

Estimation of (co) variance components and genetic parameters for growth traits in Arman sheep

M.S. Mokhtari*, M. Moradi Shahrebabak, H. Moradi Shahrebabk and M. Sadeghi

Department of Animal Science, University College of Agriculture and Natural Resources, University of Tehran, P. O. Box 31587-77871, Karadj, Iran

* Corresponding author, E-mail address: msmokhtari@ut.ac.ir

Abstract (Co) variance components and genetic parameters for growth traits in Arman sheep were estimated, using data collected during an 11-year period (1999-2010), by applying the restricted maximum likelihood (REML) procedure under univariate and bivariate animal models. The studied traits were body weight of lamb at birth (BW), body weight at 3 months of age as weaning weight (WW), body weight at 6 months (6MW), body weight at 9 months (9MW), yearling weight (YW), average daily gain from birth to weaning (ADG) and the Kleiber ratio (KR) from birth to weaning. Significant random effects for each trait were determined by AIC test fitting the additive direct genetic effect, additive maternal effect, covariance between additive direct and additive maternal effect, maternal permanent environmental and maternal temporary environmental (common litter) effects under nine animal models. Univariate analyses were carried out under the most appropriate model, determined by AIC test. Direct heritability estimates for BW, WW, ADG, KR, 6MW, 9MW and YW were 0.03 ± 0.02 , 0.15 ± 0.02 , 0.16 ± 0.02 , 0.04 ± 0.03 , 0.15 ± 0.04 , 0.08 ± 0.04 and 0.16 ± 0.02 , respectively. Maternal additive genetic effect was fitted only for BW, WW and ADG; corresponding estimates of 0.20 ± 0.02 , 0.13 ± 0.01 and 0.07 ± 0.03 were obtained for maternal heritability of BW, WW and ADG, respectively. Maternal permanent environmental effects had a small contribution in expression of pre-weaning growth traits and 6MW, and led to estimates of 0.05 ± 0.02 , 0.06 ± 0.04 , 0.12 ± 0.03 , 0.07 ± 0.02 and 0.06 ± 0.03 for maternal permanent environmental variance as a proportion of phenotypic variance (c^2) of BW, WW, ADG, KR and 6MW, respectively. The magnitude of ratio of common litter variance to phenotypic variance (l^2) was 0.07 ± 0.02 and 0.09 ± 0.02 for BW and WW, respectively. Direct genetic correlations were positive and ranged from 0.08 for KR-YW to 0.83 for WW-ADG; the phenotypic ones ranged from 0.19 for KR-9MW to 0.96 for WW-ADG. The results showed that the inclusion of maternal effects in genetic evaluation of early growth traits in Arman sheep is of crucial importance.

Keywords: maternal effects, body weights, animal model, (co) variance components

Received: 2 Jan. 2013, accepted: 5 Mar. 2013, published online: 28 Apr. 2013

Introduction

Small ruminants play an important role in the livelihood of a sizeable portion of the human population in the tropics, where they are mainly kept by local pastoralists under low-input production systems. Therefore, coordinated attempts, in terms of managerial practices and genetic improvement to promote production efficiency, are of crucial importance (Kosgey and Okeyo, 2007). Mutton production in Iran, as the main source of red meat, does not meet the increasing demand. Iranian native sheep are mainly kept under low-efficient production

systems, relying on limited low-quality rangeland plantation. Such low efficiency necessitates designing appropriate breeding programs for improved performance

of lambs as an appropriate alternative for enhancing meat production. Sheep population in Iran is comprised of 26 breeds, providing favorable opportunities for enhancing production efficiency through crossbreeding strategies that exploit breed diversities, heterosis, and breed complementarity (Freking and Leymaster, 2004). There has been a revival of interest in the creation of composite populations through crossbreeding prolific exotic sheep breeds with local breeds, with the aim of exploiting production efficiency to the benefit of the livestock industries (Shrestha, 2005).

Arman sheep was synthesized by crossbreeding four sheep breeds, including Baluchi, Ghezel (two Iranian native breeds), Chios and Suffolk in Abbasabad bre-

eeding station, located in Khorasan Razavi province, north-east Iran. This was aimed mainly at increasing litter size, mutton production and tolerance to harsh and unfavorable environmental conditions, prevalent in the area. The project was started in 1975 and breed fixation was accomplished by selection and inbreeding.

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 used as efficient selection criteria in sheep breeding system. Riggio et al. (2008) estimated the genetic parameters of the body weight in Scottish Blackface sheep and suggested that taking live body weight of older lambs into account as a selection criterion would increase selection accuracy. Such appropriate selective procedure requires accurate estimates of (co)variance components and genetic parameters. Genetic parameters for growth traits of different sheep breeds have been reported (Safari et al., 2005; Miraei-Ashtiani et al., 2007; Rashidi et al., 2008; Gowane et al., 2010; Mohammadi et al., 2010). The results of these studies indicated that the inclusion of maternal effects in the models considered for genetic evaluation of growth traits, especially for pre-weaning traits, is of crucial importance. They showed that exclusion of maternal effects leads to upward biased estimates for (co)variance components. Thus, accurate estimation of (co)variance components is a prerequisite for designing breeding program and genetic evaluation system.

Because of paucity of such estimates for growth traits in Arman sheep, as a new composite sheep breed in Iran, the objective of the current research was to estimate the (co)variance components and corresponding genetic parameters for growth traits in this breed.

Materials and methods

Flock management

The animals were kept under conventional managerial practices similar to local flocks. Breeding season extends from late August to late October. Therefore, lambing occurs late in January to late March. Breeding rams and ewes were selected mainly based on phenotypic appraisal such as visual body conformation at yearling age and nearest three generations of pedigree information on birth type of their lambs. Maiden ewes were exposed to fertile rams at approximately 18 months of age under a fully supervised mating strategy. Ewes in estrus were identified using teaser rams, at a ratio of 20-25 ewes per ram. The ewes were kept for a maximum of 7 parities (until 8 years of age), and the rams for a maximum of 2 mating seasons. To avoid inbr-

eeding, rams were allocated, in rotation, to each group of ewes. Lambs were ear-tagged and weighed at lambing or within 24 h of birth. The ewes and their lambs were housed in separate pens for a few days. The lambs were creep-fed and grazed on the range. They were kept together until weaning; approximately at 3 months of age. All lambs were weaned on the same day, but not necessarily at the same age. During spring and summer, the flock was kept in pastures and in the autumn it was grazed on wheat and barley stubbles. During winter, the lambs were kept indoors and hand-fed. Supplementary feed, offered to all animals during winter and to ewes late in pregnancy, consisted of wheat and barley straw, alfalfa hay, sugar beet pulp and concentrate.

Studied traits

The data set was collected during an 11-year period, from 1999 to 2010, at Abbasabad Sheep Breeding Station, Khorasan Razavi province, north-eastern Iran. Investigated traits were body weight of lambs at birth (BW), body weight at 3 months of age as weaning weight (WW), body weight at 6 months of age (6MW), body weight at 9 months of age (9MW), yearling age (YW), average daily gain from birth to weaning (ADG) and the Kleiber ratio (KR) from birth to weaning; defined as $ADG/WW^{0.75}$. The structure of the data set is set out in Table 1.

Statistical analysis

Fixed effects

Significance testing of fixed effects, included in the operational model for each trait, was carried out using the general linear model (GLM) procedure (SAS Institute, 2002), and the least squares means of the traits were determined. Considered fixed effects in the model were gender of lamb (male and female), birth year in 11 classes (1999–2010), dam age at lambing in 6 classes (2-7 years old), birth type in 3 classes (singletons, twins and triplets and more) 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

The restricted maximum likelihood (REML) procedure, under a derivative free algorithm, was used to estimate the (co)variance components and corresponding genetic parameters applying WOMBAT program

Quantitative genetics of growth traits in sheep

(Meyer, 2007). Tested models (in matrix notation) were as follow:

$y = Xb + Z_1a + e$		Model 1
$y = Xb + Z_1a + Z_3c + e$		Model 2
$y = Xb + Z_1a + Z_3c + Z_4l + e$		Model 3
$y = Xb + Z_1a + Z_2m + e$	Cov(a,m)=0	Model 4
$y = Xb + Z_1a + Z_2m + e$	Cov(a,m)=Aσ _{am}	Model 5
$y = Xb + Z_1a + Z_2m + Z_3c + e$	Cov(a,m)=0	Model 6
$y = Xb + Z_1a + Z_2m + Z_3c + e$	Cov(a,m)=Aσ _{am}	Model 7
$y = Xb + Z_1a + Z_2m + Z_3c + Z_4l + e$	Cov(a,m)=0	Model 8
$y = Xb + Z_1a + Z_2m + Z_3c + Z_4l + e$	Cov(a,m)=Aσ _{am}	Model 9

In which, y is a vector of records for studied traits; b , a , m , c , l and e are vectors of fixed, direct genetic, maternal genetic, maternal permanent environmental, maternal temporary environmental (common litter) 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 . Temporary environmental effects, also called common environmental effects, constitute a portion of the maternal environmental effects that is common among full-sibs in a particular year and differs amongst years.

It was assumed that direct additive genetic, maternal additive genetic, maternal permanent environmental, maternal temporary environmental and residual effects were normally distributed with a mean 0 and variance of $A\sigma_a^2$, $A\sigma_m^2$, $I_d\sigma_c^2$, $I_l\sigma_l^2$ and $I_n\sigma_e^2$, respectively. Additionally, σ_a^2 , σ_m^2 , σ_c^2 , σ_l^2 and σ_e^2 are direct additive genetic variance, maternal additive genetic variance, maternal permanent environmental variance (half sibs across years), maternal temporary environmen-

tal variance (full sibs within a year) and residual variance, respectively. A is the additive numerator relationship matrix, I_d , I_l and I_n are identity matrices with orders equal to the number of dams, litters and records, respectively; σ_{am} refers to the covariance between maternal and direct genetic effects.

An Akaike's information criterion (AIC) test was used to determine the most appropriate model for estimating the (co)variance components for each trait (Akaike, 1974) according to the following formula:

$$AIC_i = -2 \log L_i + 2 p_i \quad (1)$$

in which, $\log L_i$ 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 smallest AIC was chosen as the most appropriate model. Total heritability (h^2_t) of the studied traits was calculated from the following formula:

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

in which σ_a^2 , σ_m^2 , σ_{am} and σ_p^2 are direct additive genetic variance, maternal additive genetic variance phenotypic variance, covariance between direct and maternal additive genetic variance and phenotypic variance, respectively.

Maternal across year repeatability for ewe performance (t_m) was estimated as using the following formula (Gowane et al., 2010):

$$t_m = 1/4 h^2_d + h^2_m + c^2 + (m r_{am} h) \quad (3)$$

in which, h^2_d , h^2_m , c^2 , r_{am} , m and h are denote direct heritability, maternal heritability, ratio of maternal permanent environmental variance to phenotypic variance, correlation between direct and maternal additive genetic effects, square root of direct heritability and square root of maternal heritability, respectively. Genetic and phenotypic correlations were estimated using bivariate analyses and applying the best model, determined in univariate analyses. When the value of $-2 \log$ likelihood variance in the AIREML function was below 10^{-8} ; convergence was assumed to have been achieved.

Table 1. Summary of descriptive statistics for the traits studied in Arman sheep

Traits ¹	No. of records	Mean	S.D. ²	% C.V. ³	No. of dams	No. of sires	Average no. of records per dam	Average no. of records per sire	No. of dams with record	No. of sires with records
BW (kg)	2194	4.02	0.85	21.14	604	63	3.63	34.82	446	44
WW (kg)	1991	21.86	5.47	25.02	590	63	3.37	31.60	394	41
ADG (g/day)	1991	190.04	59.71	31.42	590	63	3.37	31.60	394	41
KR	1991	18.51	3.10	16.75	590	63	3.37	31.60	394	41
6MW (kg)	1711	32.16	6.73	20.92	569	63	3.01	27.16	333	37
9MW (kg)	1453	35.78	6.09	17.02	505	59	2.88	24.63	265	31
YW (kg)	1357	41.74	7.69	18.42	490	59	2.77	23.00	249	28

¹ BW: Birth weight, WW: Weaning weight (three-month weight), ADG: Average daily gain from birth to weaning, KR: Kleiber ratio from birth to weaning, 6MW: Six-month weight, 9MW: nine-month weight, YW: Yearling weight

² S.D.: Standard deviation, ³C.V.: Coefficient of variation

Results

Fixed effects and model comparison

Descriptive statistics are summarized in Table 1. Approximately 9.25% of the lambs died from birth to weaning age. Least squares means of the traits are shown in Table 2. Singleton, twin and triplet lambs constituted 29.6%, 59.0% and 11.4% of all lambs, respectively. As indicated in Table 2, birth year, and lamb gender and birth type had significant effects on all studied traits ($P < 0.01$). Dam age significantly influenced the pre-weaning ($P < 0.01$) but not the post-weaning traits ($P > 0.05$). Age of lambs (in days) at 3, 6, 9 and 12 months of age as a linear covariate, significantly influenced the WW, 6MW, 9MW and YW, respectively.

The AIC values for different tested models are presented in Table 3. The most appropriate model for BW and WW included direct additive genetic, maternal additive genetic, maternal permanent environmental and common litter effects, without considering covariance between direct additive and maternal additive genetic effects (Model 8). The most appropriate model for ADG was Model 6; including the direct additive, maternal additive and maternal permanent environmental effects. The Model including direct additive genetic effects and maternal permanent environmental effects (Model 2) was chosen as the best model for KR and 6MW. Maternal effects did not influence 9MW and YW; resulting in selection of the simplest model, which included direct additive genetic effects as the sole random effects.

Estimates of genetic parameters

Estimation of genetic parameters, based on the best

model under univariate analyses, is shown in Table 4. Total heritability estimates ranged from 0.04 for KR to 0.19 for WW and ADG; while those related to repeatability of ewe performance varied from 0.02 for 9MW to 0.26 for BW. Correlation estimates are set out in Table 5. Direct additive genetic correlations were positive and ranged from 0.08 ± 0.10 for KR-YW to 0.83 ± 0.18 for WW-ADG. Maternal additive genetic correlations ranged from 0.21 ± 0.08 for BW-ADG to 0.38 ± 0.21 for BW-WW. The estimated maternal permanent environmental correlations were low (0.09 ± 0.12 for BW-6MW) to high (0.72 ± 0.15 for BW-ADG). A high estimate of 0.85 ± 0.26 was obtained for maternal temporary environmental correlation between BW and WW. Phenotypic correlations ranged from 0.19 ± 0.11 (KR-9MW) to 0.96 ± 0.14 (WW-ADG) and environmental ones from 0.08 ± 0.09 (KR-YW) to 0.78 ± 0.14 (WW-ADG).

Discussion

Superiority of male lambs to female lambs in terms of studied traits can be partly ascribed to differences in endocrine status that tends to become more pronounced as lambs approach maturity (Matika et al., 2003; Yilmaz et al., 2007). The significant effects of dam age on the studied traits can be explained to some extent by differences in maternal effects and maternal behavior of ewes at different ages (Abbasi et al., 2012). Differences in animal husbandry management, feed availability, climatic conditions and breeding systems through years, are possible causes for the significant effect of the year on these traits (Matika et al., 2003). Competition for milk consumption among members of twins or triplets can lead to significant effect of birth type of lambs on pre-weaning traits (Yil-

Table 3. AIC values for pre-weaning and post-weaning growth traits in Arman lambs under different univariate animal models

Model ¹	Traits ²						
	BW	WW	ADG	KR	6MW	9MW	YW
Model 1	851.558	8150.68	17619.812	6135.500	7634.726	6286.416	6342.490
Model 2	847.032	8146.336	17613.606	6125.578	7633.756	6287.746	6344.450
Model 3	855.406	8151.118	17618.378	6133.184	7636.756	6289.746	6346.045
Model 4	851.034	8148.274	17615.332	6127.488	7661.996	6304.988	6370.098
Model 5	850.416	8150.168	17616.990	6129.466	7660.776	6306.744	6372.088
Model 6	813.316	8103.808	17570.676	6153.808	7662.340	6306.962	6373.098
Model 7	812.370	8105.808	17572.664	6155.808	7663.042	6307.042	6374.754
Model 8	812.210	8086.406	17573.982	6157.746	7651.370	6306.204	6360.716
Model 9	816.200	8088.336	17575.926	6159.700	7653.226	6310.098	6362.727

¹ The best model determined for each trait is shown in boldface

² For trait abbreviations see footnote to Table 1

Quantitative genetics of growth traits in sheep

maz et al., 2007). The significant effect of birth type on 6MW, 9MW and YW may be due to the existence of twin and triplet lambs at post-weaning period (at 6, 9 and 12 months of age).

As indicated in Table 2, BW and WW of twins were higher than those of triplets but there were no significant differences among twin and triplet lambs in terms of 6MW, 9MW and YW. Significant influences of fixed effects on body weight of different sheep breed have been well documented (Yazdi et al., 1997; Abegaz et al., 2005; Rashidi et al., 2008; Jafaroghli et al., 2010).

Duguma et al. (2002) pointed out that if maternal effects constitute a sizable part of genetic variation for a trait and ignored in genetic evaluations, then upward biased estimates will be obtained. In the present study, most ewes had their own records, approximately 74% at birth to 51% at yearling age (Table 1). According to Maniatis and Pollot (2003), accuracy of partitioning maternal effects into genetic and environmental components may be affected by the number of records per dam and the proportion of dams having records.

Estimated value for direct heritability of BW was in agreement with the estimates of Rashidi et al. (2008) in Kermani sheep and Jafaroghli et al. (2010) in Moghani sheep. The low direct heritability estimate for BW denotes the fact that direct genetic effects constituted a negligible portion of the phenotypic variance for BW in Arman lambs; suggesting that slow genetic progress would be expected through direct selection. Such low direct heritability is possibly due to inclusion of maternal effects in the selected model. Contrary to the present findings, Safari et al. (2005) reported weighted mean of direct heritability, obtained from the literature, for BW of meat, dual-purpose and wool type sheep at 0.15, 0.19 and 0.21, respectively.

Estimated direct heritability values for WW and ADG

were almost similar in magnitude. Direct heritability estimate of WW is in line with those in the literature (Miraei-Ashtiani et al., 2007; Gowane et al., 2010; Mohammadi et al., 2010; Mohammadi et al., 2011). Direct heritability values for ADG was generally in accord with estimates of Rashidi et al. (2008) in Kermani sheep (0.15) and Mohammadi et al. (2011) in Sanjabi sheep (0.14). Safari et al. (2005) reported weighted mean estimate of 0.18 for direct heritability of WW in both dual-purpose and meat-type breeds of sheep which are in general agreement with the estimated value in the present study. A low direct heritability value was estimated for KR (0.04); in agreement with those obtained by Rashidi et al. (2008) in Kermani sheep and by Matika et al. (2003) in Sabi sheep. The Kleiber ratio has been proposed as an efficient selection criterion for feed efficiency under low-input range conditions which provides a good indication of how economically an animal grows (Scholtz and Roux, 1988). During the post-weaning period, direct heritability estimates decreased from 0.15 at 6 months of age to 0.08 at 9 months of age, increasing to a value of 0.16 at yearling age. Direct heritability estimate value for 6MW was generally concordant with the estimates of Vatankhah and Talebi (2008) in Lori-Bakhtiari sheep (0.19) and Abegaz et al. (2005) in Horro sheep (0.18). Higher (Miraei-Ashtiani et al., 2007; Mokhtari et al., 2008; Gowane et al., 2010) and lower (Eskandarinasab et al., 2010; Mohammadi et al., 2010) estimates were also reported. A low estimate of 0.08 obtained for direct heritability of 9MW is in general agreement with the value of 0.03 in Kermani sheep (Rashidi et al., 2008). Obtained direct heritability estimate of YW (0.16) generally agreed with estimate of Mokhtari et al. (2008) in Kermani sheep (0.15) and Miraei-Ashtiani et al. (2007) in Sangsari sheep (0.10). Higher estimates also were reported by others (Snyman

Table 4. Genetic parameter estimates for pre-weaning and post-weaning growth traits under the most appropriate univariate animal model

Trait ¹	Model fitted	$h^2_d \pm S.E.$	$h^2_m \pm S.E.$	$c^2 \pm S.E.$	$l^2 \pm S.E.$	h^2_t	t_m	σ_p^2
BW	8	0.03 ± 0.02	0.20 ± 0.02	0.05 ± 0.02	0.07 ± 0.02	0.13	0.26	0.52
WW	8	0.15 ± 0.02	0.13 ± 0.01	0.06 ± 0.04	0.09 ± 0.03	0.19	0.23	21.60
ADG	6	0.16 ± 0.02	0.07 ± 0.03	0.12 ± 0.03	-	0.19	0.23	98.59
KR	2	0.04 ± 0.03	-	0.07 ± 0.02	-	0.04	0.08	7.92
6MW	2	0.15 ± 0.04	-	0.06 ± 0.03	-	0.15	0.10	32.15
9MW	1	0.08 ± 0.04	-	-	-	0.08	0.02	28.02
YW	1	0.16 ± 0.02	-	-	-	0.16	0.04	39.83

σ_p^2 : phenotypic variance; h^2_d : direct heritability; h^2_m : maternal heritability; c^2 : ratio of maternal permanent environmental effects to phenotypic variance; l^2 : ratio of common litter effects to phenotypic variance; S. E.: standard error; h^2_t = Total heritability = $(\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am}) / \sigma_p^2$; $t_m = (1/4 h^2_d + h^2_m + c^2 + m r_{am} h)$

¹ For trait abbreviations see footnote to Table 1

et al., 1995; Yazdi et al., 1997; Abegaz et al., 2005).

Accurate genetic evaluation of growth traits requires adopting models that contain direct, maternal genetic and maternal environmental effects. Where multiple births are relatively common, partitioning maternal environmental effects into across year effect (maternal permanent environmental) and litter effect (within year common environmental effect specified to the litter) is of paramount importance in terms breeding (Safari et al., 2005). Safari et al. (2005) suggested that for traits affected by maternal effects, interpretation of genetic parameters under animal model is mainly dependent on both data structure and the analytical model used.

Maternal additive genetic effects disappeared after weaning. The estimated value for maternal heritability of BW was in concordance with estimates of Rashidi et al. (2008) in Kermani sheep (0.24) and Eskandarinasab et al. (2010) in Afshari sheep (0.22). Lower estimates also were reported by Mohammadi et al. (2010) in Sanjabi sheep (0.14) and by Mohammadi et al. (2011) in Zandi sheep (0.13). As expected, maternal effects constitute an integral part of variation for BW, probably refl-

ecting the differences in uterine environment and space for growth of the fetus (Gowane et al., 2010). Maternal heritability estimate for WW was lower than the direct one (0.13 vs. 0.15) and generally agreed with estimate of Zamani and Mohammadi (2008) in Iranian Mehraban sheep (0.08). Higher (Mohammadi et al., 2010) and lower estimate (Ozcan et al., 2005; Miraei-Ashtiani et al., 2007) were also reported. Low maternal heritability values obtained for ADG was in general agreement with Ozcan et al. (2005) in Turkish Merino sheep (0.04) and Ghafouri-Kesbi et al. (2011) in Zandi sheep (0.03). Maternal permanent environmental effects influenced all pre-weaning traits and 6MW. These effects may be due to the effects of uterine environment and multiple birth on milk production of ewes, level of nutrition at late gestation and maternal behavior (Maria et al., 1993; Snyman et al., 1995). Estimated values for c^2 of BW, ADG and WW were generally in agreement with estimates of Abbasi et al. (2012) in Iranian Baluchi sheep. Mokhtari et al. (2008) reported a value of 0.09 for c^2 of 6MW in Kermani sheep which is in accordance with the value in the present study. Consistent with our estimates, Abegaz et al.

Table 5. Correlation estimates among studied traits under bivariate animal models

Traits ¹	r_p	r_a	r_m	r_c	r_l	r_e
BW-WW	0.37 ± 0.10	0.49 ± 0.25	0.38 ± 0.21	0.27 ± 0.12	0.85 ± 0.26	0.17 ± 0.18
BW-ADG	0.35 ± 0.12	0.25 ± 0.21	0.21 ± 0.08	0.72 ± 0.15	-	0.14 ± 0.11
BW-KR	0.27 ± 0.10	0.09 ± 0.12	-	0.14 ± 0.11	-	0.12 ± 0.10
BW-6MW	0.30 ± 0.08	0.34 ± 0.17	-	0.09 ± 0.12	-	0.22 ± 0.08
BW-9MW	0.25 ± 0.09	0.30 ± 0.13	-	-	-	0.19 ± 0.10
BW-YW	0.26 ± 0.08	0.18 ± 0.11	-	-	-	0.12 ± 0.09
WW-ADG	0.96 ± 0.14	0.83 ± 0.18	0.29 ± 0.11	0.64 ± 0.19	-	0.78 ± 0.14
WW-KR	0.57 ± 0.11	0.55 ± 0.19	-	0.59 ± 0.11	-	0.67 ± 0.15
WW-6MW	0.45 ± 0.08	0.55 ± 0.12	-	0.24 ± 0.11	-	0.45 ± 0.12
WW-9MW	0.32 ± 0.11	0.44 ± 0.13	-	-	-	0.36 ± 0.11
WW-YW	0.28 ± 0.10	0.53 ± 0.11	-	-	-	0.28 ± 0.12
ADG-KR	0.39 ± 0.12	0.75 ± 0.31	-	0.56 ± 0.13	-	0.27 ± 0.08
ADG-6MW	0.26 ± 0.08	0.35 ± 0.22	-	0.27 ± 0.09	-	0.41 ± 0.11
ADG-9MW	0.22 ± 0.11	0.46 ± 0.29	-	-	-	0.27 ± 0.16
ADG-YW	0.26 ± 0.12	0.35 ± 0.15	-	-	-	0.23 ± 0.14
KR-6MW	0.33 ± 0.09	0.25 ± 0.19	-	0.38 ± 0.16	-	0.35 ± 0.18
KR-9MW	0.19 ± 0.11	0.16 ± 0.11	-	-	-	0.25 ± 0.10
KR-YW	0.27 ± 0.14	0.08 ± 0.10	-	-	-	0.08 ± 0.09
6MW-9MW	0.45 ± 0.10	0.51 ± 0.12	-	-	-	0.41 ± 0.15
6MW-YW	0.47 ± 0.09	0.47 ± 0.22	-	-	-	0.33 ± 0.12
9MW-YW	0.35 ± 0.11	0.59 ± 0.24	-	-	-	0.49 ± 0.17

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

¹ For trait abbreviations see footnote to Table 1

Quantitative genetics of growth traits in sheep

(2005) reported a value of 0.13 for I^2 estimate of weaning weight in Horro sheep. Abbasi et al. (2012) reported a value of 0.19 for I^2 of BW in Baluchi sheep which is higher than the value recorded in the present study.

Total heritability estimates are model sensitive (Gowane et al., 2010). Abegaz et al. (2005) pointed out that when maternal effects are important in the expression of a trait total heritability is of crucial importance in terms of breeding and is useful in estimation of selection response based on phenotypic values. The obtained estimates of h^2 , and t_m for BW and for WW were in general agreement with values reported by Gowane et al. (2010) in Malpura sheep. Estimates of t_m for post-weaning body weights were generally higher than values in Malpura sheep (Gowane et al., 2010).

Birth weight had positive and low to medium direct genetic correlations with other traits, ranging from 0.09 (BW, KR) to 0.49 (BW, WW). Gowane et al. (2010) reported positive and medium direct genetic correlation estimates for BW, weaning weight, 6 months weight, 9 months weight and yearling weight in Malpura sheep, close to estimates in the present study.

Direct genetic correlation estimate of BW with other body weight traits decreased with age. A low direct genetic correlation estimate was obtained for BW-KR which was in agreement with estimate of Mohammadi et al., (2010) in Sanjabi sheep (0.02). Medium estimate of 0.25 for direct genetic correlation of BW and ADG was in agreement with estimate of Mohammadi et al. (2010) in Sanjabi sheep (0.19) and Mohammadi et al. (2011) in Zandi sheep (0.21). Higher estimate were reported by Rashidi et al. (2008) in Kermani sheep.

Direct genetic correlation estimate between WW and ADG was high (0.83) and of similar magnitude to estimates of Duguma et al. (2002) in Tygerhoek Merino sheep (0.99) and Rashidi et al. (2008) in Kermani sheep (0.86). 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. Lower estimate of 0.59 for direct genetic correlation between WW and ADG also was reported by Maria et al. (1993). Medium and positive direct genetic correlations were found between WW and other traits (Table 5). Estimated values for direct genetic correlations of WW with 6MW, 9MW and YW generally agreed with the estimates of Gowane et al. (2010) in Malpura sheep.

Weaning weight had a medium and positive direct genetic correlation with KR (0.55); the corresponding estimate was generally in agreement with estimate of Mohammadi et al. (2010) in Sanjabi sheep (0.73). A relatively large direct genetic correlation estimate was

obtained for ADG-KR (0.75) which was in agreement with those obtained by Rashidi et al. (2008) in Kermani sheep (0.76) and Mohammadi et al. (2011) in Zandi sheep (0.84). Direct genetic correlations of post-weaning body weight traits with ADG were higher than those of post-weaning ones with KR. Similar pattern were recorded by Mohammadi et al. (2010) in Sanjabi sheep.

Estimated direct genetic correlations among post-weaning body weights (6MW, 9MW and YW) were positive and medium in magnitude and generally lower than other published estimates (Mokhtari et al., 2008; Mohammadi et al., 2010). In general, the existence of positive direct genetic correlations among the studied traits suggested that genetic factors which influence these traits were in similar direction. Positive estimates for maternal genetic correlation among pre-weaning traits (except for KR) indicated that maternal additive genetic effects, which favor the growth of fetus, could have favorable influences on post-natal growth traits in Arman lambs. Body weight and growth rate from birth to weaning are influenced by similar genes in terms of maternal genetic effects. Obtained estimates of maternal genetic correlation were in agreement with estimates of Abbasi et al. (2012) in Baluchi sheep. Positive values were recorded for maternal permanent environmental correlations among pre-weaning growth traits and 6MW, suggesting that good management conditions and favorable maternal behavior would have beneficial effects on body weight of lambs from birth to 6 months of age (Gowane et al., 2010). Maternal temporary environmental correlations, found only between BW and WW, were high in magnitude. Phenotypic and/or environmental correlation estimates among the studied traits generally agreed with those of Abegaz et al., (2005) in Horro sheep and Mohammadi et al., (2010) in Sanjabi sheep. Positive genetic (direct and/or maternal), phenotypic and environmental correlations among body weight traits indicated that there was no genetic, phenotypic and environmental antagonist relationship among considered traits. Therefore, selection for any of these body weights is likely to result in positive response in terms of genetic and phenotypic values.

Conclusions

Different models for estimation of (co)variance components and genetic parameters were compared. Low direct genetic variations were found for all studied traits. Thus, a relatively low genetic gain would be expected through mass selection. As Arman sheep is a

crossbred one it seems that non-additive genetic effects have sizeable impacts on the expression of body weight and growth rate. The results revealed that maternal environmental effects should be partitioned into permanent and temporary components until six months of age.

Acknowledgement

The cooperation of the staff of Abbasabad Sheep Breeding Station for providing data is greatly acknowledged.

References

- Abbasi, M.A., Abdollahi-Arpanahi, R., Maghsudi, A., Vaez Torshizi, R., Nejati-Javaremi, A., 2012. Evaluation of models for estimation of genetic parameters and maternal effects for early growth traits of Iranian Baluchi sheep. *Small Ruminant Research* 104, 62-69.
- Abegaz, S., van Wyk, J.B., Olivier, J.J., 2005. Model comparisons and genetic and environmental parameter estimates of growth and the Kleiber ratio in Horro sheep. *South African Journal of Animal Science* 35, 30-40.
- Akaike, H., 1974. A new look at the statistical model identification. *IEEE Transactions, Automatic Control* 19, 716-723.
- Duguma, G., Schoeman, S.J., Cloete, S.W.P., Jordan, G.F., 2002. Genetic parameter estimates of early growth traits in the Tygerhoek Merino flock. *South African Journal of Animal Science* 32, 66-75
- Eskandarinasab, M., Ghafouri-Kesbi, F., Abbasi, M.A., 2010. Different models for evaluation of growth traits and Kleiber ratio in an experimental flock of Iranian fat-tailed Afshari sheep. *Journal of Animal Breeding and Genetics* 127, 26-33.
- Ghafouri-Kesbi, F., Abbasi, M.A., Afraz, F., Babaei, M., Baneh, H., Abdollahi-Arpanahi, R., 2011. Genetic analysis of growth rate and Kleiber ratio in Zandi sheep. *Tropical Animal Health and Production* 43, 1153-1159
- Gowane, G.R., Ashish Chopra., Ved Prakash., Arora, A.L., 2010. Estimates of (co)variance components and genetic parameters for body weights and first greasy fleece weight in Malpura sheep. *Livestock Science* 131, 94-101.
- Jafaroghli, M., Rashidi, A., Mokhtari, M.S., Shadparvar, A.A., 2010. (Co)Variance components and genetic parameter estimates for growth traits in Moghani sheep. *Small Ruminant Research* 91, 170-177.
- Freking, B. A., Leymaster, K. A. 2004. Evaluation of Dorset, Finnsheep, Romanov, Texel, and Montadale breeds of sheep. IV. Survival, growth, and carcass traits of F1 lambs. *Journal of Animal Science* 82, 3144-3153.
- Kosgey, I.S. Okeyo, A.M., 2007. Genetic improvement of small ruminants in low-input, smallholder production systems: Technical and infrastructural issues. *Small Ruminant Research* 70, 76-88.
- Maniatis, N., Pollott, G.E., 2003. The impact of data structure on genetic (co)variance components of early growth in sheep, estimated using an animal model with maternal effects. *Journal of Animal Science* 81, 101-108.
- Maria, G.A., Boldman, K.G., Van Vleck, L.D., 1993. Estimates variances due to direct and maternal effects for growth traits of Romanov sheep. *Journal of Animal Science* 71, 845-849.
- Matika, O., van Wyk, J.B., Erasmus, G.J., Baker, R.L. 2003. Genetic parameter estimates in Sabi sheep. *Livestock Production Science* 79, 17-28.
- Meyer, K., 2007. WOMBAT: A tool for mixed model analyses in quantitative genetics by Restricted Maximum Likelihood (REML). *Journal of Zhejiang University Science B* 11, 815-821.
- Miraei-Ashtiani, S.R., Seyedalian, S.A.R., Moradi Shahrabak, M., 2007. Variance components and heritabilities for body weight traits in Sangsari sheep, using univariate and multivariate animal models. *Small Ruminant Research* 73, 109-114.
- Mohammadi, K., Rashidi, A., Mokhtari, M.S., Beigi Nassiri, M.T., 2011. The estimation of (co)variance components for growth traits and Kleiber ratios in Zandi sheep. *Small Ruminant Research* 99, 116-121.
- Mohammadi, Y., Rashidi, A., Mokhtari, M.S., Esmailzadeh, A.K., 2010. Quantitative genetic analysis of growth traits and Kleiber ratios in Sanjabi sheep. *Small Ruminant Research* 93, 88-93.
- Mokhtari, M.S., Rashidi, A., Mohammadi, Y., 2008. Estimation of genetic parameters for post-weaning traits of Kermani sheep. *Small Ruminant Research* 80, 22-27.
- Ozcan, M., Ekiz, B., Yilmaz, A., Ceyhan, A., 2005. Genetic parameter estimates for lamb growth traits and greasy fleece weight at first shearing in Turkish Merino sheep. *Small Ruminant Research* 56, 215-222.
- Rashidi, A., Mokhtari, M.S., Safi Jahanshahi, A., Mohammad Abadi, M.R., 2008. Genetic parameter estimates of pre-weaning growth traits in Kermani sheep. *Small Ruminant Research* 74, 165-171.
- Riggio, V., Finocchiaro, R., Bishop, S.C., 2008. Genetic parameters for early lamb survival and growth in Scottish Blackface sheep. *Journal of Animal Science* 86, 1758-1764.
- Safari, E., Fogarty, N.M., Gilmour, A.R., 2005. A review of genetic parameter estimates for wool, growth, meat and reproduction traits in sheep. *Livestock Production Science* 92, 271-289.

Quantitative genetics of growth traits in sheep

- SAS Institute Inc., 2002. SAS User's Guide, Version 9.1, Statistics. Cary, NC.
- Scholtz, M.M., Roux, C.Z., 1988. The Kleiber ratio (growth rate/metabolic mass) as possible selection criteria in the selection of beef cattle. In: Proceedings of the 3rd World Congress on Sheep and Beef Cattle Breeding, Vol. 2, Paris, France, pp. 373–375.
- Shrestha, J.N.B., 2005. Conserving domestic animal diversity among composite populations. *Small Ruminant Research* 56, 3-20.
- Snyman, M.A., Erasmus, G.J., van Wyk, J.B., Olivier, J.J., 1995. Direct and maternal (co)variance components and heritability estimates for body weight at different ages and fleece traits in Afrino sheep. *Livestock Production Science* 44, 229–235.
- Vatankhah, M., Talebi, M.A., 2008. Heritability estimates and correlations between production and reproductive traits in Lori-Bakhtiari sheep. *South African Journal of Animal Science* 38, 110-118.
- Yazdi, M.H., Engstrom, G., Nasholm, A., Johansson, K., Jorjani, H., Liljedahl, L.E., 1997. Genetic parameters for lamb weight at different ages and wool production in Baluchi sheep. *Animal Science* 65, 247–255.
- Yilmaz, O., Denk, H., Bayram, D., 2007. Effects of lambing season, sex and birth type on growth performance in Norduz lambs. *Small Ruminant Research* 68, 336-339.
- Zamani, P., Mohammadi, H., 2008. Comparison of different models for estimation of genetic parameters of early growth traits in Mehraban sheep. *Journal of Animal Breeding and Genetics* 125, 29-34.

Communicating editor: Alex Safari