Genetic and non-genetic parameters for growth traits and Kleiber ratios in Dorper x indigenous sheep

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Abstract

Genetic improvement program will only be successful when accompanied by a good understanding of the influence of environmental factors, knowledge of the genetic parameters, and the genetic relationships between the traits of interest. Thus, this study aimed to evaluate the influence of non-genetic factors on growth traits and Kleiber ratios and to estimate genetic parameters for early growth traits in Dorper x indigenous sheep. The effects of fixed factors were analyzed by the general linear model procedure of SAS and the genetic parameters were estimated by AI-REML algorithm using a WOMBAT computer program fitted animal model. The log-likelihood ratio test was used for selecting the best-fitted model from four models. The overall least-squares means for birth weight (BW), weaning weight (3MW), six-months (6MW), nine-month (9MW), and yearling (12WT) were 3.03 ± 0.02 , 14.5 ± 0.18 , 20.4 ± 0.26 , 24.8 ± 0.31 , and 28.3 ± 0.40 kg, respectively. The overall least-square means for Kleiber ratio from birth to weaning (KR1), weaning to six-month (KR2), six to nine-month (KR3) and nine-month to yearling age (KR4) were 16.8 ± 0.10 , 6.41 ± 0.17 , 4.55 ± 0.21 and 3.38 ± 0.20 g/kg of metabolic weight, respectively. The inclusion of maternal genetic effect exerted a significant influence on BW and it explains 20% of the phenotypic variation. The total heritability (h^2_t) estimates for BW, 3MW, ADG1 and KR1 were 0.10, 0.14, 0.16 and 0.12, respectively. The phenotypic correlation varied from -0.11 to 0.98 whereas the direct genetic correlation ranged from -0.32 to 0.98 . The mean inbreeding coefficient was 0.105% with annual rate of 0.02%. The heritability estimates for growth traits and Kleiber ratio suggests that slow genetic progress would be expected from the selection. However it is, integration of selection with crossbreeding program with this level of variation would enhance the genetic gain. Therefore, selection should be conducted based on breeding values estimated from multiple information sources to increase the selection response.

Introduction

Sheep farming is a significant part of Ethiopia's livestock sector. There are around nine sheep breeds (Gizaw et al. 2008) and the total population is about 31.30 million (CSA 2018). The productivity of indigenous sheep breeds, on the other hand, is uneven in comparison to the human population. As a result, to supply the growing demand for animal protein, it has been suggested that sheep productivity be increased by employing more productive genotypes. Consequently, the Romney, Corriedale, Hampshire, Rambouillet, and Awassi sheep breeds have been imported to Ethiopia in various years since 1944 (Getachew et al. 2016). However, the contribution of these breeds except Awassi sheep was negligible (Tesema and Shenkute 2019). Consequently, the project entitled Ethiopian Sheep and Goat Productivity Improvement Program (ESGPIP) launched crossbreeding of indigenous ewes with Dorper sire breed in different parts of the country with a goal of improvement of meat production since 2007. Tumele sheep is one of the indigenous sheep populations which crossed with Dorper sheep and the resulted in crossbred rams were disseminated to farmers since 2012 to improve the growth performance and meat production.

Live weight and growth rate are economically critical traits, requiring particular attention in any breeding program intended to improve meat production. Besides growth, the selection of sheep for feed utilization is a better strategy to increase the efficiency of meat production (Faid-Allah et al. 2016). Selection for this trait directly is impossible particularly in the tropics due to the absence of feed intake data for the individual animals. However, the possibility of improving feed efficiency using the Kleiber ratio is noted by several scholars (Arthur et al. 2001; Faid-Allah et al. 2016; Ghafouri-Kesbi and Gholizadeh 2017; Mokhtari et al. 2019).

The integration of crossbreeding program with selective breeding is imperative to enhance genetic gain and reduce the declining performance of crossbreds in subsequent generations (Gizaw et al. 2012). Many factors affect growth traits and Kleiber ratio, including additive genetic effects, maternal genetic effects, and non-genetic factors (Farokhad et al. 2010). The design of such type of combined genetic improvement program will only be successful when accompanied by a good understanding of the influence of different environmental factors, knowledge of the genetic parameters, and the genetic relationships between the traits of interest. Genetic parameter estimation for various pure breeds was conducted by several scholars (Farokhad et al. 2010; Mohammadi et al. 2010; Ghafouri-Kesbi et al. 2011; Prakash et al. 2012; Khorsand et al. 2014; Mandal et al. 2015; Faid-Allah et al. 2016; Areb et al. 2021). However, there is a lack of estimates for crossbred sheep. Because of the scarcity of such estimates for growth and Kleiber ratio in Dorper crossbred sheep, the objectives of this study were to evaluate the influence of non-genetic factors on growth traits and Kleiber ratios and to estimate genetic parameters for early growth traits and Kleiber ratio in Dorper x indigenous crossbred sheep.

Materials And Methods

Location

The study was conducted at the goat farm of Sirinka Agricultural Research Center which is located 508 km away from Addis Ababa at an altitude of 1850 m.a.s.l and at 11°45' 00" N and 39°36' 36" E. The mean annual rainfall amount of the area is on average about 950 mm. The area is a moderately warm temperature zone with a mean daily temperature ranges from 13.7–26.4°C.

Flock management

Flocks were reared under semi-intensive management i.e. graze for 6:00 hrs and supplemented with 0.1 to 0.4 kg based on their age and physiology when returned from grazing. Sheep were vaccinated against Anthrax, Sheep and Goat pox, and Pestis Des Petites Ruminants diseases. They were treated regularly for internal and external parasites (Tesema et al. 2020). A natural controlled mating method was used and one ram was assigned to 20–30 ewes. The assigned rams were kept with ewes for 45 days during the daytime. During mating, herdsman were assigned to each mating group to collect the mating data and pedigree information. The pure indigenous ewes were crossed with pure Dorper rams to produce the F1 crossbreds with 50% blood level. To evaluate the performance of crossbreds with different exotic gene levels, female crossbreds with 50% blood level were crossed with pure Dorper rams to produce crossbreds with 75 % Dorper blood level.

Data collection and studied traits

Data were collected for Dorper-indigenous crossbred sheep born from 2009 to 2018. A growth trait includes birth weight (BW), weaning (3MW), six-month (6MW), nine-month (9MW), and yearling weight (12MW). Birth weight was taken within 24 hours of the birth of a lamb, and 3-, 6-, 9-, and 12-month weights were taken on exact dates. In addition, average daily gain (g/day) from birth to weaning (ADG1), from weaning to 6 months (ADG2), from 6 month to 9 months (ADG3), and from 9 months to yearling age (ADG4) were computed and considered in this study. Kleiber ratios in different growth phases (KR1, KR2, KR3, and KR4) were computed as follows: $KR1 = ADG1/3MW^{0.75}$, $KR2 = ADG2/6MW^{0.75}$, $KR3 = ADG3/9MW^{0.75}$ and $KR4 = ADG4/12MW^{0.75}$.

Data analysis

Data on growth performance and Kleiber ratio were analyzed using the general linear model procedure of SAS (2002). The model considered fixed effects of type of birth in two classes (single and twin), sex of lamb in two classes (male and female), the blood level of lambs in two classes (50% and 75%), year of lambing in ten classes (2009–2018) and season of birth in three classes (dry, short rain and main rain). Tukey-Kramer test was employed for making all possible comparisons of means.

Genetic parameters for BW, 3MW, ADG1, and KR1 were estimated by the Average Information Restricted Maximum Likelihood (AI-REML) method fitting an animal model using a WOMBAT computer program (Meyer et al. 2012). The genetic parameters for post-weaning growth traits were not estimated due to a lack of enough sample size. A detailed description of the data is presented in Table 1.

Table 1
Description of data structure for early growth traits in
Dorper x indigenous sheep

Items	Traits			
	BW	3MW	ADG1	KR1
Number of records	537	453	449	449
Number of sire	21	20	20	20
Number of dam	260	229	229	229
NPR/ sire	25.6	22.6	22.4	22.4
NPR/ dam	2.06	1.97	1.96	1.96
Mean	3.03	14.5	127.2	16.8
SD	0.68	3.87	41.2	2.30
Minimum	1.2	8.60	40.0	9.97
Maximum	5.0	27.5	260.8	23.2
C.V. %	19.3	22.9	28.1	12.2

SD, standard deviation; CV, coefficient of variation; BW, birth weight; 3MW, weaning weight; ADG1, birth to weaning average daily weight gain; KR1, birth to weaning Kleiber ratio

Four univariate animal models were used for genetic analysis as shown below:

$$y = X\beta + Z_1 a + \varepsilon \quad (1)$$

$$y = X\beta + Z_1 a + Z_2 m + \varepsilon \text{ with } \text{Cov}(a, m) = 0 \quad (2) \quad y = X\beta + Z_1 a + Z_2 c + \varepsilon \quad (3)$$

$$y = X\beta + Z_1 a + Z_2 m + Z_3 c + \varepsilon \text{ with } \text{Cov}(a, m) = 0 \quad (4)$$

Where, **y** is the vector of records; **β**, **a**, **m**, **c** and **ε** are vectors of fixed (fixed effects which had a significant effect), additive direct genetic, maternal additive genetic, permanent environmental effects of the dam and residual

effects, respectively; $\mathbf{X}$, $\mathbf{Z}_1$, $\mathbf{Z}_2$ and $\mathbf{Z}_3$ are incidence matrices that relate these effects to the records. The (co)variance structure for the model was:

$$\text{Var}(\mathbf{a}) = \mathbf{A}\sigma_a^2, \text{Var}(\mathbf{m}) = \mathbf{A}\sigma_m^2, \text{Var}(\mathbf{c}) = \mathbf{I}_D\sigma_c^2, \text{Var}(\boldsymbol{\varepsilon}) = \mathbf{I}_K\sigma_e^2 \text{ and } \text{Cov}(\mathbf{a}, \mathbf{m}) = \mathbf{A}\sigma_{am},$$

Where, $\mathbf{A}$ is the numerator relationship matrix between animals; $\mathbf{I}_D$ and $\mathbf{I}_K$ are identity matrices with orders equal to the number of dams and the number of kids, respectively.

Likelihood ratio test (LRT) was used to determine the most appropriate model for each trait. 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 (Chen et al. 2006; Wilson et al. 2010).

$$\chi^2_{1df} = 2[\text{ML}(\mathbf{x})_f - \text{ML}(\mathbf{x})_r]$$

Where; $\text{ML}(\mathbf{x})_f$ = maximum likelihood for full model, $\text{ML}(\mathbf{x})_r$ = maximum likelihood for reduced model.

Genetic and phenotypic correlations were estimated using bivariate analysis. The genetic trend was obtained by regression of the average breeding values on birth year (Tesema et al. 2020). The inbreeding coefficient for individual animals was estimated and extracted from the additive relationship matrix. The total heritability (h^2_t) was estimated according to Willham (1972).

$$h^2_t = \sigma_a^2 + 0.5 \sigma_m^2 + 1.5 \sigma_{am}$$

$$\sigma_p^2$$

Where; σ_a^2 = additive genetic variance, σ_m^2 = maternal genetic variance, σ_p^2 = phenotypic variance, σ_{am} = the covariance between additive direct and maternal genetic effects.

Results And Discussion

Live weight and the effect of non-genetic factors

The live weights at various ages of Dorper crossbred lambs are presented in Table 2. The birth weight (BW), weaning weight (3MW), six-month weight (6MW) of crossbred lambs in this study are higher than the report of Abebe et al. (2016) for Dorper-Afar (2.57 kg BW, 9.45 kg 3MW and 13.2 kg 6MW) and Dorper-Menz crossbred sheep (2.77 kg BW, 12.3 kg 3MW and 17.2 kg 6MW). Likewise, a relatively lowest yearling weight (22.5 kg) than the current result was reported for Washera x Farta sheep (Mekuriaw et al. 2013). However, the yearling weight of crossbred lambs in this study is lower than the result (31.3 kg for Dorper x Menz sheep) reported by Abebe et al. (2016). Generally, the live weight of crossbred sheep observed in the present study is superior to most of the non-improved indigenous breeds (Washera, Farta, Horo, Adilo, Menz, Wollo sheep) reported by several scholars (Tibbo 2006; Gizaw and Getachew 2009; Mekuriaw et al. 2013; Gemiyo et al. 2014). The export market needs lambs weighing 25–30 kg at yearling age. In this study, the crossbred lambs could attain the minimum requirement of the export market standard starting from 9 months of age.

Birth type exerted a significant ($P < 0.05$) influence on the weight of crossbred lambs at various ages. Single-born lambs had a higher live weight in all growth phases than twin-born lambs. This result is in agreement with several studies (Mohammadi et al. 2010; Mekuriaw et al. 2013; Lakew et al. 2014; Mandal et al. 2015). The superiority of singletons could be attributed to the pre-and post-natal availability of nutrients i.e. enough capacity of the maternal uterus space to gestate offspring and less competition for milk among the singletons than twin born. This carry-over effect is there up to yearling age (Abegaz et al. 2002) and males will be superior to female counterparts up to yearling age.

The sex of lambs is the other important source of variation and males appear to grow faster than respective female lambs. The superiority of males has been reported by several authors (Tibbo 2006; Lakew et al. 2014; Teklebrhan et al. 2014; Mandal et al. 2015). This difference could be due to more influence of sex hormones (androgen) on muscle development of males than females. However, oestrogen limits skeleton growth in females (Ghafouri-Kesbi and Gholizadeh, 2017). Besides, ewes that carry male lambs had higher cotyledon numbers and heavier placental weight than ewes that carry females (Jawasreh et al. 2009), this may be the other possible reason for the superiority of males.

The growth performance of crossbreds was not increased with exotic gene level, i.e. crossbred lambs with 50% exotic gene level and 75% exotic gene-level had similar ($P > 0.05$) live weight in all growth phases. Hence, the higher exotic inheritance must be accompanied by improved management to enable them to express their full genetic potential. Otherwise, using 50% crossbreds would be compatible with the existing management.

Table 2
Live weight of Dorper x indigenous sheep at a specific age (LSM $\pm$ SE)

Source of variation	BW		3MW		6MW		9MW		12MW	
	N	LSM $\pm$ SE	N	LSM $\pm$ SE	N	LSM $\pm$ SE	N	LSM $\pm$ SE	N	LSM $\pm$ SE
Overall	531	3.03 $\pm$ 0.02	450	14.5 $\pm$ 0.18	349	20.4 $\pm$ 0.26	284	24.8 $\pm$ 0.31	210	28.3 $\pm$ 0.40
CV		19.3		22.9		21.2		17.5		15.5
Birth type		***		***		***		**		**
Single	440	3.13 $\pm$ 0.03	377	14.9 $\pm$ 0.14	290	20.6 $\pm$ 0.28	232	25.2 $\pm$ 0.33	173	28.7 $\pm$ 0.45
Twin	91	2.55 $\pm$ 0.07	73	12.2 $\pm$ 0.43	59	19.5 $\pm$ 0.68	52	23.1 $\pm$ 0.79	37	26.3 $\pm$ 0.79
Blood level		ns		ns		ns		ns		ns
50%	450	3.03 $\pm$ 0.03	388	14.4 $\pm$ 0.18	308	20.3 $\pm$ 0.28	258	24.6 $\pm$ 0.32	196	28.1 $\pm$ 0.14
75%	81	3.00 $\pm$ 0.07	62	15.2 $\pm$ 0.59	41	21.4 $\pm$ 0.66	26	26.3 $\pm$ 1.28	14	29.6 $\pm$ 1.94
Sex		**		***		**		***		***
Female	270	2.93 $\pm$ 0.04	233	13.9 $\pm$ 0.21	186	19.6 $\pm$ 0.32	165	23.6 $\pm$ 0.34	138	27.3 $\pm$ 0.45
Male	261	3.13 $\pm$ 0.04	217	15.1 $\pm$ 0.29	163	24.1 $\pm$ 0.42	119	26.5 $\pm$ 0.53	72	30.0 $\pm$ 0.75
Season		***		ns		**		ns		ns
Dry	171	2.97 $\pm$ 0.05 ^b	151	14.9 $\pm$ 0.36	121	21.5 $\pm$ 0.53 ^a	77	25.5 $\pm$ 0.59	56	28.6 $\pm$ 0.66
Main rain	114	2.65 $\pm$ 0.05 ^c	91	13.4 $\pm$ 0.41	59	20.0 $\pm$ 0.66 ^b	51	25.4 $\pm$ 0.86	37	28.9 $\pm$ 0.95
Short rain	246	3.25 $\pm$ 0.04 ^a	208	14.7 $\pm$ 0.22	169	19.8 $\pm$ 0.31 ^b	156	24.2 $\pm$ 0.39	117	27.8 $\pm$ 0.57
Year		***		***		***		***		***
2009	72	3.10 $\pm$ 0.06 ^{abc}	68	15.3 $\pm$ 0.44 ^{bcd}	55	19.6 $\pm$ 0.62 ^{cde}	52	26.6 $\pm$ 0.66 ^{abc}	38	31.2 $\pm$ 0.77 ^{ab}
2010	66	3.39 $\pm$ 0.07 ^a	64	14.8 $\pm$ 0.31 ^{cd}	58	20.3 $\pm$ 0.42 ^{cd}	54	22.1 $\pm$ 0.45 ^{de}	42	22.3 $\pm$ 0.44 ^e

Ns, P > 0.05; ***, P < 0.001; **, P < 0.01; *, P < 0.05

Source of variation	BW		3MW		6MW		9MW		12MW	
	N	LSM $\pm$ SE	N	LSM $\pm$ SE	N	LSM $\pm$ SE	N	LSM $\pm$ SE	N	LSM $\pm$ SE
2011	59	3.26 $\pm$ 0.06 ^{ab}	57	12.8 $\pm$ 0.31 ^{ef}	45	17.8 $\pm$ 0.47 ^{de}	30	23.0 $\pm$ 0.58 ^{de}	28	28.5 $\pm$ 0.70 ^{bc}
2012	66	3.16 $\pm$ 0.07 ^{ab}	52	14.1 $\pm$ 0.50 ^{de}	29	20.2 $\pm$ 0.71 ^{cd}	25	23.5 $\pm$ 1.08 ^{cde}	15	27.4 $\pm$ 1.67 ^{cd}
2013	24	3.18 $\pm$ 0.11 ^{ab}	14	16.6 $\pm$ 0.99 ^{ab}	10	23.1 $\pm$ 1.66 ^{ab}	5	28.5 $\pm$ 2.51 ^a	-	-
2014	32	2.45 $\pm$ 0.11 ^f	24	12.2 $\pm$ 0.82 ^f	13	18.4 $\pm$ 1.21 ^{de}	11	24.6 $\pm$ 0.77 ^{bcd}	8	30.5 $\pm$ 1.12 ^{ab}
2015	55	2.62 $\pm$ 0.09 ^{ef}	44	16.0 $\pm$ 0.66 ^{abc}	37	22.8 $\pm$ 0.90 ^{ab}	36	27.9 $\pm$ 0.92 ^{ab}	31	31.9 $\pm$ 0.97 ^a
2016	67	3.01 $\pm$ 0.10 ^{bcd}	56	15.2 $\pm$ 0.57 ^{bcd}	49	21.8 $\pm$ 0.67 ^{bc}	40	26.7 $\pm$ 0.90 ^{abc}	29	30.8 $\pm$ 1.09 ^{ab}
2017	52	2.74 $\pm$ 0.08 ^{def}	44	12.4 $\pm$ 0.39 ^f	29	17.5 $\pm$ 0.88 ^e	26	20.8 $\pm$ 0.87 ^e	19	25.4 $\pm$ 0.99 ^d
2018	30	3.13 $\pm$ 0.11 ^{ab}	27	17.2 $\pm$ 0.93 ^a	24	24.8 $\pm$ 1.40 ^a	5	29.3 $\pm$ 4.01 ^a	-	-
Ns, P > 0.05; ***, P < 0.001; **, P < 0.01; *, P < 0.05										

BW, birth weight; 3MW, weaning weight; 6MW, six-month weight; 9MW, nine-month weight; 12MW, yearling weight

Lambs born during the short rainy season had higher birth weight than lambs born during the dry and main rainy seasons. However, the six-month weight of lambs born during the dry season was greater than lambs born in the other seasons. Although the influence had not a consistent trend, the year of lambing also exerted a considerable influence on the live weight of crossbred lambs. The lowest 3MW and 6MW were observed for lambs born during 2011, 2014, and 2017 compared to lambs born in the other years. Moderate level of drought in 2011 and 2014 and also high disease prevalence during 2017 were the possible reasons for the observed lowest performance of lambs. Besides, the variability of rainfall across the year may also be the other factor for observed variation as it is associated with the quality and quantity of forage.

Weight gain and the influence of environmental factors

The least-squares mean and standard errors for the weight gain of lambs at different growth phases are presented in Table 3. Generally, the growth rate showed a decreasing trend when the age of lambs increases. In

particular, higher weight gain of crossbred lambs was observed during the pre-weaning period. This result is consistent with several studies (Ghafouri-Kesbi et al. 2011; Jalil-Sarghale et al. 2014; Ghafouri-Kesbi and Gholizadeh 2017). This reduction could be explained by the reduction of maternal effect when the age of lambs is increased.

Single-born lambs had a higher pre-weaning growth rate than twin-born. This result is in line with Teklebrhan et al. (2014) and Abebe et al. (2016). However, the post-weaning growth rate of twins and singletons was found to be similar ($P > 0.05$). A similar observation has been made by several authors (Taye et al. 2009; Mohammadi et al. 2010; Mekuriaw et al. 2013; Lakew et al. 2014). The maternal-effect during the pre-weaning period is higher than the effect during the post-weaning period i.e. singletons are favored during pre-weaning periods than twin in terms of nutrients. Except for ADG2, the weight gain of male lambs was superior to female lambs. The superiority of males was noted elsewhere (Mohammadi et al. 2010; Ghafouri-Kesbi and Gholizadeh 2017). This could be ascribed to the secretion and function of hormones. According to Ghafouri-Kesbi and Gholizadeh (2017), oestrogen limits the growth of the long bones in females whereas testosterone has a positive effect on growth in males.

Lambs with a 50% exotic gene level had lower ($P < 0.05$) pre-weaning weight gain than lambs with a 75% exotic gene level. A similar observation has been made by Teklebrhan et al. (2014) for Dorper x Hararghe Highland and Doper x Black Head Ogaden lambs. Nevertheless, the weight gain of both genotypes was found to be similar during the post-weaning growth phases. Season and year of birth exerted a considerable influence on the weight gain of crossbred lambs. These results are in agreement with those reported in the literature (Mekuriaw et al. 2013; Lakew et al. 2014; Teklebrhan et al. 2014). The difference in weight gain across year and season of lambing could be attributed to the variability of feed availability, climatic condition and disease distribution.

Table 3
Weight gain of Dorper x indigenous sheep at different growth phases (LSM $\pm$ SE)

Source of variation	ADG1		ADG2		ADG3		ADG4	
	N	LSM $\pm$ SE	N	LSM $\pm$ SE	N	LSM $\pm$ SE	N	LSM $\pm$ SE
Overall	446	127.3 $\pm$ 1.95	345	64.1 $\pm$ 1.99	274	51.9 $\pm$ 2.26	208	44.4 $\pm$ 2.58
CV		28.1		54.5		60.1		64.0
Birth type		***		ns		ns		ns
Single	373	131.3 $\pm$ 2.09	286	61.7 $\pm$ 2.13	223	52.6 $\pm$ 2.53	171	43.8 $\pm$ 2.90
Twin	73	106.7 $\pm$ 4.59	59	75.9 $\pm$ 5.19	51	49.3 $\pm$ 5.00	31	47.1 $\pm$ 5.64
Blood level		***		ns		ns		ns
50%	384	125.9 $\pm$ 2.00	305	64.8 $\pm$ 2.01	248	52.1 $\pm$ 2.33	194	44.8 $\pm$ 2.64
75%	62	135.7 $\pm$ 6.40	40	58.9 $\pm$ 6.28	26	50.1 $\pm$ 8.54	14	38.5 $\pm$ 8.80
Sex		**		ns		**		*
Female	231	121.9 $\pm$ 2.23	184	62.1 $\pm$ 2.60	159	46.7 $\pm$ 2.75	137	40.9 $\pm$ 2.92
Male	215	133.0 $\pm$ 3.22	161	66.5 $\pm$ 3.08	115	59.3 $\pm$ 3.72	71	51.2 $\pm$ 4.99
Season		ns		***		***		ns
Dry	149	132.6 $\pm$ 3.91	121	75.5 $\pm$ 3.31 ^a	75	43.8 $\pm$ 3.49 ^b	56	43.9 $\pm$ 4.74
Main rain	91	119.3 $\pm$ 4.46	57	65.9 $\pm$ 5.25 ^a	51	59.2 $\pm$ 5.45 ^a	37	46.2 $\pm$ 5.72
Short rain	206	126.9 $\pm$ 2.41	167	55.3 $\pm$ 2.66 ^b	148	53.6 $\pm$ 3.26 ^{ab}	115	44.1 $\pm$ 3.65
Year		***		**		***		***
2009	68	136.2 $\pm$ 4.60 ^{bc}	55	53.0 $\pm$ 4.31 ^c	49	81.7 $\pm$ 4.55 ^a	38	59.4 $\pm$ 6.09 ^a
2010	64	127.0 $\pm$ 3.19 ^c	58	61.4 $\pm$ 3.16 ^{abc}	52	23.9 $\pm$ 1.86 ^d	40	2.88 $\pm$ 3.48 ^b

Ns, P > 0.05; ***, P < 0.001; **, P < 0.01; *, P < 0.05

ADG1, weight gain from birth to weaning; ADG2, weight gain from weaning to six-month; ADG3, six-month to nine month; ADG4, weight gain from nine-month to yearling age

Source of variation	ADG1		ADG2		ADG3		ADG4	
	N	LSM $\pm$ SE	N	LSM $\pm$ SE	N	LSM $\pm$ SE	N	LSM $\pm$ SE
2011	57	106.2 $\pm$ 3.28 ^d	45	55.9 $\pm$ 3.04 ^c	30	52.9 $\pm$ 5.17 ^{bc}	28	59.8 $\pm$ 6.02 ^a
2012	52	121.2 $\pm$ 5.48 ^{cd}	29	52.5 $\pm$ 5.76 ^{abc}	22	58.4 $\pm$ 8.25 ^{abc}	15	44.0 $\pm$ 4.99 ^a
2013	14	147.4 $\pm$ 10.9 ^{ab}	10	62.1 $\pm$ 10.6 ^{abc}	5	49.7 $\pm$ 11.1 ^{bc}	-	-
2014	24	106.9 $\pm$ 8.63 ^d	11	61.6 $\pm$ 8.98 ^{abc}	11	60.4 $\pm$ 12.3 ^{abc}	8	55.3 $\pm$ 10.7 ^a
2015	44	148.0 $\pm$ 7.24 ^{ab}	36	76.8 $\pm$ 7.29 ^{ab}	35	52.8 $\pm$ 6.23 ^{bc}	31	52.9 $\pm$ 6.08 ^a
2016	56	133.9 $\pm$ 5.96 ^{bc}	49	78.3 $\pm$ 6.06 ^{ab}	40	51.8 $\pm$ 6.92 ^{bc}	29	48.8 $\pm$ 7.30 ^a
2017	40	103.8 $\pm$ 5.49 ^d	28	60.9 $\pm$ 9.11 ^{abc}	26	37.9 $\pm$ 7.42 ^{cd}	19	54.6 $\pm$ 5.53 ^a
2018	27	156.7 $\pm$ 10.2 ^a	24	83.3 $\pm$ 10.9 ^a	4	74.4 $\pm$ 7.43 ^{ab}	-	-
Ns, P > 0.05; ***, P < 0.001; **, P < 0.01; *, P < 0.05								
ADG1, weight gain from birth to weaning; ADG2, weight gain from weaning to six-month; ADG3, six-month to nine month; ADG4, weight gain from nine-month to yearling age								

Kleiber ratio and the effect of non-genetic factors

Kleiber ratio (KR) could be used as a useful indicator of feed conversion and an important selection criterion for the efficiency of growth as suggested by different scholars (Kleiber 1947; Köster et al. 1994; Ghafouri-Kesbi et al. 2011). The least-squares means and standard errors for KR of lambs are presented in Table 4. The highest KR was observed from birth to weaning growth phase and the lowest KR was observed between nine-month and yearling age. Likewise, Ghafouri-Kesbi and Gholizadeh (2017) noted a higher growth rate and Kleiber ratio in the

pre-weaning growth phase than post-weaning. The KR1 observed in this study is comparable with the value (16.8) reported by Mandal et al. (2015), higher than the value (15.6) reported by Mohammadi et al. (2010), 15.3 reported by Abegaz et al. (2005), but lower than 18.2 reported by Ghafouri-Kesbi et al. (2011). The observed variation among breeds could be due to the variability of the genetic potential of breeds, weaning age of lambs, forage abundance, and other husbandry practices.

Single-born lambs had a higher Kleiber ratio during the pre-weaning growth phase and that superiority was not continued thereafter. However, multiple born lambs had a superior Kleiber ratio during the post-weaning age. This trend could be due to compensatory growth of lambs i.e. the period of amplified growth after a spell of limited development and growth. Animals that have a high KR are considered efficient users of feed (Ghafouri-Kesbi et al. 2011), i.e. single-born lambs were more efficient in feed utilization than twin contemporaries during

the pre-weaning period and the reverse is true during post-weaning. Season and year of lambing also exerted a significant influence on Kleiber ratios of crossbred sheep. The sizable influence of year and season on Kleiber ratios was documented elsewhere (Mohammadi et al. 2010; Mandal et al. 2015; Faid-Allah et al. 2016). The variation across year and season could be due to the variability of climatic conditions that directly or indirectly associated with feed availability, quality of forage, and disease prevalence.

Table 4
Kleiber ratio for Dorper x indigenous crossbred sheep (LSM $\pm$ SE)

Source of variation	KR1		KR2		KR3		KR4	
	N	LSM $\pm$ SE	N	LSM $\pm$ SE	N	LSM $\pm$ SE	N	LSM $\pm$ SE
Overall	446	16.8 $\pm$ 0.10	345	6.41 $\pm$ 0.17	274	4.55 $\pm$ 0.21	208	3.38 $\pm$ 0.20
CV		12.2		48.3		66.9		67.3
Birth type		***		**		ns		**
Single	373	16.9 $\pm$ 0.11	286	6.09 $\pm$ 0.18	223	4.58 $\pm$ 0.22	171	3.27 $\pm$ 0.22
Twin	73	15.9 $\pm$ 0.29	59	7.94 $\pm$ 0.48	51	4.45 $\pm$ 0.55	31	3.88 $\pm$ 0.52
Blood level		**		ns		ns		ns
50%	384	16.7 $\pm$ 0.11	305	6.49 $\pm$ 0.18	248	4.66 $\pm$ 0.22	194	3.44 $\pm$ 0.21
75%	62	17.2 $\pm$ 0.35	40	5.76 $\pm$ 0.56	26	3.54 $\pm$ 0.77	14	2.57 $\pm$ 1.00
Sex		ns		ns		ns		ns
Female	231	16.7 $\pm$ 0.13	184	6.37 $\pm$ 0.24	159	4.31 $\pm$ 0.29	137	3.24 $\pm$ 0.22
Male	215	16.9 $\pm$ 0.17	161	6.45 $\pm$ 0.26	115	4.89 $\pm$ 0.28	71	3.65 $\pm$ 0.41
Season		ns		***		***		ns
Dry	149	17.0 $\pm$ 0.21	121	7.42 $\pm$ 0.25 ^a	75	3.69 $\pm$ 0.33 ^b	56	3.24 $\pm$ 0.41
Main rain	91	16.6 $\pm$ 0.26	57	6.54 $\pm$ 0.48 ^a	51	5.20 $\pm$ 0.50 ^a	37	3.71 $\pm$ 0.45
Short rain	206	16.7 $\pm$ 0.13	167	5.63 $\pm$ 0.25 ^b	148	4.77 $\pm$ 0.30 ^a	115	3.34 $\pm$ 0.28
Year		***		ns		***		***
2009	68	17.3 $\pm$ 0.22 ^{abc}	55	5.46 $\pm$ 0.38	49	6.86 $\pm$ 0.34 ^a	38	4.38 $\pm$ 0.42 ^{ab}
2010	64	16.7 $\pm$ 0.17 ^{bcd}	58	6.33 $\pm$ 0.29	52	2.31 $\pm$ 0.19 ^c	40	0.25 $\pm$ 0.34 ^c
2011	57	15.5 $\pm$ 0.22 ^e	45	6.38 $\pm$ 0.28	30	4.99 $\pm$ 0.48	28	4.76 $\pm$ 0.55 ^{ab}
2012	52	16.4 $\pm$ 0.33 ^{cde}	29	5.29 $\pm$ 0.56	22	5.88 $\pm$ 1.13 ^{ab}	15	3.64 $\pm$ 0.37 ^{ab}
2013	14	17.7 $\pm$ 0.51 ^{ab}	10	5.74 $\pm$ 0.77	5	4.24 $\pm$ 1.10 ^{ab}	-	-

Ns, P > 0.05; ***, P < 0.001; **, P < 0.01; *, P < 0.05

Source of variation	KR1		KR2		KR3		KR4	
	N	LSM $\pm$ SE	N	LSM $\pm$ SE	N	LSM $\pm$ SE	N	LSM $\pm$ SE
2014	24	15.9 $\pm$ 0.50 ^{de}	11	6.65 $\pm$ 0.91	11	5.38 $\pm$ 1.08 ^{abc}	8	4.16 $\pm$ 0.73 ^{ab}
2015	44	18.1 $\pm$ 0.39 ^a	36	6.94 $\pm$ 0.64	35	4.25 $\pm$ 0.50 ^{abc}	31	3.89 $\pm$ 0.45 ^{ab}
2016	56	17.1 $\pm$ 0.31 ^{abc}	49	7.62 $\pm$ 0.58	40	3.84 $\pm$ 0.60 ^{bc}	29	3.20 $\pm$ 0.68 ^b
2017	40	15.7 $\pm$ 0.37 ^{de}	28	6.31 $\pm$ 0.85	26	4.00 $\pm$ 0.86 ^{bc}	19	-
2018	27	18.1 $\pm$ 0.52 ^a	24	7.12 $\pm$ 0.79	4	6.52 $\pm$ 1.18 ^{ab}	-	-
Ns, P > 0.05; ***, P < 0.001; **, P < 0.01; *, P < 0.05								

KR1, Kleiber ratio from birth to weaning; KR2, Kleiber ratio from weaning to six-month; KR3, Kleiber ratio from six to nine month; KR4, nine to yearling age

Estimation of genetic parameters for early growth traits

Variance components and heritability

Estimates of genetic parameters for birth weight (BW), weaning weight (3MW), pre-weaning weight gain (ADG1), and pre-weaning Kleiber ratio (KR1) along with their likelihood values for each analysis under the four different models are summarized in Table 5. As per the log-likelihood test, model 2, 3, 3, and 1 were the optimal models for BW, 3MW, ADG1, and KR1, respectively. Based on optimal models, the direct heritability (h^2_a) was varied from 0.003 for BW to 0.16 for ADG1. The h^2_a for ADG1 and KR1 in the present study is higher than the value (0.11 for ADG, and 0.10 for KR1) reported by Ghafouri-Kesbi et al. (2011). However, higher estimates (0.16 for BW, 0.27 for 3MW, 0.26 for ADG and 0.15 for KR) than the present results were noted by Mohammadi et al. (2010). Likewise, higher h^2_a (0.164) and lower c^2 (0.078) than the current result were reported by Khorsand et al. (2014) for Afshari sheep. The variability of estimates could be ascribed to the type of breeding program (crossbreeding or selection), selection intensity, data structure, the model used for estimation, and overall management of the flock.

The inclusion of maternal genetic effect exerted a significant influence on BW, reduces the h^2_a estimate and it explains 20% of the phenotypic variation. Likewise, higher maternal heritability (h^2_m) estimates ranging from 0.18 to 0.24 for BW were documented in several studies (Roshanfekr et al. 2011; Rashidi 2012; Shokrollahi and Zandieh 2012; Khorsand et al. 2014; Faid-Allah et al., 2016). This depicts that birth weight is strongly influenced by the maternal gene than by the lambs own gene and this suggests that maternal genetic effects need to be considered in selecting for early growth. However, 21% of the phenotypic variation in 3MW and 19% in ADG1 were explained by a maternal permanent environmental effect (c^2). The c^2 of 3WW in this study was higher than those reported for dual purpose (0.09), meat (0.19), and wool (0.10) sheep (Safari et al. 2005). This indicates

that maternal genetic effect is more important in birth weight than other traits. This result is in line with Prakash et al. (2012) who noted that the maternal genetic effects directly affect the lamb's birth weight and its effect usually diminishes slowly as the age of lamb increases. The influence of genetic and non-genetic maternal-effect on early growth traits suggests that intervention in ewes and considering in selection may have a considerable influence on the pre-weaning growth performance of lambs.

When the maternal genetic effect is considered in the model, the total heritability (h^2_{t}) estimate is ideal for the estimation of selection response. Higher total heritability estimates for BW than the current study were reported by Abegaz et al. (2005) for Horo sheep and Mandal et al. (2015) for Muzaffarnagari sheep. However, the estimates for 3MW (0.12) and ADG1 (0.13) of Horo sheep were lower than the present estimates. In general, the heritability estimates in this study was found within a lower range and this could be explained by the inconsistency of management, fodder quality, and malnourishment of flock, as these factors increase the proportion of phenotypic variance due to environmental variance (Mandal et al. 2015; Gholizadeh and Ghafouri-Kesbi 2017).

The present heritability estimates for pre-weaning growth traits and Kleiber ratio suggest slow genetic progress would be expected through selection. According to Cassel (2009) and Faid-Allah et al. (2016), when the heritability is below 0.15, the selection of animals based on own performance is less effective. Therefore, selection for both early growth traits and Kleiber ratio should be according to the breeding values estimated from multiple information sources such as progeny, pedigree, sibs, and other relative information besides to own performance record.

Table 5
Genetic parameter estimates for pre-weaning growth traits of Dorper x local sheep

Trait	M	σ^2_a	σ^2_m	σ^2_c	σ^2_e	σ^2_p	$h^2_a \pm$ SE	$h^2_m \pm$ SE	$c^2 \pm$ SE	e^2	h^2_t	Log (L)
BW	1	0.14			0.23	0.37	0.37 ± 0.12			0.63	0.38	-6.026
	2	0.001	0.07		0.28	0.35	0.003 ± 0.08	0.20 ± 0.06		0.79	0.10	-1.646
	3	0.001		0.08	0.26	0.34	0.003 ± 0.07		0.23 ± 0.06	0.77	0.00	-0.548
	4	0.001	0.02	0.06	0.27	0.35	0.003 ± 0.08	0.06 ± 0.11	0.17 ± 0.11	0.76	0.03	-0.395
3MW	1	2.51			9.28	11.8	0.21 ± 0.12			0.78	0.21	-777.41
	2	1.59	1.59		8.64	11.8	0.13 ± 0.13	0.13 ± 0.07		0.73	0.20	-775.65
	3	1.67		2.47	7.75	11.9	0.14 ± 0.13		0.21 ± 0.07	0.65	0.14	-773.37
	4	1.67	0.001	2.47	7.75	11.9	0.14 ± 0.13	0.00 ± 0.13	0.21 ± 0.13	0.65	0.14	-773.37
ADG1	1	255.7			1091	1346	0.19 ± 0.12			0.81	0.19	-1797.4
	2	200.9	172.8		987.2	1360	0.15 ± 0.13	0.13 ± 0.07		0.72	0.21	-1795.9
	3	221.7		265.7	886.3	1374	0.16 ± 0.13		0.19 ± 0.07	0.64	0.16	-1794.3
	4	221.4	0.009	265.4	886.8	1373	0.16 ± 0.14	0.00 ± 0.12	0.19 ± 0.13	0.65	0.16	-1794.3
KR1	1	0.54			3.87	4.41	0.12 ± 0.10			0.87	0.12	-562.43
	2	0.49	0.33		3.61	4.44	0.11 ± 0.13	0.07 ± 0.06		0.81	0.15	-561.85
	3	0.55		0.59	3.33	4.48	0.12 ± 0.13		0.13 ± 0.07	0.74	0.12	-561.12

Trait	M	σ^2_a	σ^2_m	σ^2_c	σ^2_e	σ^2_p	$h^2_a \pm$ SE	$h^2_m \pm$ SE	$c^2 \pm$ SE	e^2	h^2_t	Log (L)
	4	0.56	0.001	0.59	3.32	4.48	0.12 ± 0.13	0.00 ± 0.11	0.13 ± 0.12	0.74	0.13	-561.12

σ^2_a , direct genetic variance; σ^2_m , maternal genetic variance; σ^2_c , maternal permanent environmental variance; σ^2_e , residual variance; σ^2_p , phenotypic variance; h^2_a , heritability of direct genetic effects; h^2_m , heritability of maternal genetic effects; c^2 , maternal permanent environmental variance as a proportion of phenotypic variance; e^2 , residual variance as a proportion of phenotypic variance; h^2_t , total heritability

BW, birth weight; 3MW, weaning weight; ADG1, weight gain from birth to weaning and KR1, Kleiber ratio from birth to weaning age

Genetic and phenotypic correlation

The correlation estimates for considered traits are presented in Table 6. The phenotypic correlation varied from -0.11 to 0.98 whereas the direct genetic correlation ranges between -0.32 and 0.98. Higher direct genetic correlations for BW-3MW (0.72) and BW-ADG1 (0.52) than the current finding were noted by Jalil-Sarghale et al. (2014). The direct genetic correlation estimate for BW-3MW, BW-ADG1, 3MW-KR1, and 3MW-ADG1 were reported to be 0.29, 0.04, 0.74, and 0.96, respectively according to Abegaz et al. (2005) and these values were lower than the current estimates. The variation of correlation estimate among breeds or studies likely due to the variation of sample size, data structure, management, number of random and fixed factors considered.

The antagonistic phenotypic and genetic relationship was observed between BW and KR1. A lower genetic correlation among these traits was reported by Mohammadi et al. (2010), Mandal et al. (2015), and Faid-Allah et al. (2016). This suggests that these two traits cannot be improved simultaneously through selection and thus selection should focus on the trait of the highest importance. On the other hand, high and positive genetic correlations were observed among 3MW and other pre-weaning growth traits (ADG1 and KR1). These results are in line with previous studies (Prakash et al., 2012; Mandal et al., 2015) and this suggests that genes that influence these traits were in a similar direction or the presence of linkage between these genes and thus, selection could be carried out based on either one of them.

Table 6
Direct genetic (above the diagonal) and phenotypic (below the diagonal) correlation estimates

	BW	3MW	ADG1	KR1
BW		0.43 $\pm$ 0.32	0.10 $\pm$ 0.32	-0.32 $\pm$ 0.40
3MW	0.30 $\pm$ 0.05		0.98 $\pm$ 0.17	0.70 $\pm$ 0.25
ADG1	0.13 $\pm$ 0.05	0.98 $\pm$ 0.02		0.87 $\pm$ 0.11
KR1	-0.11 $\pm$ 0.05	0.89 $\pm$ 0.01	0.94 $\pm$ 0.01	

BW, birth weight; 3MW, weaning weight; ADG1, weight gain from birth to weaning and KR1, Kleiber ratio from birth to weaning age

Genetic trend for early growth traits

The genetic trend for pre-weaning growth traits of Dorper crossbred sheep are presented in Fig. 1. The coefficient for genetic trend for BWT, WWT, ADG, and KR were 0.01 kg/year, -0.105 kg/year, -1.103 g/year, and - 0.044 g/metabolic weight/year, respectively. This implies that except BWT, all investigated traits were decreased genetically by determined coefficient per year. In the contrary, a positive genetic trend (0.028 kg/year) was noted by Areb et al. (2021) for weaning weight of Bonga sheep under selection. This genetically reduction of pre-weaning growth traits could be due to the absence of selection for rams and ewes based on their estimated breeding value. Hence, the ram and ewes must be evaluated properly and selected based on their estimated breeding value to enhance the genetic progress.

Inbreeding coefficient (F)

The overall mean probability of the two alleles at a randomly chosen locus being identical by descent (inbreeding coefficient) was 0.105% with annual rate of 0.021% (Fig. 2). The average inbreeding level for inbred sheep was found to be 14.1%. A relatively higher inbreeding level than this result was reported by Patiabadi et al. (2016) for Iranian Shal sheep ($F = 6.28\%$), Tesema et al. (2020) for Boer crossbred goats ($F = 0.58\%$), and Areb et al. (2021) for Bonga sheep ($F = 0.36\%$). This could be ascribed to excessive use of very few rams and a high number of progenies per ram. According to Ryan (2018), the inbreeding coefficient of up to 6.25% is acceptable. Inbreeding depression is unlikely to occur in this study because the inbreeding level is below the threshold.

Conclusion

In conclusion, the growth performance of Dorper x indigenous sheep was higher than most of the non-improved indigenous sheep breeds/populations in Ethiopia. Birth type, sex, season, and year of lambing are the main determinants of growth traits and Kleiber ratios. Considering the maternal effect is vital for accurate genetic evaluation of early growth traits. The observed low heritability estimates for growth traits and Kleiber ratio suggests that slow genetic progress would be expected from the selection. However, the integration of selection with crossbreeding programs and improving the flock management would further enhance the genetic gain. Therefore, selection should be conducted based on breeding values estimated from multiple information sources to improve its efficiency.

Declarations

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Figures

Figure 1

Genetic trend for pre-weaning growth traits of Dorper crossbred sheep

Figure 2

Trend of average inbreeding coefficient by year of birth observed for Dorper crossbred sheep