

Estimates of (co)variance components and genetic parameters for growth traits of Avikalin sheep

Leslie Leo L. Prince · Gopal R. Gowane ·
Ashish Chopra · Amrit L. Arora

Accepted: 10 February 2010 / Published online: 7 April 2010
© Springer Science+Business Media B.V. 2010

Abstract (Co)variance components and genetic parameters for various growth traits of Avikalin sheep maintained at Central Sheep and Wool Research Institute, Avikanagar, Rajasthan, India, were estimated by Restricted Maximum Likelihood, fitting six animal models with various combinations of direct and maternal effects. Records of 3,840 animals descended from 257 sires and 1,194 dams were taken for this study over a period of 32 years (1977–2008). Direct heritability estimates (from best model as per likelihood ratio test) for weight at birth, weaning, 6 and 12 months of age, and average daily gain from birth to weaning, weaning to 6 months, and 6 to 12 months were 0.28 ± 0.03 , 0.20 ± 0.03 , 0.28 ± 0.07 , 0.15 ± 0.04 , 0.21 ± 0.03 , 0.16 and 0.03 ± 0.03 , respectively. Maternal heritability for traits declined as animal grows older and it was not at all evident at adult age and for post-weaning daily gain. Maternal permanent environmental effect (c^2) declined significantly with advancement of age of animal. A small effect of c^2 on post-weaning weights was probably a carryover effect of pre-weaning maternal influence. A significant large negative genetic correlation was observed between direct and maternal genetic effects for all the traits, indicating antagonistic pleiotropy, which needs special care while formulating breeding plans. A fair rate of genetic progress seems possible in the flock by selection for all

traits, but direct and maternal genetic correlation needs to be taken in to consideration.

Keywords Genetic parameters · Heritability · Maternal effects · Avikalin sheep

Introduction

Crossbreeding program for sheep in India were primarily aimed at evolving sheep breeds of high genetic merit for various economic traits such as wool and mutton, so as to improve the socio-economic status of the rural poor and safeguard their livelihood security. Under this program, “Avikalin” a synthetic dual type (carpet wool and mutton) sheep was evolved at CSWRI, Avikanagar by stabilizing the crossbred population of Rambouillet and Malpura at 50% exotic inheritance. Since the time of evolving this strain, multi-trait selection of ram lambs and inter-se breeding was practiced for the genetic improvement of desirable traits, which were mainly body weight at market age, i.e., 6-month weight and first six monthly greasy fleece weight. Wool produced from Avikalin sheep is considered as the best for carpet industry and the growth potential of this breed is at par with the native sheep breeds viz. Malpura and Sonadi, specially raised for mutton production. Many of the published genetic parameter estimates on the Indian Sheep breeds were derived from the sire models that did not take in to account partitioning of the genetic variance in to the direct and maternal components. In the present study, an effort has been made to estimate the variance and covariance components due to additive and maternal effects in Avikalin sheep for growth traits by determining the most appropriate animal model.

L. L. L. Prince (✉) · G. R. Gowane · A. Chopra · A. L. Arora
Animal Genetics and Breeding Division,
Central Sheep and Wool Research Institute,
Avikanagar-304501, via-Jaipur,
Rajasthan, India
e-mail: drlleslie@gmail.com

Materials and methods

Data

Data available for the analysis were collected from the flock of Avikalin sheep maintained at Central Sheep and Wool Research Institute (CSWRI), Avikanagar situated at 75°28'E latitude and 26°17'N longitude at an altitude of 320 m above mean sea level. Different economic traits used for the analysis were birth weight (BWT), weaning weight (WWT), 6-month weight (6WT), 12-month weight (12WT), average daily gain from birth to weaning (ADG1), from weaning to 6 months (ADG2), and from 6- to 12-month age (ADG3). Characteristics of the data structure, number of sire and dam, least squares means, standard deviations, and coefficient of variation for respective traits are summarized in Table 1. Data spreads over the years 1977 to 2008, which were further divided into five periods [(1): up to 1984, (2): 1985–1990, (3): 1991–1996, (4): 1997–2002, (5): 2003–2008] with records on total of 3,840 lambs descended from 257 sires and 1,194 dams. All the animals in this flock were kept under semi-intensive management system. The flock was a closed type where 250 breeding females were maintained over the years. Male to female ratio for breeding was around 1:25. Regarding feeding, concentrate mixture was offered ad libitum to suckling lambs from 15 days age till weaning (90 days). After about 3 weeks of age, lambs were sent for grazing in morning and evening. During post-weaning period, in addition to 8–10 h grazing and dry fodder supplementation, 300 g concentrate mixture was provided.

Statistical methods

Data were first analyzed by least squares analysis of variance (SPSS 2005) to identify the fixed effects to be

included in the model. Statistical model for all the growth traits included fixed effects of period of birth (five levels), season of birth (two levels), sex of the lamb (two levels), and dam age class (four levels: less than 2.5 years; 2.5 to 4 years; 4 to 5.5 years; above 5.5 years). Ewe weight at lambing was taken as the covariate. For BWT all the effects were significant except season of birth; for WWT, 6WT, 12WT, and ADG1 all the effects were significant. For ADG2 all the effects except dam age class were significant and for ADG3 all the effects except season of birth and ewe weight at lambing were significant. Only significant effects ($P \leq 0.05$) were included in the models which were subsequently used for the genetic analysis. (Co)variance components were estimated by restricted maximum likelihood (REML) using a derivative-free algorithm fitting an animal model (DFREML, Meyer 2000). Convergence of the REML solutions was assumed when the variance of function values ($-2\log L$) in the simplex was less than 10^{-8} . To ensure that a global maximum is reached, analyses were restarted. When estimates did not change, convergence was confirmed. Univariate animal models were fitted to estimate (co) variance components for all the traits. Different models which accounts for the direct and maternal effects were constructed as follows:

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

$$y = X\beta + Z_a a + Z_m m + \varepsilon \text{ with Cov}(a_m, m_o) = 0 \quad (2)$$

$$y = X\beta + Z_a a + Z_m m + \varepsilon \text{ with Cov}(a_m, m_o) = A\sigma_{am} \quad (3)$$

Table 1 Characteristics of data structure for economic traits of Avikalin sheep

Trait	BWT	WWT	6WT	12WT	ADG1	ADG2	ADG3
No. of records	3,840	3,361	2,971	2,213	3,359	2,869	1,774
Sires with progeny records	257	253	262	233	253	241	298
Dams with progeny records	1,194	1,124	1,176	831	1,124	1,006	674
Grand sire with progeny	306	300	288	268	300	280	236
Grand dam with progeny	755	706	689	525	706	632	383
Trait weight LSM	3.02 kg	13.89 kg	20.15 kg	25.51 kg	120.65 g	73.58 g	38.46 g
SD	0.55 kg	2.98 kg	3.92 kg	4.29 kg	31.37 g	33.18 g	25.10 g
CV%	16.54	19.62	17.95	14.07	24.40	41.88	64.70
R ² %	26.10	22.80	21.60	33.00	19.60	21.30	12.40

BWT birth weight, WWT weaning weight, 6WT 6-month weight, 12WT 12-month weight, ADG1 average daily gain from birth to weaning, ADG2 average daily gain from weaning to 6 months, ADG3 average daily gain from 6 to 12 months

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_c\mathbf{c} + \boldsymbol{\varepsilon} \quad (4)$$

$$\begin{aligned} \mathbf{y} &= \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_m\mathbf{m} + \mathbf{Z}_c\mathbf{c} + \boldsymbol{\varepsilon} \text{ with Cov}(\mathbf{a}_m, \mathbf{m}_o) \\ &= 0 \end{aligned} \quad (5)$$

$$\begin{aligned} \mathbf{y} &= \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_m\mathbf{m} + \mathbf{Z}_c\mathbf{c} + \boldsymbol{\varepsilon} \text{ with Cov}(\mathbf{a}_m, \mathbf{m}_o) \\ &= \mathbf{A}\boldsymbol{\sigma}_{am} \end{aligned} \quad (6)$$

Where \mathbf{y} is the vector of records; $\boldsymbol{\beta}$, \mathbf{a} , \mathbf{m} , \mathbf{c} , and $\boldsymbol{\varepsilon}$ are vectors of fixed, direct additive genetic, maternal additive genetic, permanent environmental effects of the dam, and residual effects, respectively; with incidence matrices \mathbf{X} , \mathbf{Z}_a , \mathbf{Z}_m , and \mathbf{Z}_c that relate these effects to the records; \mathbf{A} is the numerator relationship matrix between animals; and $\boldsymbol{\sigma}_{am}$ is the covariance between additive direct and maternal genetic effects. Assumptions for variance (\mathbf{V}) and covariance (\mathbf{Cov}) matrices involving random effects were

$$\begin{aligned} \mathbf{V}(\mathbf{a}) &= \mathbf{A}\boldsymbol{\sigma}_a^2, \mathbf{V}(\mathbf{m}) = \mathbf{A}\boldsymbol{\sigma}_m^2, \mathbf{V}(\mathbf{c}) = \mathbf{I}\boldsymbol{\sigma}_c^2, \mathbf{V}(\boldsymbol{\varepsilon}) \\ &= \mathbf{I}\boldsymbol{\sigma}_\varepsilon^2, \text{ and } \mathbf{Cov}(\mathbf{a}, \mathbf{m}) = \mathbf{A}\boldsymbol{\sigma}_{am} \end{aligned}$$

Where \mathbf{I} is an identity matrix and $\boldsymbol{\sigma}_a^2$, $\boldsymbol{\sigma}_m^2$, $\boldsymbol{\sigma}_c^2$, and $\boldsymbol{\sigma}_\varepsilon^2$ are additive direct, additive maternal, maternal permanent environmental, and residual variances, respectively. Estimates of genetic parameters ($\boldsymbol{\sigma}_a^2$ = additive genetic variance; $\boldsymbol{\sigma}_m^2$ = maternal additive genetic variance; $\boldsymbol{\sigma}_{am}$ = genetic covariance between direct and maternal effect; $\boldsymbol{\sigma}_c^2$ = permanent environmental variance due to dam; $\boldsymbol{\sigma}_\varepsilon^2$ = error variance; $\boldsymbol{\sigma}_p^2$ = phenotypic variance; h^2 = direct heritability; m^2 = maternal heritability; r_{am} = direct-maternal genetic correlation; c^2 = the permanent environmental variance due to dam as a proportion of phenotypic variance) were obtained with DFREML (Meyer 2000). Maternal across year repeatability for ewe performance, ($t_m = (1/4)h^2 + m^2 + c^2 + mr_{am}h$) was calculated (Al-Shorepy 2001). The total heritability (h_T^2) was calculated using the formula $h_T^2 = (\boldsymbol{\sigma}_a^2 + 0.5\boldsymbol{\sigma}_m^2 + 1.5\boldsymbol{\sigma}_{am})/\boldsymbol{\sigma}_p^2$ to estimate the expected response to selection (Willham 1972).

The best model suited for each trait considering the likelihood ratio test (Meyer 1992) was chosen and used to study the genetic parameters. Significance of an effect was tested at $P < 0.05$ by comparing the differences in log likelihoods with values for a chi-square distribution with degrees of freedom equal to the difference in the number of (co)variance components fitted for the two models. The model with fewest random terms was chosen where log L values did not differ significantly.

Results and discussion

Least squares mean (LSM) along with the standard deviation (SD) and percent coefficient of variation for different traits under study are given in Table 1. The LSM \pm SE for various traits were BWT, 3.02 ± 0.008 kg; WWT, 13.89 ± 0.05 kg; 6WT, 20.15 ± 0.07 kg; 12WT, 25.51 ± 0.09 kg; ADG1, 120.65 ± 0.54 g; ADG2, 73.58 ± 0.62 g; and ADG3, 38.46 ± 0.60 g. The percent coefficient of variation ranged amid 14.07% to 19.62% from BWT to 12WT. It ranged from 24.40% to 64.70% for ADG1 to ADG3.

(Co)variance components and genetic parameter estimates derived by univariate analysis for various traits of Avikalin sheep are presented in Tables 2, 3, and 4. As per the likelihood ratio test, the best model for BWT was model-1 that included only direct additive genetic effect. For WWT, 6WT and 12WT, and ADG1 and ADG2, model-4 was the best model which included direct additive effect and permanent environmental effects of the dam. For ADG-3, model-1 was the best that included only direct genetic effect.

Pre-weaning weights

(Co)variance components along with the genetic parameters for BWT from six different models are given in Table 2. The model including only direct additive effect (model-1) was sufficient to explain the variation in the birth weight, as addition of maternal effects did not improve the likelihood than model-1. Additive direct heritability (h^2) for BWT was 0.28 ± 0.03 . Moderate estimate of direct heritability suggests further scope for improvement due to selection in the flock for higher birth weight. Our h^2 estimate for BWT was in accordance with the average weighted estimates of Zamani and Mohammadi (2008) in Mehraban sheep, Kushwaha et al. (2009) in Chokla sheep. Estimate of 0.168 was reported earlier for Avikalin sheep by Maroof et al. (2005). Low estimates than current study were earlier reported by Safari and Fogarty (2003); Mandal et al. (2006b); Behreini et al. (2007); Kariuki et al. (2010); and Gowane et al. (2010).

Comparison of maternal effects with literature is difficult due to differences in the model fitted. Maternal heritability (m^2) from model-2 was 0.25 ± 0.02 and estimate of permanent environmental maternal effect (c^2) from model-4 was 0.22 ± 0.02 . In more comprehensive model-5, we found $h^2 = 0.14 \pm 0.03$, $m^2 = 0.08 \pm 0.03$, and $c^2 = 0.16 \pm 0.03$; indicating that the maternal effect constitutes more of the maternal environment rather than maternal genes. Actual partitioning of the maternal variance in additive and permanent environment effect was practically difficult as earlier discussed by Mandal et al. (2006a). Notter and Hough (1997) suggested that partitioning of maternal

Table 2 Estimates of (co)variance components (kg^2) and genetic parameters for pre-weaning weights

Items ^a	Model-1	Model-2	Model-3	Model-4	Model-5	Model-6
TRAIT: BWT						
σ_a^2	0.07	0.03	0.05	0.04	0.04	0.05
σ_m^2	–	0.06	0.09	–	0.02	0.04
σ_{am}	–	–	–0.03	–	–	–0.03
σ_c^2	–	–	–	0.05	0.04	0.04
σ_e^2	0.17	0.15	0.14	0.15	0.15	0.14
σ_p^2	0.24	0.25	0.25	0.24	0.24	0.24
h^2	0.28 (0.03)	0.13 (0.03)	0.20 ^b	0.15 (0.03)	0.14 (0.03)	0.21 ^b
m^2	–	0.25 (0.02)	0.34 ^b	–	0.08(0.03)	0.15 ^b
r_{am}	–	–	–0.480	–	–	–0.57
c^2	–	–	–	0.22 (0.02)	0.16 (0.03)	0.16 ^b
h_T^2	0.28	0.26	0.18	0.15	0.18	0.13
t_m	0.07	0.28	0.26	0.26	0.27	0.26
log L	705.51	–144.63	–136.58	606.94	–129.06	78.02
TRAIT: WWT						
σ_a^2	1.55	1.51	3.73	1.50	1.50	3.71
σ_m^2	–	0.15	1.62	–	0.05	1.46
σ_{am}	–	–	–2.24	–	–	–2.18
σ_c^2	–	–	–	0.19	0.15	0.14
σ_e^2	5.88	5.79	4.48	5.74	5.74	4.44
σ_p^2	7.43	7.45	7.58	7.43	7.44	7.57
h^2	0.21 (0.03)	0.20 (0.04)	0.49 ^b	0.20 (0.03)	0.20 (0.03)	0.49 ^b
m^2	–	0.02 (0.01)	0.21 ^b	–	0.01 (0.01)	0.19 ^b
r_{am}	–	–	–0.91	–	–	–0.94
c^2	–	–	–	0.03 (0.02)	0.02 (0.02)	0.02 ^b
h_T^2	0.21	0.21	0.16	0.20	0.20	0.15
t_m	0.05	0.07	0.04	0.08	0.08	0.04
log L	–5,442.81	–5,707.02	–5,672.97	–5,410.67	–5,737.51	–5,703.57

Values in the parentheses are standard errors. Column in bold represents estimates from best model as per LRT

BWT birth weight, *WWT* weaning weight

^a σ_a^2 , σ_c^2 , σ_m^2 , σ_e^2 , and σ_p^2 are additive direct, maternal permanent environmental, maternal genetic, residual variance, and phenotypic variance, respectively, h^2 is heritability, c^2 is σ_c^2/σ_p^2 , t_m is maternal across year repeatability for ewe performance, h_T^2 is total heritability, *log L* is log likelihood for the model obtained from DFREML (Meyer 2000)

^b The approximation used to define standard errors of parameter estimates failed

effects into additive and permanent environmental components requires large amount of data with repeated records on individual ewes and presence of related ewes in the data. Even after meeting these requirements, results were inconsistent as per Al-Shorepy and Notter (1998). Similar picture is seen in the current data set too. The evidence for the maternal genetic effect for birth weight was not observed as such in the present analysis. Genetic correlation between direct and maternal effects was large and negative (–0.48 to –0.57). The estimates of repeatability of ewe performance (t_m) for birth weight were high in magnitude. The total heritability (h_T^2) ranged from 0.15 to 0.28 over different models. Estimates of h_T^2 and t_m were sensitive to

the model fitted. Moderate h_T^2 and t_m suggest scope of improvement in the trait through selection. The estimate for m^2 , c^2 , r_{am} , h_T^2 , and t_m were within the range of estimates presented in review by Safari et al. (2005) for various sheep breeds and by Mohammadi and Edriss (2007) in Mehraban sheep. Lower estimates of m^2 and c^2 were reported by Riggio et al. (2008) and Gowane et al. (2010).

Direct heritability estimates for WWT ranged from 0.20 to 0.49, depending on the model used. Estimate of m^2 for WWT in model-2 (0.019±0.01) was lower than the m^2 for BWT, indicating decline of maternal effect from birth to weaning. In model 3, inflated h^2 estimate were observed, probably due to very high negative covariance between

Table 3 Estimates of (co)variance components (kg^2) and genetic parameters for post-weaning weights

Items ^a	Model-1	Model-2	Model-3	Model-4	Model-5	Model-6
TRAIT: 6WT						
σ_a^2	3.79	3.66	7.87	3.65	3.64	7.86
σ_m^2	–	0.33	3.51	–	0.91	3.21
σ_{am}	–	–	–4.73	–	–	–4.62
σ_c^2	–	–	–	0.43	0.36	0.29
σ_e^2	9.26	9.10	6.57	8.97	8.97	6.48
σ_p^2	13.05	13.08	13.22	13.05	13.06	13.21
h^2	0.29 (0.35)	0.28 (0.04)	0.60 ^b	0.28 (0.08)	0.28 (0.04)	0.60 ^b
m^2	–	0.03 (0.02)	0.27 ^b	–	0.01 (0.02)	0.24 ^b
r_{am}	–	–	–0.90	–	–	–0.92
c^2	–	–	–	0.03 (0.01)	0.03 (0.03)	0.02 ^b
h_T^2	0.29	0.30	0.19	0.28	0.30	0.19
t_m	0.07	0.09	0.06	0.10	0.11	0.06
log L	–5,623.74	–5,821.73	–5,780.22	–5,452.98	–5,854.98	–5,813.78
TRAIT:12WT						
σ_a^2	2.02	1.92	4.31	1.91	1.91	4.28
σ_m^2	–	0.34	2.32	–	0.3E-3	1.86
σ_{am}	–	–	–2.76	–	–	–2.62
σ_c^2	–	–	–	0.52	0.52	0.48
σ_e^2	10.86	10.65	9.074	10.45	10.45	8.93
σ_p^2	12.88	12.95	12.95	12.89	12.89	12.94
h^2	0.16 (0.04)	0.15 (0.04)	0.33 ^b	0.15 (0.04)	0.15 ^b	0.33 ^b
m^2	–	0.03 (0.02)	0.18 ^b	–	0.00 ^b	0.14 ^b
r_{am}	–	–	–0.87	–	–	–0.93
c^2	–	–	–	0.04 (0.02)	0.04 ^b	0.04 ^b
h_T^2	0.16	0.17	0.10	0.15	0.15	0.10
t_m	0.04	0.07	0.05	0.08	0.08	0.06
log L	–4,283.55	–4,292.30	–4,277.15	–4,216.21	–4,357.35	–4,342.41

Values in the parentheses are standard errors. Column in bold represents the estimates from best model as per LRT

6WT 6-month weight, 12WT 12-month weight

^{a,b}As indicated for Table 2

direct and maternal effect, which resulted in -0.92 estimate of r_{am} . These models did not increase the likelihood anyway. Addition of permanent environmental effect in the model significantly increased the log likelihood of the model-4 over other models ($P < 0.01$). In this model 2.6% of the phenotypic variance was attributed to maternal permanent environmental effect.

Direct heritability for WWT from model-4 was 0.20 ± 0.03 , which was similar to the earlier estimates by Hanford et al. (2003) for Targhee sheep (0.22), weighted mean estimates by Safari et al. (2005) for various sheep breeds (0.18 to 0.21), Mandal et al. (2006b) in Muzaffarnagri sheep (0.21), and Zamani and Mohammadi (2008) for Mehraban sheep (0.18). Higher h^2 indicates further scope of genetic improvement in the sheep for weaning weight. Lower estimates than current study were obtained by

Maroof et al. (2005) for Avikalin sheep (0.077), Ekiz et al. (2004) for Turkish Merino sheep (0.06), and Riggio et al. (2008) for Scottish Blackface sheep (0.14). The c^2 estimate of 0.026 ± 0.017 in the present study indicates the decline of maternal effect from birth to weaning in Avikalin sheep. Estimates for c^2 within the range were reported by Safari et al. (2005) for various wool and dual-purpose breeds (0.06, 0.07), Hanford et al. (2003) for Targhee sheep (0.06). Ekiz et al. (2004) and Ozcan et al. (2005) both reported $c^2 = 0.08$ in Turkish Merino sheep. In the current study estimate of h_T^2 was 0.20, which was slightly lower than the report of Hanford et al (2003) for Targhee sheep (0.27).

For pre-weaning weights, r_{am} estimates were negative and higher which means improvement in one will result in reduction of another. Similar conclusion was observed for

Table 4 Estimates of (co)variance components (g^2) and genetic parameters for average daily gains (ADG1, ADG2, and ADG3)

Items ^a	Model-1	Model-2	Model-3	Model-4	Model-5	Model-6
TRAIT: ADG1 (birth to weaning)						
σ_a^2	188.48	186.88	434.96	186.29	183.23	433.87
σ_m^2	–	7.29	158.39	–	1.60	148.04
σ_{am}	–	–	–240.55	–	–	–236.36
σ_c^2	–	–	–	10.34	9.08	9.78
σ_e^2	678.29	673.65	530.16	670.47	67.38	527.22
σ_p^2	866.77	867.82	882.96	867.10	87.29	882.56
h^2	0.22 (0.03)	0.22 (0.03)	0.49 ^b	0.21 (0.03)	0.21 (0.03)	0.49 ^b
m^2	–	0.01 (0.02)	0.18 ^b	–	0.00 (0.00)	0.17 ^b
r_{am}	–	–	–0.92	–	–	–0.93
c^2	–	–	–	0.01 (0.02)	0.01 (0.00)	0.01 ^b
h_T^2	0.22	0.22	0.17	0.21	0.21	0.17
t_m	0.05	0.06	0.03	0.06	0.06	0.03
log L	–13,397.80	–13,673.11	–13,642.86	–13,332.05	–13,738.47	–13,708.21
TRAIT: ADG2 (weaning to 6 months)						
σ_a^2	154.40	154.22	388.95	154.41	154.18	177.74
σ_m^2	–	0.00	132.12	–	0.2E-4	0.59
σ_{am}	–	–	–226.69	–	–	–10.28
σ_c^2	–	–	–	0.9E-3	0.4E-4	0.5E-3
σ_e^2	795.39	795.53	662.98	795.38	795.56	781.84
σ_p^2	949.79	949.74	957.36	949.79	949.73	949.89
h^2	0.16 (0.03)	0.16 ^b	0.41 ^b	0.16 ^b	0.16 ^b	0.19 ^b
m^2	–	0.00 ^b	0.14 ^b	–	0.00 ^b	0.00 ^b
r_{am}	–	–	–1.00 ^b	–	–	–1.00
c^2	–	–	–	0.00 ^b	0.00 ^b	0.00 ^b
h_T^2	0.16	0.16	0.12	0.16	0.16	0.18
t_m	0.04	0.04	0.01	0.04	0.04	0.05
log L	–11,618.86	–11,801.16	–11,770.11	–11,583.93	–11,836.11	–11,832.35
TRAIT: ADG3 (6 to 12 months)						
σ_a^2	20.11	18.82	39.32	20.25	18.55	35.10
σ_m^2	–	5.10	24.53	–	5.18	21.40
σ_{am}	–	–	–31.05	–	–	–25.68
σ_c^2	–	–	–	0.00	0.00	0.8E-5
σ_e^2	599.20	60.47	584.42	599.06	595.27	586.44
σ_p^2	619.31	62.39	617.21	619.32	619.40	617.26
h^2	0.03 (0.03)	0.03 (0.03)	0.06 ^b	0.03 ^b	0.03 ^b	0.06 ^b
m^2	–	0.01 (0.02)	0.04 ^b	–	0.01 ^b	0.04 ^b
r_{am}	–	–	–1.00	–	–	–0.94
c^2	–	–	–	0.00 ^b	0.00 ^b	0.00 ^b
h_T^2	0.03	0.03	0.01	0.03	0.03	0.01
t_m	0.01	0.02	0.01	0.01	0.02	0.02
log L	–6,794.21	–6,927.39	–6,923.48	–6,801.10	–6,918.77	–6,915.30

ADG1 average daily gain from birth to weaning, ADG2 average daily gain from weaning to 6 months, ADG3 average daily gain from 6 to 12 months

Values in the parentheses are standard errors. Column in bold represents the estimates from best model as per LRT

^{a,b} As indicated for Table 2

Muzaffarnagri sheep (Mandal et al. 2006b). Antagonism between the effects of an individual's genes for growth and those of its dam for a maternal contribution may be due to natural selection for an intermediate optimum (Tosh and Kemp 1994). According to Roff (2002), antagonistic pleiotropy has long been considered a probable mechanism for the maintenance of genetic variance. Inclusion of sire \times year interaction in the model could lead to a reduction in the negative correlation estimate between the animal effects (Robinson 1996; Berweger et al. 1999). The data structure in the present study however did not include this interaction.

One more peculiar thing observed for pre-weaning traits was, in the presence of large negative estimate of r_{am} , direct and maternal estimates tend to be higher than in models that assume r_{am} to be zero. As noted by Notter and Hough (1997), estimates that do not involve r_{am} can be properly used for genetic prediction only if the user also accepts and incorporates the additive maternal covariance in to the prediction model.

Post-weaning weights

Estimates of (co)variance components calculated for the weights at 6 and 12 months of age are presented in Table 3. The direct heritability estimate from the best model (model-4) for post-weaning weights were 0.28 ± 0.07 at 6WT and 0.15 ± 0.04 for 12WT. Current estimates of h^2 agree well with the estimates by Safari et al. (2005) for various wool, meat, and dual-purpose breeds (0.30, 0.28, and 0.22, respectively) and Ozcan et al. (2005) for Turkish Merino sheep (0.25). Heritability estimate of 0.162 and 0.203 was reported earlier for Avikalın sheep by Maroof et al. (2005) for 6WT and 12WT, respectively. Evidence of maternal genetic variance for post-weaning weights was negligible when comparison of model-2, model-4 versus model-5 is made. As discussed earlier, partitioning of the total maternal effect in to its direct and permanent environmental components was difficult in advanced stages of life too. At 6WT, estimates of h^2 , m^2 , and c^2 from inclusive model-5 are 0.28 ± 0.04 , 0.007 ± 0.02 , and 0.028 ± 0.024 , respectively. At 12WT, model-5 yielded $h^2 = 0.15$, $m^2 = 0.0002$, and $c^2 = 0.04$. Addition of maternal genetic component or its covariance with direct genetic effect in the model did not increase likelihood and thus had no effect on goodness of fit. Maternal permanent environmental effect explained 3% and 4% of the total phenotypic variation in 6WT and 12WT. This is indicative of the fact that post-weaning has carryover maternal permanent environmental effects still as a source of variation. Impact of animal's own genotype for body weight at post-weaning stage is important than other effects, hence for genetic evaluation of post-weaning weights, maternal effects need not be considered. Reports where maternal effects were found to be declining with the

advancement of age were given by Mandal et al. (2006b) and Riggio et al. (2008).

Significant negative and high correlation between animal and maternal genetic effects was observed for post-weaning weights (-0.87 to -0.93) from models that included σ_{am} . This estimate matched with the reports by Ozcan et al. (2005) for Turkish Merino sheep and Mandal et al. (2006b) for Muzaffarnagri sheep, whereas most of the literature values for r_{am} at post-weaning weights are also negative but of low magnitude (Abegaz et al. 2002; Safari et al. 2005). In spite of the fact that maternal genetic variance tends to converge to zero as the age advances, high and negative r_{am} is suggestive that there is some hidden mechanism underlying phenotypic relation, which restricts genetic covariance at higher negative magnitude. Relation of animal and maternal genes would definitely have negative r_{am} at birth, for the reason that it has to maintain intermediate optimum at birth. The authors wish to advance the hypothesis that this relationship cannot change completely for growth at advanced age because the set of genes responsible for growth will be the same throughout the life, and thus the relationship it will have with the maternal genes at birth will also not change much except for the phenomenon of switch on or switch off of different genes as per requirement of the growth milieu. At birth, σ_{am} could express itself due to individuals own genotype's interaction with strong maternal effect, resulting in restricting the body size of lamb to avoid lambing problems. However, as animal grows older, the maternal effect fades (decline in m^2) significantly and individuals' own genes play major role in defining the phenotype. More expression of direct additive genes at later stage of life, dominating the σ_{am} , will result in independent growth pattern of the individual without interference of the high and negative r_{am} .

Estimates of t_m were comparatively low (0.10 to 0.08) for 6WT and 12WT. Our estimates were similar to reports of Mandal et al. (2006b); little higher estimates were reported earlier by Abegaz et al. (2002), Safari et al. (2005), and Kushwaha et al. (2009). Total heritability estimates were 0.28 and 0.15 from model-4 for 6WT and 12WT, respectively. Estimates were linked with the σ_{am} in models which included covariance giving lesser estimates. Our estimates were within the range of earlier estimates by Abegaz et al. (2002), Ozcan et al. (2005), and Safari et al. (2005). Result suggests scope of further genetic improvement in post-weaning traits.

Average daily gain

(Co)variance estimates for average daily gains are presented in Table 4. Based on logarithm of the likelihood function, model-4 was best for ADG1 and ADG2, whereas for ADG-3, model-1 was the best. Additive genetic heritability for

pre-weaning gain (ADG1) from most suitable model was 0.21 ± 0.03 . For ADG1, maternal effects had lesser role to play ($h^2 = 0.21 \pm 0.03$, $m^2 = 0.002 \pm 0.00$, $c^2 = 0.01 \pm 0.001$; estimates from model-5) for determining growth rate. Our estimates for h^2 were similar to estimates by Mohammadi and Edriss (2007) for Mehraban sheep but they obtained little higher maternal effects for pre-weaning growth rate. Genetic correlation of direct and maternal animal effects (r_{am}) was also high and negative (-0.92). This may also be due to the reasons discussed for pre-weaning weights. Total heritability estimates and t_m were robust for change of model, except models with σ_{am} . Model-4 gave estimates of $t_m = 0.06$ and $h_T^2 = 0.21$.

For post-weaning gain (ADG2 and ADG3), direct additive heritability (h^2) from the best model (model-4 for ADG2 and model-1 for ADG3) were 0.16 and 0.03, respectively, indicating reasonable scope of improvement in the trait through selection for ADG2, but not for ADG3. It is notable that for determining daily gain after 6-month age, genetic factors have lesser role to play, and growth rate is determined more by environmental factors. Similar result for h^2 estimate of ADG2 were reported by Safari et al. (2005) for weighted mean of different studies (0.15 ± 0.01 to 0.17 ± 0.01) for daily gain. For post-daily gain, Kariuki et al. (2010) reported h^2 estimate of 0.30 for ADG of 6 to 12 months. In our study, maternal variance was found to be fading as the animal grows older. Most inclusive model, without σ_{am} , reflects negligible evidence of maternal effect on these traits. Safari et al. (2005) reported lower estimate for maternal effects for daily gain ($m^2 = 0.05 \pm 0.01$, $c^2 = 0.05 \pm 0.01$) based on weighted mean of various studies. Similar to post-weaning weights, the r_{am} was found to be very high. In contrast to our study, Safari et al. (2005) reported very low estimate of r_{am} for daily gain (-0.02 ± 0.08), based on weighted mean of 18 studies. For improvement in daily gain up to 6 months only direct animal effects are important, whereas after 6 months even direct effect plays non-significant role giving leeway to environmental factors. This indicates that for harvesting more daily gain it is necessary to moderate the stress factors and insulate animals from majority of variance inducing factors.

Conclusion

Additive genetic variability for all the growth traits was moderate indicating further scope for genetic improvement through selection. Maternal heritability was evident only at early ages and it converged to zero at adult age. Small magnitude of permanent environment effects due to dam for all traits except (ADG2 and ADG3) was observed. Its evidence at later ages might be due to carryover effect of maternal care during weaning. Maternal effects need not be

considered for genetic evaluation of daily gain and post-weaning weights. Strong negative direct and maternal genetic correlation indicates the need to take this effect in to consideration while planning a breeding strategy.

Acknowledgments Authors acknowledge the contribution of Shri Ashok Prasad (T-4) for their help in data management. Contribution of all the investigators associated with the project till now is deeply acknowledged. Support provided by the Director, Central Sheep and Wool Research Institute for execution of the project is deeply acknowledged.

References

- Abegaz, S., Negussie, E., Duguma, G. and Rege, J.E.O., 2002. Genetic parameter estimates for growth traits in Horro sheep, *Journal of Animal Breeding and Genetics*, 119, 35–45
- Al-Shorepy, S.A., 2001. Estimates of genetic parameters for direct and maternal effects on birth weight of local sheep in United Arab Emirates, *Small Ruminant Research*, 39, 219–224
- Al-Shorepy, S.A. and Notter, D.R., 1998. Genetic parameters for lamb birth weight in spring and autumn lambing, *Animal Science*, 67, 327–332
- Behreini, B.M.R., Shahroudi, F.E., VanVleck, L.D., 2007. Estimates of genetic parameters for growth traits in Kermani sheep, *Journal of Animal Breeding and Genetics*, 124:296–301
- Berweger, B. M., Moll, J. and Kunzi, N., 1999. Comparison of models to estimate maternal effects for weaning weight of Swiss Angus cattle fitting a sire-herd interaction as an additional random effect, *Livestock Production Science*, 60, 203–208
- Ekiz, B., Ozcan, M., Yilmaz, A. and Ceyhan, A., 2004. Estimates of genetic parameters for direct and maternal effects with six different models on birth and weaning weights of Turkish Merino lambs, *Turkish Journal of Veterinary and Animal Science*, 28, 383–389
- Gowane, G.R., Chopra, A., Prince, L.L.L., Paswan, C. and Arora, A.L., 2010. Estimates of (co)variance components and genetic parameters for body weights and first greasy fleece weight in Bharat Merino sheep, *Animal*, 4(3):425–431
- Hanford, K.J., Van Vleck, L.D. and Snowden, G.D., 2003. Estimates of genetic parameters and genetic change for reproduction, weight, and wool characteristics of Targhee sheep, *Journal of Animal Science* 81, 630–640
- Kariuki, C.M., Ilatsia, E.D., Kosgey, I.S. and Kahi, A.K. (2010) Direct and maternal (co)variance components, genetic parameters and annual trends for growth traits in Dorper sheep in semi-arid Kenya. *Tropical Animal Health and Production* 42:473–481
- Kushwaha, B.P., Mandal, A., Arora, A.L., Kumar, R., Kumar, S. and Notter, D.R., 2009. Direct and maternal (co)variance components and heritability estimates for body weights in Chokla sheep, *Journal of Animal Breeding and Genetics*, 126, 278–287
- Mandal, A., Naser, F.W.C., Rout, P.K., Roy, R. and Notter, D.R., 2006a. Estimation of direct and maternal (co)variance components for Preweaning growth traits in Muzaffarnagri sheep, *Livestock Science*, 99, 79–89
- Mandal, A., Naser, F.W.C., Rout, P.K., Roy, R. and Notter, D.R., 2006b. Genetic parameters for direct and maternal effects on body weights of Muzaffarnagri sheep, *Animal Science*, 82, 133–140
- Maroof, A., Singh, C. V., Sushil Kumar and Arora, A. L., 2005. Comparison of different methods of heritability estimates for body weights and wool yield traits in Avikalin crossbred sheep, *Indian Journal of Small Ruminants*, 11, 121–126

- Meyer, K., 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle, *Livestock Production Science*, 31, 179–204
- Meyer, K., 2000. DFREML programs to estimate variance components by restricted maximum likelihood using derivative free algorithm-user notes
- Mohammadi, H. and Edriss, M.A., 2007. Genetic parameters of early growth traits in Mehraban breed of sheep, *Pakistan Journal of Biological Sciences*, 10, 373–377
- Notter, D.R. and Hough, J.D., 1997. Genetic parameter estimates for growth and fleece characteristics in Targhee sheep, *Journal of Animal Science*, 75, 1729–1737
- Ozcan, M., Ekiz, B., Yilmaz, A and 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
- Riggio, V., Finocchiaro, R. and Bishop, S.C., 2008. Genetic parameters for early lamb survival and growth in Scottish Blackface sheep, *Journal of Animal Sciences*, 86, 1758–1764
- Robinson, D. L., 1996. Estimation and interpretation of direct and maternal genetic parameters for weights of Australian Angus cattle, *Livestock Production Science*, 45,1–11
- Roff, D. A., 2002. *Life History Evolution*, Sinauer Associates, Sunderland, MA.
- Safari, A. and Fogarty, N.M., 2003. Genetic parameters for sheep production traits: estimates from the literature, *Technical Bulletin 49*. New South Wales Agriculture, Orange, Australia.
- Safari, E., Fogarty, N.M. and 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
- SPSS 2005. *SPSS for Windows, Brief Guide, Version 14.0*, SPSS Inc. Chicago, IL.
- Tosh, J. and Kemp, R.A., 1994. Estimation of variance components for lamb weights in three sheep populations, *Journal of Animal Science*, 72, 1184–1190
- Willham, R.L., 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals, *Journal of Animal Science*, 35, 1288–1293
- Zamani, P. and Mohammadi, H., 2008. Comparison of different models for estimation of genetic parameters of early growth traits in the Mehraban sheep, *Journal of Animal Breeding and Genetics*, 125, 29–34