Original study

Model comparisons and genetic parameter estimates of growth and the Kleiber ratio in Shal sheep

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Abstract

Genetic and phenotypic parameters for lamb growth traits were estimated for the Shal sheep used as animal model. Data on lamb growth performance were extracted from available performance records at the Shal sheep Station in Qazvin, Iran. Studied traits were the body weight of lambs at birth, at three months of age as weaning weight, the six months weight, nine months weight, yearling weight, average daily gain from birth to weaning and Kleiber ratio from birth to weaning. Significant random effects for each trait were determined by fitting additive direct genetic effects, additive maternal effects, the covariance between additive direct and additive maternal effects, maternal permanent environmental and maternal temporary environmental (common litter) effects of twelve animal models. Univariate analyses were carried out under the most appropriate model, determined by the Akaike information criterion test. Direct heritability estimates for birth weight, weaning weight, average daily gain, Kleiber ratio, six months weight, nine months weight and yearling weight were 0.13, 0.19, 0.18, 0.05, 0.16, 0.18 and 0.19, respectively. Maternal additive genetic effects were fitted only for birth weight and weaning weight. Corresponding estimates of 0.12 and 0.10 were obtained for maternal heritability of birth weight and weaning weight, respectively. Maternal permanent environmental effects have low contribution to the expression of Kleiber ratio and lead to estimates of 0.06 and 0.06 for permanent maternal environmental variance as a proportion of phenotypic variance (c^2) of these traits, respectively. All pre-weaning traits, except Kleiber ratio, were affected by litter effects. The magnitude of ratio of common litter variance to phenotypic variance (l^2) was 0.05, 0.12 and 0.14 for birth weight, weaning weight and average daily gain, respectively. Direct genetic

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correlations were positive and ranged from 0.09 for Kleiber ratio-yearling weight to 0.80 for weaning weight-average daily gain. Phenotypic correlations ranged from 0.18 for Kleiber ratio-yearling weight to 0.87 for weaning weight-average daily gain.

Keywords: average daily gain, common environmental effect, Kleiber ratio, genetic parameters

Abbreviations: BW: birth weight, WW: weaning weight, 6MW: six months weight, 9MW: nine months weight, YW: yearling weight, ADG: average daily gain, KR: Kleiber ratio, AIC: Akaike information criterion

Introduction

Mutton production in Iran, as the main source of red meat, does not satisfy the increasing demand of the consumers. Van Wyk *et al.* (2003) pointed out that sheep production systems have to be dynamic to satisfy the changing consumers' demands. So, enhancing the growth potential of lambs and production of more lambs per ewe are possible alternatives to increase meat production in any sheep breeding system (Miraei-Ashtiani *et al.* 2007). The Iranian sheep population comprises of about 27 breeds and ecotypes (Vatankhah *et al.* 2004). This genetic variation provides appropriate opportunities for improving breeding efficiency through breeding strategies such as crossbreeding that exploits breed diversities and breed complementary (Freking & Leymaster 2004).

Shal breed, numbering about 1.5 million animals, is one of the most important meat breeds among Iranian sheep. They are well known for their large size, tolerance to climatic changes and capability to produce twining lambs. The breed is fat-tailed, its coat colour is predominantly sugary greyish and a small number of them is also black and white. This breed has a white spot on the forehead and both sexes are not polled. The origin of the Shal sheep is the Qazvin province and it is kept mainly to produce meat (Tavakolian 1999).

Growth rate and body weight of lambs at different ages have deterministic effects on the profitability of sheep production enterprises. Therefore, these traits may be taken into account as efficient selection criterions in any sheep breeding system (Tosh & Kemp 1994). Such appropriate selective procedure requires accurate (co)variance components and genetic parameter estimates. Genetic parameters for growth traits of different sheep breeds have been reported (Prince *et al.* 2010, Di *et al.* 2011, Abegaz *et al.* 2010). The results of these studies have shown that the inclusion of maternal effects on the models considered for genetic analysis of growth traits, especially for pre-weaning traits, is of crucial importance. They confirmed that ignoring maternal effects leads to upward biased estimates for (co)variance components. Thus, accurate estimation of (co)variance components is a prerequisite for designing any breeding programme and genetic evaluation system. Because of paucity of such estimates for growth traits of Shal sheep in Iran, the main objective of the current research was the estimation of (co)variance components and corresponding genetic parameters for growth traits of Shal sheep with an emphasis on partitioning maternal effects.

Materials and methods

Animals and management

The flock was managed semi-intensively. At birth time and/or within 24 h afterwards, lambs were weighed and ear-tagged. Lambs were kept indoors from mid-February to late April and manually fed. Afterwards, lambs were grazed on pastures of low quality and productivity. Supplemental feeding comprising dried alfalfa and barley grain was offered to the animals, particularly prior to mating and late pregnancy. Weaning was at approximately 120 days of age. The lambs were weaned at the same day but not necessarily at the same age. The female lambs were exposed to the rams at approximately 18 months of age. A controlled mating strategy was designed during mating period (early November to mid-December) and ewes were mated to fertile rams at the rate of 20 ewes per ram. Ewes were kept for a maximum of seven parities (until eight years of age) and rams for a maximum of two mating seasons. Breeding rams and ewes were selected mainly based on phenotypic characteristics such as visual body conformation at yearling age and nearest three generations of pedigree information on birth type of the lambs.

Studied traits

Data used in the present study were collected during an 11-year period from 1998 to 2009 at Agricultural Jahad Organization, Qazvin province of Iran. Investigated traits were body weights of lambs at birth (BW), three months of age as weaning weight (WW), six months of age (6MW), nine months of age (9MW), yearling age (YW), average daily gain from birth to weaning (ADG) and Kleiber ratio from birth to weaning (KR) defined as ADG/WW$^{0.75}$ The structure of the data set used in the present study is presented in Table 1.

Table 1
Characteristics of the data structure

Traits	No. of Records	Mean	Standard deviation	% Coefficient of variation	No. of dams	No. of sires	No. of dams with records	No. of sires with records
BW, kg	6 221	3.46	0.83	19.87	4 060	160	3 476	134
WW, kg	4 261	22.65	3.12	15.78	3 497	145	2 974	109
ADG, g/day	4 261	213.21	48.93	22.53	3 497	145	2 974	109
KR	4 261	20.36	2.47	13.05	3 497	145	2 974	109
6MW, kg	3 112	34.14	5.29	16.80	2 481	137	2 186	101
9MW, kg	2 370	46.36	9.92	15.59	1 883	107	1 762	99
YW, kg	2 240	55.46	6.97	17.54	1 325	102	1 190	93

Statistical analysis

Fixed effects

Significance testing of fixed effects to be included in the operational model for each trait, was carried out using the general linear model (GLM) procedure of the SAS v9 software package (SAS Institute Inc., Cary, NC, USA) and least squares means for each trait were obtained. Considered fixed effects in the analytical model were sex of lamb in 2 classes (male and female), birth year in 11 classes (1998-2009), dam age at lambing in 6 classes (2-7 years old), birth type in 3 classes (single, twin and triplet) and age of lamb at 3, 6, 9 and 12 months (in days) as a linear covariate for WW, 6MW, 9MW and YW, respectively. The interactions between fixed effects were not significant and therefore excluded.

Estimation of (co)variance components and genetic parameters

(Co)variance components and corresponding genetic parameters for the studied traits were estimated using restricted maximum likelihood (REML) using ASReml (Gilmour *et al.* 2000). Tested models (in matrix notation) are as shown below:

$$y = Xb + Z_1a + e \qquad \text{Model (1)}$$

$$y = Xb + Z_1a + Z_3c + e \qquad \text{Model (2)}$$

$$y = Xb + Z_1a + Z_4l + e \qquad \text{Model (3)}$$

$$y = Xb + Z_1a + Z_3c + Z_4l + e \qquad \text{Model (4)}$$

$$y = Xb + Z_1a + Z_2m + e \qquad Cov\,(a,m) = 0 \qquad \text{Model (5)}$$

$$y = Xb + Z_1a + Z_2m + e \qquad Cov\,(a,m) = A\sigma_{am} \qquad \text{Model (6)}$$

$$y = Xb + Z_1a + Z_2m + Z_3c + e \qquad Cov\,(a,m) = 0 \qquad \text{Model (7)}$$

$$y = Xb + Z_1a + Z_2m + Z_3c + e \qquad Cov\,(a,m) = A\sigma_{am} \qquad \text{Model (8)}$$

$$y = Xb + Z_1a + Z_2m + Z_4l + e \qquad Cov\,(a,m) = 0 \qquad \text{Model (9)}$$

$$y = Xb + Z_1a + Z_2m + Z_4l + e \qquad Cov\,(a,m) = A\sigma_{am} \qquad \text{Model (10)}$$

$$y = Xb + Z_1a + Z_2m + Z_3c + Z_4l + e \qquad Cov\,(a,m) = 0 \qquad \text{Model (11)}$$

$$y = Xb + Z_1a + Z_2m + Z_3c + Z_4l + e \qquad Cov\,(a,m) = A\sigma_{am} \qquad \text{Model (12)}$$

Where y is a vector of records for traits studied; b, a, m, c, l and e are vectors of fixed, direct genetic, maternal genetic, maternal permanent environmental, maternal temporary environmental (common litter) effects and the residual effects, respectively. X, Z_1, Z_2, Z_3 and Z_4 are corresponding design matrices associating the fixed, direct genetic, maternal genetic, maternal permanent environmental and maternal temporary environmental effects to vector of y.

It is assumed that direct additive genetic, maternal additive genetic, maternal permanent environmental, maternal temporary environmental and residual effects are normally distributed with mean 0 and variance $A\sigma^2_a$, $A\sigma^2_m$, $I_d\sigma^2_c$, $I_l\sigma^2_l$ and $I_n\sigma^2_e$, respectively. Furthermore, σ^2_a, σ^2_m, σ^2_c, σ^2_l and σ^2_e are direct additive genetic variance, maternal additive genetic variance, maternal permanent environmental variance (half sibs across years), maternal temporary environmental variance (full sibs within year) and residual variance, respectively. *A* is the additive numerator relationship matrix; I_d, I_l and I_n are identity matrices that have order equal to the number of dams, litters and number of records, respectively and σ_{am} refers to the covariance between direct genetic and maternal genetic effects.

An Akaike information criterion (AIC) test was applied to determine the most appropriate model for estimating (co)variance components for each traits as follows (Akaike 1974):

$$AIC_i = -2\ log\ L_i + 2\ p_i \tag{13}$$

Where log L_i is the maximized log likelihood of the respective model *i* at convergence and p_i is the number of parameters obtained from each model. The model with the lowest AIC was taken into account as the most appropriate one. Total heritability, h^2_t, (Willham 1972) and maternal across year repeatability for ewe performance, t_m, (Gowane *et al.* 2010) were estimated as follows:

$$h^2_t = (\sigma^2_a + 0.5\sigma^2 m + 1.5\sigma_{am})/\sigma^2_p \tag{14}$$

$$t_m = 1/4\, h^2_d + h^2_m + c^2 + (m\ r_{am}\ h) \tag{15}$$

Components of the described formulas are explained in the footnote of Table 3. Genetic and phenotypic correlations were estimated using bivariate analyses applying the best model determined in univariate analyses. If the values of −2 log likelihood variance in the Simplex function were below 10^{-8}, it was assumed that convergence had been achieved (Kushwaha *et al.* 2009).

Results and discussion

Fixed effects

Descriptive statistics of the studied traits are summarized in Table 1. Least squares means of the considered traits are shown in Table 2. Single born, twin and triplet lambs constitute 52.68 %, 38.14 % and 9.18 % of total lambs, respectively. As indicated in Table 2, birth year, sex and birth type of lambs had significant effects on all studied traits ($P<0.01$). Dam age significantly influenced the considered pre-weaning traits ($P<0.01$) but not post-weaning ones ($P>0.05$). Weighing age at 3, 6, 9 and 12 months of age as a linear covariate, had significant influence on WW, 6MW, 9MW and YW, respectively.

Male lambs had higher pre-weaning growth rate and body weight than females at various ages. Such superiority can be partly ascribed to differences in the endocrine system of male and female lambs that tends to become more pronounced as lambs approach maturity. The significant effects of dam age on the studied traits can be explained to some extent by differences in maternal effects and maternal behaviour of ewes at different ages. Differences in

Table 2
Least square means ± standard error for the studied traits

Sub-class	BW, kg[1]	WW, kg	ADG, g/day	KR	6MW, kg	9MW, kg	YW, kg
Sex	**	**	**	**	**	**	**
Male	$5.13^{a} \pm 0.06$	$26.23^{a} \pm 0.11$	$220.57^{a} \pm 2.41$	$21.35^{a} \pm 0.12$	$39.63^{a} \pm 0.28$	$44.35^{a} \pm 0.35$	$59.73^{a} \pm 0.72$
Female	$4.61^{b} \pm 0.04$	$22.18^{a} \pm 0.16$	$191.07^{a} \pm 2.29$	$18.04^{a} \pm 0.16$	$34.68^{b} \pm 0.22$	$41.25^{b} \pm 0.29$	$46.26^{b} \pm 0.26$
Birth type	**	**	**	**	**	**	**
Single	$5.28^{a} \pm 0.02$	$29.52^{a} \pm 0.15$	$235.27^{a} \pm 1.94$	$21.18^{a} \pm 0.13$	$39.26^{a} \pm 0.16$	$45.38^{a} \pm 0.28$	$49.14^{a} \pm 0.36$
Twin	$4.57^{b} \pm 0.05$	$26.15^{b} \pm 13$	$205.48^{b} \pm 1.04$	$19.09^{b} \pm 0.10$	$35.47^{b} \pm 0.16$	$41.59^{b} \pm 0.38$	$44.84^{b} \pm 0.58$
>Triplet	$4.09^{c} \pm 0.02$	$23.08^{c} \pm 0.26$	$185.23^{c} \pm 2.87$	$19.15^{b} \pm 0.17$	$32.58^{b} \pm 0.59$	$38.93^{b} \pm 0.17$	$43.36^{b} \pm 0.94$
Dam age, year	**	**	**	**	ns	ns	ns
2	$4.36^{c} \pm 0.01$	24.26d ± 0.16	$196.13^{b} \pm 2.85$	$19.73^{c} \pm 0.25$	$35.47^{a} \pm 0.26$	$42.25^{a} \pm 0.37$	$44.72^{a} \pm 0.99$
3	$4.73b^{c} \pm 0.02$	$24.37b^{c} \pm 0.26$	$198.52^{b} \pm 2.71$	$19.55^{b} \pm 0.26$	$35.46^{a} \pm 0.21$	$43.16^{a} \pm 0.83$	$44.94^{a} \pm 0.72$
4	$4.83^{b} \pm 0.02$	$24.38^{c} \pm 0.72$	$193.10^{b} \pm 3.86$	$19.05^{c} \pm 0.28$	$35.26^{a} \pm 0.24$	$44.27^{a} \pm 0.36$	$45.73^{a} \pm 0.72$
5	$4.93^{b} \pm 0.03$	$26.17^{b} \pm 0.16$	$210.82^{ab} \pm 2.78$	$20.07^{a} \pm 0.27$	$36.71^{a} \pm 0.53$	$43.37^{a} \pm 0.83$	$45.93^{a} \pm 0.28$
6	$5.16^{a} \pm 0.03$	$28.94^{a} \pm 0.71$	$225.61^{a} \pm 3.83$	$19.14^{c} \pm 0.36$	$37.23^{a} \pm 0.15$	$46.17^{a} \pm 0.22$	$46.93^{a} \pm 0.82$
7	$5.10^{ab} \pm 0.05$	$27.26^{b} \pm 0.61$	$206.51^{b} \pm 4.74$	$19.21^{c} \pm 0.41$	$38.27^{a} \pm 0.15$	$46.58^{a} \pm 0.73$	$46.82^{a} \pm 0.12$
Birth year	**	**	**	**	**	**	**
Birth date[2]	-	0.21** ± 0.01	-	-	0.19** ± 0.07	0.16** ± 0.04	0.15** ± 0.03

[1]Means with similar letters in each subclass within a column do not differ; *, ** significant effect at P<0.05 and P<0.01, respectively. [2]regression coefficient on day of lambs' birth

managing practices, feed availability, climatic conditions and breeding systems through years are possible reasons for significant effects of year on the considered traits. Competition for milk consumption among twins and triplets leads to a significant effect of birth type of lambs on the studied traits. Significant influences of investigated fixed effects on body weight of different sheep breed have been confirmed by others (Ghafouri-Kesbi *et al.* 2008, Abegaz *et al.* 2010).

Model selection

The AIC values for the studied traits under different tested models are presented in Table 3. The most appropriate model for BW and WW included direct additive genetic, maternal additive genetic and common litter effects, without considering covariance between direct additive and maternal additive genetic effects (Model 9). The most appropriate model for ADG and KR was similar to that of BW and WW, ignoring maternal additive genetic effects (Model 7). The model including direct additive genetic effects and maternal permanent environmental effects (Model 2) was determined as the best model for 6MW. Maternal effects had no influence on YW and resulted in selection of the simplest model, which included direct additive genetic effects as the sole random effects for 9MW and YW.

Table 3
AIC values for studied traits under different animal models with the best model in bold face

Model	Traits						
	BW	WW	ADG	KR	6MW	9MW	YW
Model 1	2 151.346	450.425	2 519.826	9 445.481	845.215	**7 316.326**	**12 4 212.167**
Model 2	2 147.126	446.417	2 513.439	**9 435.457**	**844.214**	7 327.735	12 4 214.673
Model 3	2 153.432	449.726	2 516.370	9 441.487	846.374	7 328.156	12 4 214.525
Model 4	2 155.387	451.167	2 518.269	9 443.047	847.254	7 329.926	12 4 216.156
Model 5	2 151.090	448.642	2 515.256	9 437.168	872.345	7 424.725	12 4 215.015
Model 6	2 150.211	450.625	2 516.268	9 439.356	871.732	7 416.615	12 4 242.156
Model 7	2 113.617	405.478	**2 470.217**	9 443.099	873.356	7 416.616	12 4 243.235
Model 8	2 112.763	405.629	2 472.374	9 445.056	874.601	7 417.672	12 4 244.168
Model 9	**2 112.079**	**404.283**	2 471.302	9 445.337	873.056	7 418.175	12 4 244.158
Model 10	2 114.427	486.160	2 473.306	9 447.728	870.581	7 420.727	12 4 245.145
Model 11	2 114.189	486.048	2 473.302	9 447.168	863.158	7 416.549	12 4 250.145
Model 12	2 116.165	488.300	2 475.306	9 449.269	864.917	7 420.164	12 4 252.156

Estimates of genetic parameters under univariate analysis

Estimation of genetic parameters for the studied traits based on the best model under univariate analyses are presented in Table 4. Direct heritability values were estimated 0.13, 0.19, 0.18, 0.05, 0.16, 0.18 and 0.19 for BW, WW, ADG, KR, 6MW, 9MW and YW, respectively. Al-Shorepy (2001) pointed out that birth weight is an economically important trait because of its effect on pre-weaning growth rate and increase of economic success in any sheep production enterprise.

Table 4
Genetic parameter estimates for traits studied fitting the most appropriate model

Traits	Model fitted	$h_d^2 \pm$ SE	$h_m^2 \pm$ SE	$c^2 \pm$ SE	$l^2 \pm$ SE	h_t^2	t^m	s_p^2
BW	9	0.13±0.03	0.12±0.03	-	0.05±0.02	0.17	0.20	20.33
WW	9	0.19±0.02	0.10±0.01	-	0.12±0.04	0.24	0.26	24.48
ADG	7	0.18±0.02	-	-	0.14±0.03	0.18	0.05	85.13
KR	2	0.05±0.01	-	0.06±0.03	-	0.05	0.07	10.51
6MW	2	0.16±0.03	-	0.06±0.02	-	0.16	0.10	14.95
9MW	1	0.18±0.02	-	-	-	0.18	0.04	14.53
YW	1	0.19±0.02	-	-	-	0.19	0.05	30.40

s_p^2: phenotypic variance; h_d^2: direct heritability; h_m^2: maternal heritability; c^2: ratio of maternal permanent environmental effects to phenotypic variance; l^2: ratio of common litter effects to phenotypic variance; SE: standard error; h_t^2 =Total heritability = $(\sigma^2_a + 0.5\sigma^2_m + 1.5\sigma_{am}) / \sigma^2_p$; $t_m = (1/4\, h_d^2 + h_m^2 + c^2 + m\, r_{am}\, h)$

The low direct heritability estimated for BW denotes the fact that direct genetic effects constitute a negligible part of phenotypic variance for BW of Shal lambs, suggesting that slow genetic progress would be expected through direct selection. Such low direct heritability is possibly due to the inclusion of maternal effects in the selected model.

Maternal effects denote the mothering ability for milk production as well as intrauterine conditions and may be partitioned into genetic and non-genetic parts (Matika *et al.* 2003, Dobek *et al.* 2004). Maternal additive genetic effects disappeared after weaning. Maternal permanent environmental effects have influenced all pre-weaning traits except KR, whereas only KR and 6MW were affected by maternal temporary environmental ones.

Maternal heritability values were estimated as 0.12 and 0.10 for BW and WW, respectively. The estimates of maternal permanent environmental variance, as a proportion of phenotypic variance (c^2) estimates, were low for KR (0.06) and 6MW (0.06). The estimate of common litter effect (l^2) was 0.05 for BW, 0.12 for WW and 0.14 for ADG. The estimated value for maternal heritability of BW (0.13) was in concordance with estimates of Mohammadi *et al.* (2011) in Zandi sheep.

As it was expected, maternal effects formed an integral part of variation for BW, probably reflecting differences in the uterine conditions, mainly with respect to the quality and capacity of the uterine space for the growth of the foetus (Gowane *et al.* 2010). Maternal heritability estimate for BW was lower than direct heritability one. These results are in agreement with studies of several authors (Noor *et al.* 2001, Mohammadi *et al.* 2012). Maternal heritability estimate for WW was lower than the direct one (0.10 *vs.* 0.19) and generally agreed with the estimate of Zamani & Mohammadi (2008) in Iranian Mehraban sheep (0.08). Lower estimates (Ozcan *et al.* 2005, Unal *et al.* 2006) also have been reported.

Estimated direct heritability values for WW (0.19) and ADG (0.18) were relatively similar in magnitude. Direct heritability estimate of WW accords well with literature (Gowane *et al.* 2010, Gowane *et al.* 2011, Mohammadi *et al.* 2012).

A low direct heritability value was estimated for KR (0.05), which generally accords well with those obtained by Matika *et al.* (2003) in Sabi sheep. The Kleiber ratio is proposed as an efficient selection criterion for feed efficiency under low-input range conditions and provides a good indication of how economically an animal grows (Mohammadi *et al.* 2011). Proportion of maternal temporary environmental variance, as a fraction of phenotypic variance (l^2) for BW, WW and ADG, was estimated as 0.05, 0.12 and 0.14, respectively.

At post-weaning period direct heritability estimate decreased from 0.16 at six months of age to 0.18 at nine months of age and increased to a value of 0.19 at yearling age. Direct heritability estimated value for 6MW was generally concordant with estimates of Abegaz *et al.* (2005) in Horro sheep (0.18). Higher (Gowane *et al.* 2010) and lower (Eskandarinasab *et al.* 2010) values were also reported. Maternal permanent environmental effects may have arisen from uterine environmental and multiple birth effects on milk production of ewes, the level of nutrition at final stages of gestation and maternal behaviour of ewes.

There are little information regarding genetic parameters of 9MW in the literature and published values are mainly related to Iranian local sheep breeds (Mohammadi *et al.* 2011). Maternal effects disappeared after six months of age. The obtained direct heritability estimate of YW (0.19) generally agrees with the estimate of Mohammadi *et al.* (2012) in Makooei sheep (0.22).

Total heritability estimates (h_t^2) were low to medium and ranging from 0.05 for KR to 0.24 for WW. Values of maternal across year repeatability for ewe performance (t_m) generally decreased with age and varied from 0.04 for 9MW to 0.26 for WW. Total heritability estimates are model sensitive (Gowane *et al.* 2010). Abegaz *et al.* (2005) pointed out that total heritability is important for breeding when maternal effects are important for the expression of a trait, and is useful for the estimation of selection response based on phenotypic values. The obtained estimates of h_t^2 and t_m for BW (0.17 and 0.20) and for WW (0.24 and 0.26) were in general agreement with estimated values reported by Gowane *et al.* (2010) in Malpura sheep. Such moderate estimates suggest scope of improvement in BW and WW through mass selection (Gowane *et al.* 2010). Estimates of h_t^2 for ADG and KR were 0.18 and 0.05 while those of t_m were 0.05 and 0.07. Obtained estimates of h_t^2 for 6MW, 9MW and YW were 0.16, 0.18 and 0.19 whereas those of t_m were 0.10, 0.04 and 0.05 for 6MW, 9MW and YW, respectively. Estimates of t_m for post-weaning body weights were generally higher than the estimated values by Gowane *et al.* (2010) in Malpura sheep.

Correlation estimates

Correlation estimates among the studied traits are presented in Table 5. There was no antagonistic relationship between the considered traits in terms of phenotypic, genetic and environmental correlations. Thus, selection for any of these traits will bring out a positive response to selection for others. Direct additive genetic correlations were positive and ranged from 0.09 for KR-YW to 0.80 for WW-ADG.

Birth weight had positive and low to medium direct genetic correlations with other studied traits, ranging from 0.17 (BW-KR) to 0.62 (BW-WW). Direct genetic correlation estimate of BW with other body weight traits decreased with age.

Direct genetic correlation estimate between WW and ADG was high and positive (0.80) and corresponds to estimates of Duguma *et al.* (2002) in Tygerhoek Merino sheep (0.99). Duguma *et al.* (2002) pointed out that WW and ADG are genetically the same trait. Thus, selection can be carried out based on either one of them. Medium and positive direct genetic

Table 5
Correlation estimates among body weight traits

Traits	r_p	r_a	r_m	r_c	r_l	r_e
BW-WW	0.29±0.05	0.62±0.12	0.30±0.09	-	0.79±0.22	0.18±0.07
BW-ADG	0.28±0.10	0.22±0.16	-	-	0.68±0.18	0.17±0.09
BW-KR	0.24±0.14	0.17±0.04	-	-	-	0.11±0.08
BW-6MW	0.28±0.04	0.53±0.12	-	-	-	0.23±0.10
BW-9MW	0.23±0.02	0.42±0.11	-	-	-	0.16±0.08
BW-YW	0.20±0.09	0.32±0.15	-	-	-	0.19±0.07
WW-ADG	0.87±0.15	0.80±0.15	-	-	-	0.69±0.18
WW-KR	0.62±0.14	0.64±0.12	-	-	-	0.58±0.12
WW-6MW	0.39±0.05	0.52±0.11	-	-	-	0.43±0.10
WW-9MW	0.28±0.14	0.39±0.15	-	-	-	0.25±0.14
WW-YW	0.23±0.11	0.33±0.09	-	-	-	0.20±0.13
ADG-KR	0.43±0.16	0.79±0.19	-	-	-	0.37±0.16
ADG-6MW	0.34±0.11	0.46±0.16	-	-	-	0.45±0.19
ADG-9MW	0.28±0.13	0.39±0.15	-	-	-	0.36±0.14
ADG-YW	0.19±0.09	0.29±0.15	-	-	-	0.28±0.14
KR-6MW	0.42±0.12	0.30±0.16	-	0.27±0.12	-	0.29±0.15
KR-9MW	0.21±0.10	0.14±0.13	-	-	-	0.35±0.13
KR-YW	0.18±0.05	0.09±0.08	-	-	-	0.06±0.03
6MW-9MW	0.52±0.13	0.62±0.18	-	-	-	0.37±0.11
6MW-YW	0.43±0.06	0.45±0.17	-	-	-	0.29±0.10
9MW-YW	0.36±0.12	0.45±0.13	-	-	-	0.39±0.16

r_p: phenotypic correlation; r_a: direct genetic correlation; r_m: maternal genetic correlation; r_c: maternal permanent environmental correlation; r_l: common litter effect correlation; r_e: environmental correlation

correlations were found between WW and other traits (Table 4). Estimated values for direct genetic correlations of WW with 6MW, 9MW and YW generally agreed with estimates of Gowane *et al.* (2010) in Malpura sheep. Weaning weight had a medium and positive direct genetic correlation with KR (0.64).

A relatively high direct genetic correlation estimate was obtained for ADG-KR (0.79) which was consistent with those obtained by Mohammadi *et al.* (2012) in Zandi sheep. Direct genetic correlations of post-weaning body weight traits with ADG were higher than those of post-weaning ones with KR. Direct genetic correlation estimate of 6MW-YW (0.45) was similar to the estimate of Miraei-Ashtiani *et al.* (2007) in Sangsari sheep (0.55). The existence of positive direct genetic correlations among the studied traits suggests that genetic factors which influence these traits were in similar direction.

An estimate of 0.30 for maternal genetic correlation between BW and WW was found, indicating that maternal additive genetic effects, which favour the growth of foetus, could have some favourable effects on post-natal growth traits of Shal lambs. Body weight from birth to weaning is influenced by similar genes of the ewe in terms of maternal genetic effects.

Positive and medium estimated value for maternal permanent environmental correlation between KR and 6MW (0.27) suggest that the existence of good management conditions and favourable maternal behaviour results in a beneficial effect on body weight of lambs at 6 months of age (Gowane *et al.* 2010). Maternal temporary environmental correlations were high in magnitude and found only among pre-weaning traits except KR.

Estimates of phenotypic correlation were positive and ranged from low (0.18 for KR-YW) to high (0.87 for WW-ADG) values. Environmental correlation estimates were ranged from 0.06 for KR-YW to 0.69 for WW-ADG. Corresponding correlation estimates generally agreed with those of Abegaz *et al.* (2005) in Horro sheep. Positive genetic phenotypic and environmental correlations among body weight traits indicate that there is no genetic, phenotypic and environmental antagonistic relationship between the considered traits.

In conclusion, the present study contributes to the comparison of different models for estimation of (co)variance components and genetic parameters in Shal sheep. There was found low direct genetic variation for all studied traits. Thus, a relatively low genetic gain would be expected through mass selection and the investigation of indirect selection criteria such as reproduction traits for improvement of growth traits is of paramount importance. Only BW and WW were affected by maternal additive genetic effects. It was obviously shown that the maternal environmental effects should be portioned into permanent and temporary components until six months of age.

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