Estimation of dominance genetic effects on pre-weaning efficiency-related traits in Baluchi sheep

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Abstract

This study was conducted to estimate the relative contribution of dominance genetic effects to efficiency-related traits including Kleiber ratio (KR), efficiency of growth (EF) and relative growth rate (RGR) in Baluchi sheep. To this end, each trait was analysed with a series of 12 animal models which were identical for fixed and additive genetic effects but differed for combinations of dominance genetic and maternal effects. The Akaike's information criterion (AIC) was used to rank models. (Co)variances between traits were estimated using bivariate analyses. For all traits studied, according to AIC values, models containing the dominance genetic effects provided a better data fit than otherwise identical models. By including dominance genetic effects in the model, additive genetic variance did not change, but a significant decrease was observed in the residual variance (24, 19 and 25% for KR, EF and RGR, respectively). Estimates of dominance heritability (h_d^2) were 0.20 ± 0.05, 0.17 ± 0.05 and 0.19 ± 0.07 for KR, EF and RGR, respectively, more than corresponding estimates of additive heritability (h_a^2) as 0.14 ± 0.02, 0.09 ± 0.03 and 0.13 ± 0.02, respectively. Dominance genetic correlations between traits were 0.89 ± 0.17 (KR-EF), 0.86 ± 0.20 (KR-RGR) and 0.93 ± 0.21 (EF-RGR). Additive genetic correlations between traits were 0.84 ± 0.05 (KR-EF), 0.78 ± 0.04 (KR-RGR) and 0.83 ± 0.04 (EF-RGR). The Spearman correlation between additive breeding values including and excluding dominance genetic effects were close to unity either for all animals or top ranked animals. Since presence of dominance genetic effects increased the model power to fit the data, inclusion of these effects in the genetic evaluation models for Baluchi sheep was recommended.

Introduction

Sheep were the first farm animals domesticated by humans about 8–10 thousand years ago. The small size, the ability to be domesticated and the high performance for meat, milk and wool production were the reasons to domesticate sheep. Aryans were the first people which domesticate sheep. Studies show that sheep were domesticated in the land that is now called Kurdistan, and most of the domestic sheep in the world originated from wild flocks of sheep scattered in this area. Therefore, Iran can be considered as the primary land of sheep breeding (Deng *et al.*, 2020). Baluchi is a domesticated breed of sheep originating from southwest Pakistan, eastern Iran and southern Afghanistan. This breed comprises 12% of the total sheep population in Iran and because of its large population, has a significant contribution to the total meat and mutton production. The animals of this breed are known with small size, fat tail, carpet wool and white colour. They are good foragers and adapted to a wide range of harsh environmental conditions in the north-eastern parts of Iran which known as North-, South- and Razavi-Khorasan provinces (Bahreini-Behzadi *et al.*, 2014).

In Iran, during recent decades, we have witnessed an increasing demand for lamb and mutton mainly because of population growth. Due to the fact that the supply of meat from sheep does not cover the demand, breeding schemes have been conducted to increase sheep production. Since there are limitations on increasing sheep population, efforts have been focused on increasing performance per head. However, most selection programmes have focused on growth and reproductive traits, ignoring traits related to efficiency of feed utilization. In the intensive systems that are expanding in Iran, in addition to growth and reproduction traits, traits related to feed efficiency are of great importance, because in these systems, the cost of feed is a significant part of the production system, up to 60%. Therefore, any improvement in efficiency of feed utilization will lead to higher profitability of the production system (Ghafouri-Kesbi and Gholizadeh, 2017). To improve feed efficiency, selection based on traits such as Kleiber ratio (KR) (Kleiber, 1947), efficiency of growth (EF) (Dass *et al.*, 2004) and relative growth rate (RGR) (Fitzhugh and Taylor, 1971), as indirect indicators of efficiency

of feed utilization, have been suggested. KR, EF and RGR are useful measurements to identify animals which have lower maintenance requirements.

The narrow-sense heritability of a trait (h^2), defined as the proportion of the phenotypic variance accounted for by the additive genetic effects, is an important indicator of the extent to which a trait can be improved by selection. Information on heritability is crucial in the formulation of optimum breeding objectives and an effective genetic improvement programme. So far, for estimating heritability of economic traits in sheep efforts have mainly focused on estimating direct and maternal additive genetic variance, ignoring additional components such as dominance effects (Sing et al., 2016; Ghafouri-Kesbi and Gholizadeh, 2017; Javanrouh et al., 2021). The results of recently published articles show that the dominance genetic effects significantly contribute to the phenotypic variation of production and reproduction traits of domestic animals in a range between 1 and 25% (Jasouri et al., 2017; Ebrahimi et al., 2019; Sadeghi et al., 2020, 2021). Including the dominance genetic effects in the genetic evaluation model can (1) lead to a better understanding of the genetic architecture of traits, (2) increase the accuracy of genetic evaluation, and (3) improve the efficiency of breeding programmes via determining the relative importance of dominance genetic effects (Varona et al., 2018). Therefore, it would be reasonable to include dominance genetic effect in models for genetic evaluation of economic traits in sheep. Although genetic parameters for growth- and efficiency-related traits of Baluchi sheep have been estimated by Ghafouri-Kesbi and Gholizadeh (2017), no attempt has been made to quantify relative contribution of dominance genetic effects to phenotypic variation of efficiency-related traits in this breed. Therefore, this study was conducted to estimate dominance genetic effects on Kleiber ratio, efficiency of growth and relative growth rate in Baluchi sheep.

Material and methods

Data

The data used in the present study were retained from Abbasabad Baluchi Sheep breeding station (flock 1), Mashhad, Khorasan Razavi, Iran. This experimental population of Baluchi sheep was founded in early 1960s. In general, the flock is reared by following conventional industrial procedures. The mating period commenced in August and September and lasted for 51 days. Lambing took place from beginning of February to the end of March. At birth, the relevant information about newborn such as sex, birth type, birth date, birth weight, sir ID and dam ID were recorded. In addition, body weights were recorded at monthly intervals starting from birth until 4 months of age. Body weights for 6, 9 and 12 months of age were also recorded. Lambs were weaned on average age of 90 days. They were raised separately from older animals until one year of age. During this period, they were not subjected to any form of culling unless they were physically unsound. Animals are kept indoors during winter and received a ration consisted of wheat and barley straw, alfalfa hay, sugar beet pulp and concentrate. According to the requirement, the food of the ewes was supplemented with concentrates during pregnancy and the nursing period. To protect animals from various diseases, vaccinations were performed twice a year. The sheep were dewormed with drugs and dipped in anti-parasite bath twice a year.

Traits

Raw data included birth weight (BW) and weaning weight (WW). Weaning weights were adjusted for 90 days of age. Pre-weaning average daily gain (ADG) was calculated as total gain divided by the number of days in the period. The estimates of ADG was then used to calculate corresponding Kleiber ratios as KR = ADG/WW$^{0.75}$. Body weights were used to calculate efficiency of growth as EF = [(WW–BW)/BW] × 100. Relative growth rate from birth to weaning (RGR) was calculated as: RGR = [Log$_e$(WW)–Log$_e$(BW)]/90.

Statistical analysis

To identify fixed effects for each trait, GLM procedure of SAS (2004) was fitted to the data. Fixed effects included birth year, lambing age of dam, lamb sex and birth type. These fixed effects were significant ($P < 0.05$) for all traits and were subsequently included in the linear mixed models. To estimate (co)variance components and genetic parameters, the WOMBAT programme (Meyer, 2020) was used. Each trait was analysed with 12 univariate animal models, including various combinations of additive genetic, dominance genetic, maternal additive genetic and maternal permanent environmental effects (Table 1). As the simplest model, model 1 included only random animal effects, and model 12 which was the most complete animal model, included additive genetic, dominance genetic, maternal additive genetic, maternal permanent environmental and covariance between direct and maternal additive genetic effects. The general representation of the model 12 was as follows:

$$y = X\beta + Z_1a + Z_2d + Z_3c + Z_4m + e, \ cov(a, m) \neq 0$$

where **y** is the vector of observations. β is the vector of fixed effects fitted with design matrix **X**. Z_1, Z_2, Z_3, and Z_4 are incidence

Table 1. The random (co)variance components fitted in the 12 models to efficiency-related traits in Baluchi sheep

Model number	σ_a^2	σ_d^2	σ_m^2	σ_c^2	$\sigma_{a,m}$	σ_e^2
1	✓					✓
2	✓	✓				✓
3	✓			✓		✓
4	✓	✓		✓		✓
5	✓		✓			✓
6	✓	✓	✓			✓
7	✓		✓		✓	✓
8	✓	✓	✓		✓	✓
9	✓		✓	✓		✓
10	✓	✓	✓	✓		✓
11	✓		✓	✓	✓	✓
12	✓	✓	✓	✓	✓	✓

σ_a^2, additive genetic variance; σ_d^2, dominance genetic variance; σ_c^2, maternal permanent environmental variance; σ_m^2, maternal additive genetic variance; $\sigma_{a,m}$, direct-maternal additive genetic co-variance; σ_e^2, residual variance.

matrices relating observations to additive genetic, dominance genetic, maternal permanent environmental and maternal additive genetic, respectively. The (co)variance matrix for the random effects was as follows:

$$Var\begin{bmatrix} a \\ d \\ c \\ m \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & 0 & 0 & \mathbf{A}\sigma_{am} & 0 \\ 0 & \mathbf{D}\sigma_d^2 & 0 & 0 & 0 \\ 0 & 0 & \mathbf{I}_c\sigma_c^2 & 0 & 0 \\ \mathbf{A}\sigma_{am} & 0 & 0 & \mathbf{A}\sigma_m^2 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{I}_e\sigma_e^2 \end{bmatrix}$$

where a, d, c, m and e are vectors for additive genetic, dominance genetic, maternal permanent environmental, maternal additive genetic and residual effects, respectively. σ_a^2, σ_d^2, σ_c^2, σ_m^2 and σ_e^2 are additive genetic variance, dominance genetic variance, maternal permanent environmental variance, maternal additive genetic variance and residual variance, respectively. $\mathbf{A}$ and $\mathbf{D}$ are the additive and dominance numerator relationship matrix, respectively. $\mathbf{I}_c$ and $\mathbf{I}_e$ are identity matrices of appropriate dimensions. The matrix $\mathbf{D}$ and its inverse were constructed using *nadive* package (Wolak, 2022) in R (R Development Core, 2023) and then fitted by GIN option in WOMBAT (Meyer, 2020). The information criterion of Akaike (AIC) (1974) was computed to rank the models according to their power to fit the data. Let p denotes the number of random (co)variance parameters to be estimated, and *Log L* is the maximum likelihood, then the information criterion is defined as AIC $= -2$ *Log L* $+ 2p$. The model yielding the smallest AIC fits the data best.

Correlations between traits were estimated by bivariate analyses. The models applied in the bivariate analyses were those selected as best for underlying traits in the univariate analyses (model 4). The matrix notation for the bivariate model was as follows:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 \\ 0 & \mathbf{X}_2 \end{bmatrix}\begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{a1} & 0 \\ 0 & \mathbf{Z}_{a2} \end{bmatrix}\begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{d1} & 0 \\ 0 & \mathbf{Z}_{d2} \end{bmatrix}$$
$$\times \begin{bmatrix} \mathbf{d}_1 \\ \mathbf{d}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{c1} & 0 \\ 0 & \mathbf{Z}_{c2} \end{bmatrix}\begin{bmatrix} \mathbf{c}_1 \\ \mathbf{c}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix},$$

where $\mathbf{y}_1$ and $\mathbf{y}_2$ denote traits 1 and 2, respectively.

Estimates of additive breeding values (EBVs) were derived using the best linear unbiased prediction procedure (BLUP) in WOMBAT (Meyer, 2020). The effect of inclusion of dominance genetic effects in the model on additive breeding values was tested by estimating Spearman correlation coefficients between EBVs obtained with the best model and the best model without dominance genetic effects. It was done for all animals and 10 and 50% of top animals.

Results

Table 2 shows the pedigree structure of the studied population of the Baluchi sheep. The pedigree included 11 658 animals which were progenies of 258 sires and 3137 dams and distributed over 17 generations. Characteristics of the data structure are shown in Table 3. The mean of KR, EF and RGR were 19.81, 456.87% and 1.88, respectively. According to phenotypic coefficient of variation (CV), with 24.16 and 9.77%, EF and KR were, respectively, the most and least variable traits.

Estimates of variance components and genetic parameters for KR, EF and RGR are listed in Tables 4–6, respectively. For all

Table 2. Pedigree structure of the Baluchi sheep

No. of generations (including base generation)	17
No. of animals in the pedigree file	11 658
No. of animals with progeny	3395
No. of animals without progeny	8263
No. of non-base animals	10 827
No. of non-base animals with known sire and dam	10 494
No. of non-base animals only with known sire	13
No. of non-base animals only with known dam	320
No. of sire	258
No. of dam	3137
No. of grand sire	210
No. of grand dam	588
No. of great grand sire	181
No. of great grand dam	980

traits studied, model 1 which included only additive genetic effects had least power to fit the data as evidenced by higher AIC values. Model 3 which contained the maternal permanent environmental effects fitted the data substantially better than model 1, proved by the significant decrease in the AIC. Also it resulted in decrease in additive genetic variance by 7.2, 21.4 and 11.5% for KR, EF and RGR, respectively. Amending models already containing the additive and maternal permanent environmental effects with the dominance genetic effects led to a clearly better fit of data according to the AIC values (model 4). The dominance genetic effects contributed 59, 65 and 59% to the total genetic variance of KR, EF and RGR, respectively. By including dominance genetic effects in the model, additive genetic variance did not change, but residual variance decreased significantly by 24, 19 and 25% for KR, EF and RGR, respectively. In other

Table 3. Summary statistics for efficiency-related traits in Baluchi sheep

Item	KR	EF (%)	RGR
No. of records	6451	6451	6451
No. of animals	7210	7210	7210
No. of sires with progeny	176	176	176
No. of sires with progeny and record	89	89	89
Average number of progeny per sire	36.65	36.65	36.65
No. of dams with progeny	2047	2047	2047
No. of dams with progeny and record	1452	1452	1452
Average number of progeny per dam	3.15	3.15	3.15
Mean	19.81	456.87	1.88
Min	9.21	89	0.70
Max	24.57	750	2.766
S.D.	1.94	110.39	0.23
CV (%)	9.77	24.16	12.23

KR, Kleiber ratio; EF, efficiency of growth; RGR, relative growth rate; S.D, standard deviation; CV, phenotypic coefficient of variation.

Table 4. Estimates of variance components and genetic parameters for Kleiber ratio (best model shown in bold)

Model	σ_a^2	σ_d^2	σ_c^2	σ_m^2	$\sigma_{a,m}$	σ_e^2	σ_p^2	σ_a^2	h_d^2	h_m^2	h_c^2	e^2	$r_{a,m}$	AIC
1	0.403					2.185	2.588	0.15 ± 0.032				0.85 ± 0.031		6924.18
2	0.402	0.511				1.670	2.582	0.15 ± 0.031	0.20 ± 0.051			0.67 ± 0.052		6922.24
3	0.373		0.046			2.163	2.585	0.14 ± 0.025			0.02 ± 0.014	0.84 ± 0.033		6901.55
4	**0.365**	**0.521**	**0.048**			**1.666**	**2.600**	**0.14 ± 0.023**	**0.20 ± 0.054**		**0.02 ± 0.013**	**0.64 ± 0.046**		**6899.13**
5	0.375			0.030		2.182	2.586	0.15 ± 0.011		0.01 ± 0.022		0.84 ± 0.031		6916.59
6	0.370	0.528		0.029		1.672	2.599	0.14 ± 0.025	0.20 ± 0.063	0.01 ± 0.024		0.64 ± 0.052		6914.45
7	0.368			0.023	0.024	2.181	2.595	0.14 ± 0.026			0.01 ± 0.025	0.87 ± 0.024	0.22 ± 0.282	6917.54
8	0.365	0.519		0.025	0.021	1.661	2.591	0.14 ± 0.020	0.19 ± 0.061		0.01 ± 0.027	0.69 ± 0.063	0.26 ± 0.292	6915.38
9	0.370		0.041	0.006		2.165	2.583	0.14 ± 0.032		≈0.00	0.02 ± 0.013	0.84 ± 0.02		6902.55
10	0.374	0.503	0.043	0.005		1.668	2.603	0.14 ± 0.035	0.19 ± 0.070	≈0.00	0.02 ± 0.012	0.65 ± 0.052		6900.13
11	0.365		0.040	0.005	0.039	2.151	2.594	0.15 ± 0.033		≈0.00	0.02 ± 0.014	0.84 ± 0.043	0.47 ± 0.275	6903.48
12	0.366	0.501	0.042	0.004	0.036	2.190	2.598	0.14 ± 0.028	0.20 ± 0.073	≈0.00	0.02 ± 0.012	0.66 ± 0.068	0.49 ± 0.314	6901.09

σ_a^2, additive genetic variance; σ_d^2, dominance genetic variance; σ_c^2, maternal permanent environmental variance; σ_m^2, maternal genetic variance; $\sigma_{a,m}$, direct-maternal additive genetic covariance; σ_e^2, residual variance; σ_p^2, phenotypic variance; h_a^2, additive heritability; h_d^2, dominance heritability; h_c^2, maternal permanent environmental effect; h_m^2, maternal heritability; $r_{a,m}$, direct-maternal additive genetic correlation; **AIC**, Akaike's information criterion.

Table 5. Estimates of variance components and genetic parameters for efficiency of growth (best model shown in bold)

Model	σ_a^2	σ_d^2	σ_c^2	σ_m^2	$\sigma_{a,m}$	σ_e^2	σ_p^2	h_a^2	h_d^2	h_m^2	h_c^2	e^2	$r_{a,m}$	AIC
1	820.87					6228.76	7048.88	0.12 ± 0.032				0.88 ± 0.032		32 981.27
2	821.04	1187.16				5048.13	7056.54	0.12 ± 0.024	0.17 ± 0.053			0.66 ± 0.072		32 978.72
3	645.26		260.13			6220.52	7025.97	0.09 ± 0.035			0.04 ± 0.021	0.87 ± 0.024		32 962.01
4	**643.08**	**1186.33**	**257.44**			**4961.40**	**7045.92**	**0.09 ± 0.032**	**0.17 ± 0.052**		**0.04 ± 0.023**	**0.70 ± 0.063**		**32 959.46**
5	613.26			228.99		6199.85	7040.14	0.09 ± 0.028		0.03 ± 0.023		0.88 ± 0.036		32 969.99
6	613.57	1180.81		227.87		5028.91	7051.24	0.90 ± 0.029	0.17 ± 0.054	0.03 ± 0.022		0.71 ± 0.065		32 967.28
7	540.66			175.78	131.71	6205.36	7053.45	0.07 ± 0.023			0.02 ± 0.024	0.87 ± 0.036	0.4 ± 0.17	32 970.39
8	542.15	1180.47		175.54	132.52	5021.87	7049.34	0.07 ± 0.024	0.17 ± 0.056		0.02 ± 0.025	0.69 ± 0.064	0.4 ± 0.19	32 967.32
9	603.21		144.37	135.12		6147.47	7030.18	0.09 ± 0.027		0.02 ± 0.019	0.02 ± 0.011	0.87 ± 0.034		32 961.78
10	583.39	1176.55	141.52	134.37		5018.83	7053.32	0.08 ± 0.024	0.17 ± 0.057	0.02 ± 0.016	0.02 ± 0.014	0.70 ± 0.062		32 963.21
11	582.77		132.67	135.23	91.98	6199.52	7042.78	0.08 ± 0.026		0.02 ± 0.015	0.02 ± 0.010	0.88 ± 0.020	0.2 ± 0.17	32 962.55
12	511.53	1183.30	133.77	100.55	92.02	5026.63	7046.24	0.07 ± 0.025	0.19 ± 0.049	0.01 ± 0.013	0.02 ± 0.015	0.71 ± 0.061	0.2 ± 0.17	32 959.93

σ_a^2, additive genetic variance; σ_d^2, dominance genetic variance; σ_c^2, maternal permanent environmental variance; σ_m^2, maternal genetic variance; $\sigma_{a,m}$, direct-maternal additive genetic covariance; σ_e^2, residual variance; σ_p^2, phenotypic variance; h_a^2, additive heritability; h_d^2, dominance heritability; h_c^2, maternal permanent environmental effect; h_m^2, maternal heritability; $r_{a,m}$, direct-maternal additive genetic correlation; **AIC**, Akaike's information criterion.

Table 6. Estimates of variance components and genetic parameters for relative growth rate (best model shown in bold)

Model	σ^2_a	σ^2_d	σ^2_c	σ^2_m	$\sigma_{a,m}$	σ^2_e	σ^2_p	h^2_a	h^2_d	h^2_m	h^2_c	e^2	$r_{a,m}$	AIC
1	0.0061					0.0347	0.0408	0.15 ± 0.033				0.85 ± 0.023		−6680.28
2	0.0062	0.0083				0.0261	0.0406	0.15 ± 0.034	0.20 ± 0.072			0.64 ± 0.054		−6684.02
3	0.0054		0.0010			0.0344	0.0409	0.13 ± 0.023			0.02 ± 0.014	0.84 ± 0.037		−6695.19
4	**0.0055**	**0.0079**	**0.0011**			**0.0263**	**0.0408**	**0.13 ± 0.025**	**0.19 ± 0.073**		**0.02 ± 0.012**	**0.64 ± 0.073**		**−6698.85**
5	0.0054			0.0010		0.0346	0.0410	0.13 ± 0.019		0.02 ± 0.015		0.84 ± 0.016		−6678.91
6	0.0053	0.0081		0.0011		0.0265	0.0410	0.13 ± 0.026	0.19 ± 0.074	0.02 ± 0.016		0.64 ± 0.064		−6691.65
7	0.0054			0.0008	0.0005	0.0345	0.0411	0.12 ± 0.027		0.01 ± 0.021		0.84 ± 0.037	0.3 ± 0.14	−6688.32
8	0.0054	0.0080		0.0008	0.0005	0.0262	0.0408	0.13 ± 0.028	0.20 ± 0.071	0.01 ± 0.018		0.64 ± 0.075	0.4 ± 0.16	−6692.12
9	0.0054		0.0010	0.0007		0.0348	0.0415	0.13 ± 0.024		0.01 ± 0.016	0.02 ± 0.013	0.82 ± 0.023		−6695.84
10	0.0050	0.0078	0.0010	0.0007		0.0269	0.0417	0.12 ± 0.026	0.19 ± 0.074	0.01 ± 0.015	0.02 ± 0.014	0.64 ± 0.071		−6697.87
11	0.0051	0.0083	0.0011	0.0005	0.0003	0.0260	0.0413	0.13 ± 0.024	0.20 ± 0.076	0.01 ± 0.014	0.02 ± 0.011	0.84 ± 0.030	0.2 ± 0.10	−6695.82
12	0.0056	0.0080	0.0012	0.0004	0.0003	0.0265	0.0410	0.07 ± 0.025	0.20 ± 0.076	0.01 ± 0.011	0.06 ± 0.011	0.66 ± 0.073	0.1 ± 0.14	−6698.76

σ^2_a, additive genetic variance; σ^2_d, dominance genetic variance; σ^2_c, maternal permanent environmental variance; σ^2_m, maternal genetic variance; $\sigma_{a,m}$, direct-maternal additive genetic covariance; σ^2_e, residual variance; σ^2_p, phenotypic variance; h^2_a, additive heritability; h^2_d, dominance heritability; h^2_c, maternal permanent environmental effect; h^2_m, maternal heritability; $r_{a,m}$, direct-maternal additive genetic correlation; **AIC**, Akaike's information criterion.

word, dominance genetic effects distangelled from residual variance. For all traits studied, according to AIC values, model 4 which included additive genetic, dominance genetic and maternal permanent environmental effects described the data best and was selected as the best model.

Estimates of additive heritability (h^2_a), extracted from the best models, were 0.14 ± 0.02, 0.09 ± 0.03 and 0.13 ± 0.02 for KR, EF and RGR, respectively. Dominance heritability (h^2_d) was 0.20 ± 0.05, 0.17 ± 0.05 and 0.19 ± 0.07 for KR, EF and RGR, respectively. Maternal permanent environmental effect (h^2_c) was 0.02 ± 0.01, 0.04 ± 0.02 and 0.02 ± 0.01 for KR, EF and RGR, respectively.

Correlation between breeding values obtained from the best model (model 4) and the best model without dominance genetic effects (model 3) for all animals, top 50% ranked animals and top 10% ranked animals were large and positive for all traits studied (Table 7), indicating no changes in the EBVs after inclusion of dominance genetic effects in the model. On average, 9.3 animals out of the top 10 animals and 96.3 animals out of the top 100 animals remained in their groups (top 10 and top 100 animals) after including dominance genetic effects in the model (Table 8).

Correlations between traits are listed in Table 9. Additive genetic correlation (r_a), dominance genetic correlation (r_d), maternal permanent environmental correlation (r_c) and phenotypic correlation (r_p) were all large and positive, ranged from 0.74 ± 0.01 to 0.93 ± 0.21.

Discussion

In regions where the quantity and quality of available natural feeds are limited, efficiency of feed utilization should be considered in selection programmes. As shown in Table 2, there is variation between animals regarding efficiency of feed utilization. Animals with higher KR, EF and RGR have lower maintenance requirement, i.e. they spend most of the consumed feed on meat production. Since part of this phenotypic variation among animals regarding efficiency-related traits has genetic background, these traits can be improved genetically via selection programmes.

Our findings showed significant contribution of dominance genetic effects to phenotypic variation of efficiency-related traits of Baluchi sheep, more than additive genetic variance. Non-additive genetic effects are usually ignored in animal breeding programmes due to data structure (e.g. incomplete pedigree), computational limitations and over-parameterization of the models (Sadeghi et al., 2021). It is the first paper on the importance of dominance genetic effects on efficiency-related traits in sheep. Improvement in general properties of the animal model by including dominance genetic effects has been shown by Jasouri et al. (2017) in chicken and Sadeghi et al. (2020) and Sadeghi et al. (2021) in goat. Using genomic data, Karimi et al. (2023) reported the importance of including dominance genetic effects in genomic selection models. They reported that ignoring

Table 7. Correlations between breeding values predicted by models 3 and 4

Parameters	KR	EF	RGR
All animals	0.999	1.00	0.999
Top 50% ranked	0.999	0.999	0.998
Top 10% ranked	0.993	0.995	0.999

KR, Kleiber ratio; EF, efficiency of growth; RGR, relative growth rate.

Table 8. The number of animals that remained in their groups (top 10 and top 100 animals) after including the dominance genetic effects in the model

Trait	Top 10	Top 100
KR	10	96
EF	9	95
RGR	9	98
Overall mean	9.3	96.3

KR, Kleiber ratio; EF, efficiency of growth; RGR, relative growth rate.

dominance genetic effects resulted in inaccurate, biased and dispersed estimates of genomic breeding values.

Previous reports show that including other constituents of genetic variance such as maternal genetic effects (Singh *et al.*, 2016), X chromosome linked genetic effects (Mohammadi and Latifi, 2020; Noorian *et al.*, 2020) and imprinting effects (Amiri Roudbar *et al.*, 2018) in animal model caused a decline in the additive genetic variance and heritability estimates. But our results showed a different behaviour for dominance genetic variance as it distangelled from the residual variance and did not affect the additive genetic variance. Heidaritabar *et al.* (2016) reported that dominance and epistasis effects were important for egg production traits in layers and when these effects were ignored from the genomic evaluation models, they were accumulated in residual variance. In Adani goat, Sadeghi *et al.* (2020) studied the effect of dominance genetic effects on body weight traits and reported that by including dominance genetic effects, residual variance decreased in a range between 28.2% (weaning weight) and 59.2% (birth weight). Also, Sadeghi *et al.* (2021) reported decrease in residual variance between 20.6% (average daily gain from 6 to 9 months of age) and 50.21% (average daily gain from weaning to 3 months of age) in Adani goat. These results confirm our findings. Decrease in residual variance is an indicator of improvement in general properties of the model. By decrease in residual variance, the σ_a^2/σ_e^2 ratio increased. Whenever this ratio is low, phenotypic response to selection would be slower because environmental variation could offset phenotypic response to selection even when there is high additive variation in the trait of interest (Ghafouri-Kesbi and Notter, 2016).

There is no previous report on dominance heritability for efficiency-related traits in sheep which makes comparison difficult. In other livestock, however, dominance heritability has been estimated for economic traits. For example, Heidaritabar *et al.* (2016) in brown layers estimated h_d^2 for egg production, average egg weight, albumin height, egg colour, yolk weight and age at sexual maturity as 0.14, 0.22, 0.22, 0.20, 0.13 and 0.13, respectively. Jasouri *et al.* (2017) investigated the contribution of dominance genetic effects to phenotypic variation of body weight

traits and egg production traits of Iranian native fowl and reported h_d^2 for body weight at birth, 8 and 12 weeks of age as 0.06, 0.08 and 0.01, respectively. In addition, for the age at sexual maturity, average egg weight and number of eggs, h_d^2 was 0.06, 0.06 and 0.08, respectively. In Adani goats, Sadeghi *et al.* (2020) estimated h_d^2 for body weight at birth, weaning, 6, 9 and 12 months of age as 0.15, 0.17, 0.11, 0.19 and 0.25, respectively. For these traits, the additive heritability (h_a^2) was in the range between 0.17 (weaning weight) and 0.38 (birth weight). Sadeghi *et al.* (2021) estimated h_d^2 for pre- and post-weaning average daily gain of Adani goat as 0.15 and 0.11, respectively. Current results and other reports show that part of phenotypic variation in economic traits of livestock has dominance genetic background which is comparable with additive genetic effects. However, our results contradicted other reports showing smaller dominance heritability compared with additive heritability for growth-related traits in goat (Sadeghi *et al.*, 2020; Sadeghi *et al.*, 2021) and growth and egg production traits in chicken (Heidaritabar *et al.*, 2016; Jasouri *et al.*, 2017). One of Fisher's hypotheses associated with his theory of dominance (Fisher, 1958) predicted that traits closely associated with fitness should have a significant dominance variance component, both due to the erosion of the additive component of variance and the evolution of directional dominance. Efficiency-related traits may have been correlated with fitness in the ancestral populations from which the contemporary Baluchi sheep has been drawn.

Spearman correlation between the additive breeding values from models with and without the dominance genetic effects was high and close to unity, which implied that the additive estimated breeding values between models are coherent. A correlation lower than 1.00 means that ranking of animals may change across models. Toro and Varona (2010) stated that considering the effects of non-additive genetic effects in genomic evaluation models reduces error and increases the accuracy of estimated breeding values which reflected in greater expected response to selection. Sadeghi *et al.* (2020) and Sadeghi *et al.* (2021) reported increase in accuracy of additive breeding values after including dominance effect in the model for genetic evaluation of Adani goat for body weight and average daily gain. Of course, they did not study the change in ranking of animals across models with and without dominance effect. As a result, inclusion of dominance effect did not change ranking of top animals but has the potential to increase the accuracy of additive breeding values which is relevant to maximize genetic progress (Legarra and Reverter, 2018). Therefore, it seems reasonable to recommend inclusion of dominance genetic effects in the model for genetic evaluation of Baluchi lambs for efficiency-related traits.

Genetic correlation is the correlation of phenotypic effects by genetic variants across the genome on two phenotypes. It quantifies the overall genetic similarity and provides insights into the polygenic genetic architecture of complex traits (Zhang *et al.*,

Table 9. Correlations between studied traits

Trait 1	Trait 2	r_a	r_d	r_c	r_p
KR	EF	0.84 ± 0.053	0.89 ± 0.173	0.75 ± 0.043	0.80 ± 0.013
	RGR	0.78 ± 0.042	0.86 ± 0.198	0.79 ± 0.047	0.74 ± 0.014
EF	RGR	0.83 ± 0.045	0.93 ± 0.211	0.85 ± 0.054	0.91 ± 0.016

r_a, additive genetic correlation; r_d, dominance genetic correlation; r_c, maternal permanent environmental correlation; r_p, phenotypic correlation; KR, Kleiber ratio; EF, efficiency of growth; RGR, relative growth rate.

2021). A positive genetic correlation between efficiency-related traits allows improving all traits simultaneously and that one of them is enough to be in the multi-trait selection programmes. In agreement with our findings, in Baluchi sheep, Ghafouri-Kesbi and Gholizadeh (2017) estimated additive genetic correlation between pre-weaning KR and pre-weaning EF and RGR as 0.89 and 0.65, respectively. Dominance genetic correlations between studied traits were positive and high. Lack of previous reports on dominance genetic correlations between economic traits in livestock makes comparison difficult. Considering KR and EF, positive additive genetic correlation means that the value of KR in parents is correlated to the value of EF in offspring. Regarding dominance genetic correlation, the value of KR in the parent does not correlate to the EF value in offspring. While the additive genetic correlation would accelerate the response (if both traits were under the same direction of selection), the dominance correlation is not heritable, so it does not contribute to the response to selection (and hence doesn't accelerate the response).

In conclusion, all efficiency-related traits were affected by dominance genetic effects, with contributions more than additive genetic and maternal effects. Models with dominance genetic effects fitted the data substantially better than otherwise identical models. Accounting for the dominance genetic effects in the model led to significant decrease in residual variance which was an indicator of improvement in general properties of the model. Dominance correlations between traits were positively high. Correlation between breeding values estimated by models with and without dominance effects were close to unity, indicating a little chance for re-ranking of top animals after inclusion of dominance genetic effect in the model. However, since inclusion of dominance genetic effect in the model resulted in better data fit, improvement in general properties of the model and increase in the accuracy of breeding values, inclusion of these effects in the genetic evaluation models in sheep would be useful.

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