBBP independently and from a pooled dataset. Analysis within the CBBPs was helpful to evaluate the performances of each CBBP cooperatives and provide location-specific optimization measures. However, genetic parameter estimation was done using the pooled dataset.

To determine the most appropriate model, both likelihood ratio tests (LRTs) and Akaike information criteria (AIC) were used. The significance of model comparison was done from univariate analysis of animal models with and without including the effects as a random effect and compared log-likelihoods (Maximum log L) by chi-square (χ^2) distribution for $\alpha = 0.05$ with one degree of freedom (Wilson et al., 2010).

$$\chi_{1df}^2 = 2(L(\mathbf{x})_f - L(\mathbf{x})_r)$$

The LRT was distributed as a χ^2 statistic with degrees of freedom equal to ($p_f - p_r$), where; $L(\mathbf{x})_f$ = maximum likelihood for full model, $L(\mathbf{x})_r$ = maximum likelihood for reduced model, P_f = number of parameters for full the model, and P_r = number of parameters for the reduced model.

If the χ^2 distribution value is significant at ($P < 0.05$), the full model is the best fit model for the data (Wilson et al., 2010). Using LRT, only models that differ by at least one parameter are comparable, thus AIC was also used to rank the models having the same number of parameters (Akaike, 1974).

$$\text{AIC} = -2\text{Log } L + 2p$$

where p denotes the number of random (co)variance parameters to be estimated and $\text{Log } L$ is the maximum likelihood. The model yielding the smallest AIC value fits the data best (Akaike, 1974). Estimation of genetic and phenotypic correlation was done using multi-trait analysis and applying the most appropriate model which was determined in the univariate model.

Results

Fixed effects

The overall least square means \pm SE for BWT, WWT, SMWT, NMWT and YWT of Bonga sheep were 3.10 ± 0.010 , 16.1 ± 0.07 , 24.7 ± 0.20 , 30.4 ± 0.40 and 34.0 ± 0.84 (kg), respectively (Table 2). Similarly, the overall least square means for ADG1, ADG2, ADG3 and ADG4 for Bonga sheep were 141.9 ± 0.80 , 98.7 ± 2.40 , 87.6 ± 4.30 and 58.7 ± 8.50 g, respectively (Table 3). The effect of year of birth, birth type, CBBP cooperative, and sex of animal was significant ($P < 0.0001$) on all studied traits (Table 2).

Model comparison

Both LRT and AIC methods were used to choose the best fit model for the dataset (Table 4). Including maternal additive genetic effect (model 3) to direct animal genetic effect (model 1) significantly improved the log L for SMWT, NMWT and YWT. However, for BWT and WWT, both maternal genetic and permanent environmental effects of dam were important. Therefore, model six was the best fit model for preweaning weight (BWT and

Table 2
Least square means \pm SE for different BW traits as affected by different fixed effects of Bonga sheep.

Fixed effect	N	BWT	N	WWT	N	SMWT	N	NMWT	N	YWT
Overall	16 116	3.10 \pm 0.010	11 470	16.1 \pm 0.07	4 238	24.7 \pm 0.20	1 351	30.4 \pm 0.40	563	34.0 \pm 0.84
CV %		17.6		15.9		14.8		12.4		15
Year		$P < 0.0001$		$P < 0.0001$		$P = 0.0049$		$P < 0.0001$		$P = 0.0007$
CBBP Cooperative		$P < 0.0001$		$P < 0.0001$		$P < 0.0001$		$P < 0.0001$		$P < 0.0001$
Abeta	1 721	3.06 \pm 0.01 ^{de}	1 071	15.1 \pm 0.1 ^{de}	156	23.5 \pm 0.4 ^d	98	27.9 \pm 0.5 ^c	50	31.0 \pm 1.1 ^c
Alargeta	1 460	3.30 \pm 0.01 ^b	1 242	17.6 \pm 0.1 ^a	673	24.1 \pm 0.3 ^{cd}	272	30.3 \pm 0.4 ^b	63	33.1 \pm 1 ^c
Angiyokola	620	3.60 \pm 0.02 ^a	427	17.9 \pm 0.2 ^a	99	26.4 \pm 0.4 ^b	–	–	11	41.8 \pm 1.9 ^a
Dacha	1 611	3.10 \pm 0.01 ^c	1 252	14.5 \pm 0.1 ^{ef}	714	23.2 \pm 0.3 ^d	413	29.4 \pm 0.4 ^b	186	32.5 \pm 0.8 ^c
Didifa	1 086	2.80 \pm 0.02 ^g	664	17.1 \pm 0.1 ^b	167	25.9 \pm 0.4 ^b	8	31.4 \pm 1.4 ^b	35	35.8 \pm 1.2 ^b
Dirbedo	1 731	3.10 \pm 0.01 ^{cd}	1 150	17.6 \pm 0.1 ^a	417	24.0 \pm 0.3 ^{cd}	190	29.3 \pm 0.4 ^b	40	31.9 \pm 1.1 ^c
Guta	1 122	2.90 \pm 0.02 ^g	605	15.8 \pm 0.1 ^c	165	25.8 \pm 0.4 ^b	77	31.9 \pm 0.6 ^b	–	–
Kicho	1 074	3.00 \pm 0.01 ^{ef}	826	14.7 \pm 0.1 ^{de}	477	23.4 \pm 0.3 ^d	3	28.5 \pm 2.3 ^{bc}	31	33.9 \pm 1.2 ^{bc}
Meduta	1 412	3.00 \pm 0.01 ^{ef}	1 006	14.5 \pm 0.1 ^{ef}	418	22.7 \pm 0.3 ^{de}	117	30.0 \pm 0.5 ^b	17	34.9 \pm 1.5 ^{bc}
Omashoga	897	3.30 \pm 0.02 ^b	710	15.4 \pm 0.1 ^{cd}	116	26.0 \pm 0.4 ^b	–	–	15	39.2 \pm 1.6 ^a
Shosha	1 632	3.30 \pm 0.01 ^b	1 183	16.7 \pm 0.1 ^b	505	25.3 \pm 0.3 ^{bc}	126	31.3 \pm 0.5 ^b	101	32.2 \pm 0.9 ^{bc}
Wanabolla	745	3.30 \pm 0.02 ^b	531	14.2 \pm 0.1 ^f	87	22.7 \pm 0.5 ^{de}	–	–	–	–
Yama	1 005	3.00 \pm 0.02 ^{ef}	803	17.8 \pm 0.1 ^a	244	28.2 \pm 0.3 ^a	47	33.6 \pm 0.7 ^a	14	37.6 \pm 1.7 ^{ab}
Season		$P = 0.4288$		$P = 0.0249$		$P = 0.0968$		$P = 0.0873$		$P = 0.5291$
Dry	7 924	3.10 \pm 0.01	5 707	16.1 \pm 0.1	2 063	24.8 \pm 0.2	735	30.5 \pm 0.4	327	33.9 \pm 0.9
Wet	8 192	3.09 \pm 0.01	5 763	16.0 \pm 0.1	2 175	24.6 \pm 0.2	616	30.2 \pm 0.4	236	34.2 \pm 0.9
Sex		$P < 0.0001$		$P < 0.0001$		$P < 0.0001$		$P < 0.0001$		$P < 0.0001$
Male	10 555	3.20 \pm 0.01	7 639	16.7 \pm 0.1	2 985	26.5 \pm 0.2	1 010	33.2 \pm 0.4	453	37.7 \pm 0.8
Female	5 561	3.00 \pm 0.01	3 831	15.4 \pm 0.1	1 253	22.9 \pm 0.2	341	27.5 \pm 0.5	110	30.4 \pm 1.0
Birth type		$P < 0.0001$		$P < 0.0001$		$P < 0.0001$		$P < 0.0001$		$P = 0.0111$
Single	7 146	3.47 \pm 0.03 ^a	5 281	17.6 \pm 0.1 ^a	2 172	25.9 \pm 0.2 ^a	718	31.4 \pm 0.4 ^a	311	35.2 \pm 0.8 ^a
Twin	8 554	3.10 \pm 0.01 ^b	5 916	15.9 \pm 0.1 ^b	1 966	24.6 \pm 0.2 ^b	599	30.8 \pm 0.4 ^b	238	33.7 \pm 0.7 ^b
\geq Triple	416	2.70 \pm 0.03 ^c	273	14.6 \pm 0.2 ^c	100	23.7 \pm 0.4 ^c	34	28.8 \pm 0.8 ^c	14	33.2 \pm 1.7 ^b
Parity		$P < 0.0001$		$P = 0.0003$		$P = 0.8529$		$P = 0.5259$		$P = 0.7386$
1	6 795	3.07 \pm 0.01 ^b	3 097	15.7 \pm 0.1 ^d	1 130	24.3 \pm 0.2	372	30.3 \pm 0.5	174	33.7 \pm 0.9
2	4 177	3.11 \pm 0.01 ^a	3 067	15.9 \pm 0.1 ^c	1 193	24.3 \pm 0.2	383	30.3 \pm 0.5	162	33.5 \pm 0.9
3	2 417	3.10 \pm 0.01 ^a	2 830	15.9 \pm 0.1 ^c	1 044	24.4 \pm 0.2	345	30.3 \pm 0.5	136	33.8 \pm 0.9
4	1 241	3.11 \pm 0.02 ^a	968	16.0 \pm 0.1 ^c	327	24.7 \pm 0.3	99	30.0 \pm 0.6	37	33.0 \pm 1.2
5	716	3.09 \pm 0.02 ^{ab}	644	16.1 \pm 0.1 ^{bc}	246	24.8 \pm 0.3	72	30.4 \pm 0.6	28	33.9 \pm 1.2
6	433	3.08 \pm 0.02 ^{ab}	405	16.5 \pm 0.2 ^{ab}	139	25.5 \pm 0.4	37	30.7 \pm 0.7	11	35.4 \pm 1.9
≥ 7	337	3.08 \pm 0.02 ^{ab}	459	16.4 \pm 0.1 ^b	159	25.1 \pm 0.4	43	30.5 \pm 0.7	15	35.2 \pm 1.6

BWT = birth weight; WWT = weaning weight; SMWT = six-month weight; NMWT = nine-month weight; YWT = yearling weight; CBBP = community-based breeding program; Means with different letters in column within fixed effects are significantly different.

WWT) whereas model three was most appropriate for SMWT, NMWT and YWT.

Genetic parameters

(Co) variance components for growth traits

The estimates of (co)variance components and genetic parameter estimates for studied traits along with maximum likelihood and AIC values for each BW are presented in Table 4. Perusal of variance components of the best fit model for each BW indicated that 0.20, 2.50, 3.09, 2.54 and 3.79 of the total variations embraced of direct additive variance (σ^2_a) for BWT, WWT, SMWT, NMWT and YWT, respectively. This indicated that maternal genetic and dam permanent environmental effects have significant contributions and should be incorporated during breeding value estimation.

Heritability estimation

Estimated direct heritabilities of Bonga sheep from selected models were 0.56 \pm 0.030 for BWT, 0.36 \pm 0.030 for WWT, 0.22 \pm 0.040 for SMWT, 0.17 \pm 0.070 for NMWT and 0.13 \pm 0.150 for YWT (Table 4). The moderate to high heritability estimation in the present study indicated the existence of moderate to high genetic variability which could be utilized for improvement of this breed through selection.

Genetic and phenotypic correlation estimates

The estimates of correlation coefficients between BW traits and average daily gains by using multivariate analysis are presented in Table 5. The genetic relation of BWT with all other growth traits

was low, whereas the genetic association between all other traits was moderate to high in magnitude. This indicated that selection of sires based on SMWT will improve all other growth traits, except BWT. Therefore, improvement in BWT will be slow and delayed compared to other traits.

Genetic trends

Genetic trends for all traits in each year from pooled data are presented in Table 6. The annual genetic gains were 0.002, 0.029, 0.059, 0.081 and 0.021 kg for BWT, WWT, SMWT, NMWT and YWT, respectively. The annual genetic trends for WWT, SMWT and NMWT were highly significant ($P < 0.0001$) but nonsignificant for BWT and YWT. The reason why BWT and YWT trends were not significant is that these are not linear trends. Similarly, the annual genetic gains were 0.317, 0.485, 0.255 and 0.371 g for ADG1, ADG2, ADG3 and ADG4, respectively. Annual genetic trends for ADG1, ADG2 and ADG3 were highly significant ($P < 0.001$) across each year but nonsignificant for ADG4.

Out of 14 CBBPs, positive genetic trends were observed in most ($n = 10$) of the CBBPs with varied rate (Table 7). These CBBP cooperatives were Alargeta, Angikolla, Omashonga, Wanabolla, Didifa, Kicho, Dacha, Guta, Shosha and Yama. The main reasons for this success were their highly reliable and effective recording system, participation of farmers in selection of breeding sires, and their efficient and regular use of selected breeding sires.

A negative trend was observed in four of the CBBPs (Table 7). Meduta, Buta, Abeta and Dirbedo showed negative genetic trends in SMWT (Table 7). Possible reasons for negative trends were a lack

Table 3
Least square means ± SE for different daily gain traits as affected by different fixed effects of Bonga sheep.

Fixed effect	N	ADG1	N	ADG2	N	ADG3	N	ADG4
Overall	11 470	141.9 ± 0.80	4 214	98.7 ± 2.40	1 312	87.6 ± 4.30	387	58.7 ± 8.50
CV%		19.6		40.6		55.4		60.9
Year		<i>P</i> < 0.0001		<i>P</i> < 0.0001		<i>P</i> < 0.0001		<i>P</i> = 0.1919
CBBP Cooperative		<i>P</i> < 0.0001		<i>P</i> < 0.0001		<i>P</i> < 0.0001		<i>P</i> = 0.8570
Abeta	1 071	131.0 ± 1.2 ^e	156	98.8 ± 3.7 ^{bc}	93	63.1 ± 4.9 ^d	43	56.1 ± 9.1
Alargeta	1 242	156.2 ± 1.2 ^b	672	77.5 ± 2.7 ^d	272	75.7 ± 4.2 ^{cd}	63	61.7 ± 9.2
Angiyokolla	427	156.2 ± 1.6 ^b	98	102.5 ± 4.5 ^{bc}	–	–	–	–
Dacha	1 252	123.5 ± 1.1 ^{gh}	713	100.0 ± 2.7 ^{bc}	408	72.0 ± 3.9 ^{cd}	183	62.0 ± 8.3
Didifa	664	155.9 ± 1.4 ^b	167	102.9 ± 3.7 ^b	7	232.0 ± 14.2 ^a	–	–
Dirbedo	1 150	158.8 ± 1.2 ^b	416	77.6 ± 2.9 ^d	187	65.0 ± 4.1 ^d	32	54.4 ± 10.0
Guta	605	141.4 ± 1.4 ^d	164	105.3 ± 3.7 ^b	75	80.8 ± 5.6 ^{bc}	–	–
Kicho	826	128.6 ± 1.3 ^{ef}	477	95.3 ± 2.8 ^c	3	56.1 ± 21.3 ^{bcd}	–	–
Meduta	1 006	125.9 ± 1.2 ^{fg}	413	90.6 ± 2.9 ^c	114	88.9 ± 4.7 ^b	16	60.2 ± 11.9
Omashong	710	133.0 ± 1.3 ^e	111	118.3 ± 4.1 ^a	–	–	–	–
Shosha	1 183	147.8 ± 1.1 ^c	503	91.1 ± 2.8 ^c	119	76.4 ± 4.9 ^{cd}	36	52.3 ± 9.9
Wanabolla	531	119.1 ± 1.5 ^h	83	104.4 ± 4.7 ^b	–	–	–	–
Yama	803	166.9 ± 1.3 ^a	241	118.0 ± 3.3 ^a	44	65.9 ± 6.6 ^{cd}	14	57.7 ± 12.4
Season		<i>P</i> = 0.0387		<i>P</i> = 0.8155		<i>P</i> = 0.7505		<i>P</i> = 0.6609
Dry	5 707	142.4 ± 0.9	2 052	98.8 ± 2.4	716	87.9 ± 4.5	239	59.2 ± 8.6
Wet	5 763	141.3 ± 0.9	2 162	98.5 ± 2.5	606	87.3 ± 4.4	148	58.2 ± 8.8
Sex		<i>P</i> < 0.0001		<i>P</i> < 0.0001		<i>P</i> < 0.0001		<i>P</i> = 0.0147
Male	7 639	147.7 ± 0.8	2 971	107.8 ± 2.4	987	95.7 ± 4.3	301	68.5 ± 8.4
Female	3 831	136.0 ± 0.9	1 243	89.5 ± 2.6	335	79.5 ± 4.7	86	48.8 ± 9.2
Birth type		<i>P</i> < 0.0001		<i>P</i> = 0.0102		<i>P</i> = 0.0267		<i>P</i> = 0.8814
Single	5 281	154.9 ± 0.7 ^a	2 160	94.8 ± 2.2 ^b	705	88.9 ± 4.0 ^b	217	53.7 ± 8.8
Twin	5 916	140.4 ± 0.7 ^b	1 954	97.3 ± 2.2 ^a	584	93.4 ± 3.9 ^a	162	49.5 ± 8.6
≥Triple	273	130.3 ± 1.8 ^c	100	103.9 ± 4.2 ^a	33	80.5 ± 7.4 ^b	8	72.8 ± 13.8
Parity		<i>P</i> = 0.2416		<i>P</i> = 0.0006		<i>P</i> = 0.1807		<i>P</i> = 0.6565
1	5 052	142.5 ± 0.8	1 812	94.0 ± 2.3 ^c	561	90.6 ± 4.3	159	61.5 ± 8.6
2	2 947	141.6 ± 0.9	1 069	97.5 ± 2.4 ^b	301	86.3 ± 4.5	86	62.3 ± 8.7
3	1 455	143.5 ± 1.0	566	98.0 ± 2.7 ^b	207	89.1 ± 4.8	67	60.8 ± 9.3
4	917	142.0 ± 1.2	335	97.2 ± 3.0 ^{bc}	104	88.1 ± 5.4	32	61.9 ± 10.0
5	559	141.6 ± 1.4	222	94.5 ± 3.3 ^{bc}	79	81.2 ± 5.8	22	56.6 ± 10.9
6	345	142.9 ± 1.7	132	107.5 ± 3.9 ^a	48	81.4 ± 6.7	12	57.2 ± 12.9
≥7	195	138.7 ± 2.2	78	101.8 ± 4.7 ^{abc}	24	96.4 ± 8.5	9	50.3 ± 13.6

ADG1 = average daily gain from birth to weaning; ADG2 = from weaning to 6 months; ADG3 = from 6 months to 9 months; ADG4 = from 9 months to yearling; CBBP = community-based breeding program; Means with different letters in column within fixed effects are significantly different.

Table 4
Estimates of (co)variance components and genetic parameters for BW traits from univariate analyses of Bonga sheep.

Variables	Traits				
	BWT	WWT	SMWT	NMWT	YWT
Best fit Model	6	6	3	3	3
σ_a^2	0.200	2.500	3.090	2.540	3.790
σ_m^2	0.120	1.520	2.130	3.770	11.920
σ_e^2	0.120	3.480	9.190	8.750	14.300
σ_c^2	0.050	1.390	–	–	–
σ_p^2	0.350	7.360	14.410	15.060	30.020
σ_{am}	–0.130	–1.540	–	–	–
h_a^2	0.56 ± 0.030	0.36 ± 0.03	0.22 ± 0.040	0.17 ± 0.070	0.13 ± 0.150
h_m^2	0.34 ± 0.050	0.20 ± 0.070	0.15 ± 0.020	0.25 ± 0.050	0.39 ± 0.100
c^2	0.15 ± 0.030	0.19 ± 0.050	–	–	–
h_f^2	0.190	0.130	0.290	0.290	0.320
r_{am}	–0.84 ± 0.040	–0.79 ± 0.100	–	–	–
log L	1 424.000	–16 658.000	–7 703.700	–2 484.600	–1 218.500
AIC	1 418.950	–16 663	–7 706.710	–2 487.610	–1 221.480

BWT = birth weight; WWT = weaning weight at 3 months; SMWT = six-month weight; NMWT = nine-month weight; YWT = yearling weight; σ_a^2 , σ_m^2 , σ_e^2 , σ_c^2 , σ_p^2 : variance of direct, maternal, residual, maternal permanent environment and phenotypic, respectively; σ_{am} : covariance between direct and maternal; h_a^2 , h_m^2 , h_f^2 : heritability of direct, maternal and total, respectively; c^2 : ratio of maternal permanent environmental variance to phenotypic variance; r_{am} : genetic correlation between direct and maternal; log L: maximum log likelihood AIC: Akaike information criteria.

of accuracy of data recording, mixing of flocks between CBBP participant and nonparticipant leading to poorly controlled mating and not efficiently using breeding sires. Also, some participants practiced fattening of un-castrated rams (purchased from the market) which graze and mate with the ewes and the regular purchase of new ewe/ewe lambs which did not originate was not from breeding sires.

Inbreeding of Bonga sheep under community-based breeding program

The average inbreeding coefficient of Bonga sheep was 0.36% with annual rate (F) of 0.13% (*P* < 0.0001) (Fig. 1). The inbreeding coefficient among inbred animals was 17%. The rate of inbreeding for the 14 CBBPs was found in the range of zero to 37.5. Relatively higher levels of inbreeding were observed at Abeta, Buta and

Table 5
Direct additive genetic effect below diagonal and phenotypic above diagonal correlation (SE) of growth traits of Bonga sheep.

Traits	BWT	WWT	SMWT	NMWT	YWT	ADG1	ADG2	ADG3	ADG4
BWT	–	0.002 (0.010)	0.009 (0.014)	0.005 (0.02)	0.024 (0.033)	0.003 (0.010)	0.008 (0.015)	0.000 (0.024)	0.025 (0.043)
WWT	0.204 (0.056)	–	0.515 (0.012)	0.403 (0.019)	0.308 (0.033)	0.923 (0.002)	–0.202 (0.016)	–0.106 (0.026)	–0.028 (0.046)
SMWT	0.225 (0.076)	0.610 (0.048)	–	0.736 (0.011)	0.492 (0.029)	0.482 (0.012)	0.694 (0.008)	–0.277 (0.026)	–0.111 (0.046)
NMWT	0.246 (0.086)	0.414 (0.065)	0.896 (0.036)	–	0.644 (0.027)	0.389 (0.019)	0.490 (0.017)	0.391 (0.021)	–0.160 (0.046)
YWT	0.113 (0.111)	0.191 (0.094)	0.457 (0.101)	0.606 (0.099)	–	0.277 (0.033)	0.356 (0.032)	0.300 (0.036)	0.604 (0.027)
ADG1	0.065 (0.057)	0.916 (0.007)	0.579 (0.050)	0.413 (0.067)	0.159 (0.095)	–	–0.200 (0.016)	–0.082 (0.026)	–0.070 (0.046)
ADG2	0.192 (0.094)	–0.188 (0.076)	0.583 (0.056)	0.668 (0.070)	0.486 (0.126)	–0.168 (0.078)	–	–0.241 (0.026)	–0.074 (0.046)
ADG3	0.040 (0.145)	–0.319 (0.125)	–0.056 (0.147)	0.387 (0.125)	0.457 (0.178)	–0.278 (0.126)	0.246 (0.189)	–	–0.080 (0.044)
ADG4	–0.018 (0.141)	–0.086 (0.122)	–0.070 (0.145)	0.007 (0.160)	0.785 (0.060)	–0.134 (0.123)	0.082 (0.182)	0.238 (0.253)	–

BWT = birth weight; WWT = weaning weight; SMWT = six-month weight; NMWT = nine-month weight; YWT = yearling weight; ADG1 = average daily gain from birth to weaning; ADG2 = from weaning to 6 months; ADG3 = from 6 months to 9 months; ADG4 = from 9 months to yearling.

Table 6
Genetic trends (kg) over years for different BW of Bonga sheep breed under community-based breeding program from pooled data.

Traits	Slope of trend	R ²	F-value	P-value
BWT	0.002	0.142	2.115	0.145
WWT	0.028	0.707	47.935	0.000
SMWT	0.058	0.618	42.661	0.000
NMWT	0.081	0.797	35.602	0.000
YWT	0.020	0.477	0.142	0.706

BWT = birth weight; WWT = weaning weight; SMWT = six-month weight; NMWT = nine-month weight; YWT = yearling weight.

Table 7
Genetic trend (kg) for Bonga sheep community-based breeding programs of different cooperatives by their selection age of six-month weight.

CBBP cooperatives	Slope of trend	R ²	F-value	P-value
Abeta	–0.022	0.006	0.03	0.861
Alargeta	0.017	0.583	0.984	0.321
Angiokolla	2.00E–06	0.009	0.109	0.741
Buta	–0.106	0.424	27.021	0.000
Dacha	0.206	0.827	37.493	0.000
Didifa	0.292	0.852	1.141	0.287
Dirbedo	–0.074	0.708	1.49	0.222
Guta	3.00E–05	0.97	4.546	0.034
Kicho	0.146	0.382	21.782	0.000
Meduta	–0.065	0.855	10.856	0.001
Omarshonga	0.453	0.563	0.125	0.723
Shosha	0.101	0.419	11.299	0.000
Wanabolla	0.082	0.471	0.014	0.904
Yama	0.059	0.783	10.203	0.001

CBBP = community-based breeding program.

Meduta CBBP cooperatives, whereas lower rates were recorded at Omashonga and Dirbedo CBBP cooperatives (Table 8).

Discussion

Factors affecting phenotypic performance

The studied BW showed a fluctuating trend over the years. Possible reasons may be a variation in environmental conditions, the number of record difference and the availability of forage and feeding over the last seven years (2012–2018). Results showed that BWT, WWT and YWT were heavier in lambs from the Angiokola cooperative, whereas lambs from the Yama cooperative had higher SMWTs and NMWTs. Variation in the BW among the cooperatives

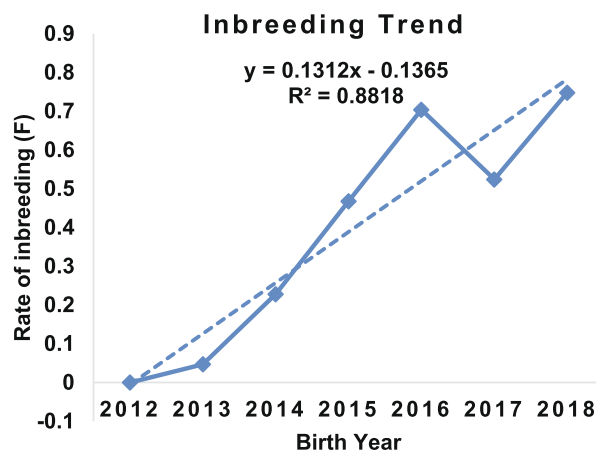


Fig. 1. Mean inbreeding trend over years in Bonga sheep breed community-based breeding program. The graph indicates normal range of inbreeding.

may be due to differences in flock management practices, availability of feed and other environmental conditions. The sex of lamb exhibited a highly significant effect ($P < 0.001$) for all BW (Table 2). Male lambs were heavier than female lambs in all BW. One possible reason may be due to hormonal and physiological differences in the two sexes (Tibbo, 2006). Also, type of birth had a significant effect ($P < 0.001$) on all BW except YWT (Table 2). Table 2 shows that a uniform trend was exhibited in the BW among singles, twins and triplets wherein the BW of single born lambs were highest and triplets lowest. The higher BW in single born lambs may be as a result of the availability of optimum nutrition during both pre- and postnatal stages of growth. The advantage of higher birth and weaning BW may then be carried forward in subsequent BW. Effect of birth year, lamb's sex, and birth type has been reported to be significant in breeds like Sabi sheep (Matika et al., 2003) and Makuie sheep (Rahimi and Rafat, 2014).

Genetic parameters, genetic gains and inbreeding

A negative covariance between direct and maternal genetic effects for a specific trait will lead to different rankings of individuals on breeding values when the maternal effect was either included or omitted in the models for the estimation of the breeding values (Bayeriyar et al., 2011). The moderate c^2 estimate for BWT and WWT indicated the importance of the maternal environment and pre- and postmaternal care of the lamb. Estimation of the association between direct and maternal genetic effects is dependent on key pedigree relationships (Maniatis and Pollott, 2003).

Table 8

Mean annual inbreeding, minimum and maximum rate of inbreeding for all and inbred animals for different Bonga sheep community-based breeding programs (CBBPs) cooperative.

CBBP cooperatives	N	All animal					N	Inbred Animal		
		Inbreeding slope	Minimum	Maximum	Average	P-value		Minimum	Maximum	Average
Abeta	1 721	0.1174	0	25	0.770	0.205	72	3.125	25	18.446
Alargeta	1 460	0.2064	0	28.125	0.300	0.000	54	1.172	28.125	8.116
Buta	6 980	0.0721	0	37.5	0.737	0.058	279	0.195	37.5	18.453
Dacha	1 611	0.1202	0	25	0.503	0.006	58	3.125	25	13.981
Didifa	1 086	0.0685	0	37.5	0.563	0.514	26	12.5	37.5	23.557
Dirbedo	1 731	0.0505	0	37.5	0.285	0.178	24	6.25	37.5	20.572
Guta	1 122	0.2276	0	25	0.509	0.002	39	3.125	25	14.663
Kicho	1 074	0.3248	0	25	0.590	0.000	31	3.125	25	20.463
Meduta	1 412	0.3013	0	25	0.710	0.000	58	3.125	25	17.295
Omashonga	897	0.2913	0	25	0.195	0.000	12	12.5	25	14.583
Shosha	1 632	0.1731	0	37.5	0.563	0.115	46	0.195	37.5	19.989
Wanabolla	745	0.1298	0	25	0.444	0.357	15	3.125	25	22.083
Yama	1 005	0.2961	0	25	0.643	0.001	32	3.125	25	20.214

The possible reasons for the observed decreasing trend in the direct heritability estimates from BWT to YWT may be ascribed to the data structure, culling during selection and sale of rams either before taking YWT or even before NMWT as these may minimize the diversity of these traits. Similarly, low estimates of heritability may be due to the strict culling of animals which might have reduced genetic variation and management factors (Matika et al., 2003). Heritability estimates for optimal models were 0.15 ± 0.01 for BWT, 0.18 ± 0.02 for WWT, and 0.20 ± 0.02 for post-weaning weight (PWWT) which were increasing with increasing age of animal for Katahdin lambs (Ngere et al., 2017). Also heritabilities increased with increasing age for Polypay sheep of BWT and WWT (0.17 ± 0.02 and 0.18 ± 0.03), respectively (Hanford and Vleck, 2006). Maternal heritability for the current study showed a decreasing trend, from BWT to SMWT which was in agreement with Katahdin lambs (0.14 for BWT, 0.10 for WWT, and 0.06 for PWWT) (Ngere et al., 2017).

Estimated heritability values of Bonga sheep were higher than other Ethiopian sheep breeds (Yacob, 2008; Abegaz et al., 2010; Gizaw et al., 2014). Similarly, the heritability was higher than some exotic sheep breeds like Turkish Merino, Kenyan Dorper and Egyptian Barki (Ozcan et al., 2005; Kariuki et al., 2010; Sallam et al., 2019). Variation in data structure, choice of models, management and environmental conditions would have influenced the differences between estimations reported in the literature for sheep breeds.

The correlation between BWT and other growth traits was low which was advantageous. If the association were strong, selection for WWT or SMWT would also increase BWT, which may be associated with dystocia (Haile et al., 2019b). Positive and strong correlations were estimated in Kenya Dorper sheep (Kariuki et al., 2010). Simultaneous improvements could be achieved for traits which have a higher heritability and a high genetic correlation. Therefore, in the current study, selection for either WWT or SMWT would result in improvement of the other because of high heritability and a medium to strong correlation.

The annual genetic trend of the current results was similar to Horro and Dorper sheep (Negussie et al., 2002; Kariuki et al., 2010). The level of inbreeding observed in this study is lower than the Food and Agriculture Organization of the United Nations (FAO) recommendation that the inbreeding rate should be maintained below the range of 0.5–1% per year to avoid risk of genetic disorders and inbreeding depression (FAO, 2010).

Generally, the evaluation of Bonga CBBPs indicated that non-genetic factors like birth year, sex, dam parity, birth type and CBBP cooperatives had a significant influence on the growth performance of the animals and need to be considered during the estima-

tion of breeding values. The direct additive, maternal genetic and maternal permanent environmental effects were important parameters to be considered during selection. The moderate to high estimates of heritability for most of the growth traits and positive genetic trends indicated scope for further improvement of these traits.

Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.animal.2021.100202>.

Ethics approval

This study was based on data collection from a breeding program and no ethical concern.

Data and model repository statement

None of the data were deposited in an official repository because Bonga Agricultural Research centre has no official repository but available in center as a softcopy.

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Declaration of interest

The authors declare that they have no conflict of interest

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