ORIGINAL ARTICLE

Direct and maternal (co)variance components and heritability estimates for body weights in Chokla sheep

B.P. Kushwaha[1], A. Mandal[2], A.L. Arora[3], R. Kumar[4], S. Kumar[3] & D.R. Notter[5]

1 Animal Breeding, Network Project on Bhadawari Buffaloes, Indian Grassland and Fodder Research Institute, Jhansi, Uttar Pradesh, India
2 Genetics and Breeding Division, Central Institute for Research on Goats, Makhdoom, Mathura, Uttar Pradesh, India
3 Animal Genetics and Breeding Division, Central Sheep & Wool Research Institute, Avikanagar, Rajasthan, India
4 Animal Breeding, National Bureau of Fish Genetic Resources, Dilkusha, Lucknow, Uttar Pradesh, India
5 Department of Animal and Poultry Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA

Summary

Estimates of (co)variance components were obtained for weights at birth, weaning and 6, 9 and 12 months of age in Chokla sheep maintained at the Central Sheep and Wool Research Institute, Avikanagar, Rajasthan, India, over a period of 21 years (1980–2000). Records of 2030 lambs descended from 150 rams and 616 ewes were used in the study. Analyses were carried out by restricted maximum likelihood (REML) fitting an animal model and ignoring or including maternal genetic or permanent environmental effects. Six different animal models were fitted for all traits. The best model was chosen after testing the improvement of the log-likelihood values. Direct heritability estimates were inflated substantially for all traits when maternal effects were ignored. Heritability estimates for weight at birth, weaning and 6, 9 and 12 months of age were 0.20, 0.18, 0.16, 0.22 and 0.23, respectively in the best models. Additive maternal and maternal permanent environmental effects were both significant at birth, accounting for 9% and 12% of phenotypic variance, respectively, but the source of maternal effects (additive versus permanent environmental) at later ages could not be clearly identified. The estimated repeatabilities across years of ewe effects on lamb body weights were 0.26, 0.14, 0.12, 0.13, and 0.15 at birth, weaning, 6, 9 and 12 months of age, respectively. These results indicate that modest rates of genetic progress are possible for all weights.

Introduction

The sheep population in India is estimated to be about 61.5 million (2003 census). About 17% of the Indian sheep population is found in Rajasthan (2003 census), which is one of the major sheep-rearing states in India. The Chokla sheep produce fine carpet wool and are found in arid and semi-arid regions of Rajasthan. The animals are hardy and well adapted

to the migratory production system that is common in the region. Animals of the characteristic Chokla type are generally found in Churu and Sikar districts, as well as in the Jhunjhunu district and bordering areas of the Bikaner, Jaipur and Nagaur districts of Rajasthan. The Chokla sheep are sometimes referred to as Rajasthani Merino. Wool produced by this breed is heterogeneous in quality, but finer than the wool of any other carpet

wool-producing sheep breed in India, with spinning counts (i.e. the number of hanks of yarn that can be spun from one pound of wool, which is used to grade the wool according to fineness) ranging from 54s to 60s, and hence is well suited for carpet manufacturing. The luster of Chokla wool is comparable with that of New Zealand wools (Parthasarthy & Kushwaha 1996). Characteristics of the breed, population numbers and distribution and production levels have been described by Kushwaha *et al.* (1997).

The growth potential of the lambs is one of the most economically important traits in sheep production. Development of effective programmes for genetic evaluation and improvement of lamb growth requires knowledge of the genetic parameters for these economically important traits. Robison (1981) noted that traits recorded in early life are likely to be affected by maternal ability. Näsholm & Danell (1994) observed that when maternal genetic effects are important, but not considered in the statistical model, heritability estimates are biased upward and the realized efficiency of selection is reduced when compared with the expected. When growth traits are included in the breeding goal, both direct and maternal components should be considered in achieving optimum progress. Several studies have attributed most of the variation in lamb weights to maternal effects (Safari *et al.* 2005; Mandal *et al.* 2006a; b; Behzadi Bahreini *et al.* 2007; Rashidi *et al.* 2008). Genetic and environmental relationships between direct and maternal effects for growth have often found to be negative in various sheep breeds (Notter 1998; Ligda *et al.* 2000). However, positive relationships have also been reported (Näsholm & Danell 1996; Yazdi *et al.* 1997; Assan *et al.* 2002). Robison (1981) postulated that understanding of the relationship between direct and maternal effects would facilitate formulation of optimum breeding programmes and improve selection efficiency. Hence, accurate estimates for the maternal genetic effects and their relationships with direct effects are required to maximize genetic gain, and the availability of restricted maximum likelihood (REML) algorithms for fitting animal models has simplified estimation of (co)variance components owing to maternal effects (Meyer 1997).

Most reported heritabilities for growth traits of sheep breeds in South Asia are based on ratios of variance components estimated by the paternal half-sib method, without consideration of maternal effects. Direct and maternal effects on body weights have been reported for Muzaffarnagari sheep (Mandal *et al.* 2006a,b), but are not available for other Indian breeds. Therefore, the present study was conducted to estimate variance and covariance components owing to direct and maternal genetic effects and maternal permanent environmental effects on body weights in Chokla sheep.

Materials and methods

Animals and data

Data were collected on Chokla sheep maintained at the Central Sheep and Wool Research Institute (CSWRI), Avikanagar, Rajasthan, India, under the All-India Coordinated Research Project (AICRP) on Sheep Improvement (renamed in 1990 as the Network Project on Sheep Improvement) over a period of 21 years (1980–2000). The institute is located 320 m above sea level at 26°17′N latitude and 75°28′E longitude in western India. The climate at the location is hot semi-arid. The maximum temperature averages 44.8°C in June and the minimum temperature averages 3.3°C in January. The average annual precipitation is 673 mm. The animals were raised under a semi-intensive feeding system. Animals were grazed for 10–12 h per day on natural pasture with supplementation of some amount of concentrate depending upon the productive status and age of the animals. Normally, a rotational grazing system was followed. During lean months of April through July, the animals were supplemented with conserved dry fodder of cenchrus (*Censhrus setigerus*), cowpea (*Vigna unguiculata*), pala leaves (*Zizypus nummularia*) and khejri (*Prosopis cineraria*) leaves. All animals were housed in pens at night. Ewes and rams were herded and housed separately except during the breeding season. More than 80% of the ewes were bred in the main autumn season (August and September), with the remainder bred in spring (March and April). Controlled single-sire mating was generally practiced, with ewes bred for the first time at 14–18 months of age. During the breeding season, ewes in oestrus were detected using a teaser ram in morning and evening. Ewes in heat were mated to the selected sires in the morning. One breeding ram was normally allowed to mate 25–30 ewes. Breeding rams were generally used for 2 years. The litter size of this breed is normally only one; twin births are very rare.

Each lamb was weighed at birth, identified by a metal ear tag and suckled its mother until weaning at 90 days of age. Animals were sheared twice a year, in March or April and in September or

October. The lambs were regularly drenched and dipped to control internal and external parasites, respectively, and animals were vaccinated against peste de petit ruminants (PPR), enterotoxaemia and foot-and-mouth disease. The data included records of 2030 lambs sired by 150 rams and out of 616 dams and born between 1980 and 2000. Traits analysed were birth weight, weaning weight and post-weaning weights at 6, 9 and 12 months of age. Means and SD of measured variables are summarized in Table 1.

Statistical analyses

(Co)variance components for direct and maternal genetic effects were estimated in single-trait animal model for body weights utilizing the DFREML program (Meyer 2000). Data were first analysed by least-squares analysis of variance (Harvey 1990) considering fixed effects of birth year, season of birth, parity of dam and sex of lambs in order to identify the fixed effects to be included in the final model. Lambs were born from 1980 through 2000 with 33 to 177 lambs born in each year. Birth season discriminated between lambs born in autumn (n = 1713) and spring (n = 317). Parity of the dam ranged from 1 to 6 with 675, 494, 366, 248, 153 and 94 lambs produced at parity 1, 2, 3, 4, 5 and 6 or above, respectively. Male (n = 1008) and female (n = 1022) kids were equally represented. All these effects were significant (p < 0.05) for all weights and hence were retained in the final model.

Six single-trait animal models incorporating various combinations of maternal genetic and permanent environmental effects were used to estimate genetic parameters for each trait:

$$y = Xb + Z_a a + e \tag{1}$$

$$y = Xb + Z_a a + Z_c c + e \tag{2}$$

$$y = Xb + Z_a a + Z_m m + e \text{ with } \mathrm{Cov}(a, m) = 0 \tag{3}$$

$$y = Xb + Z_a a + Z_m m + e \text{ with } \mathrm{Cov}(a, m) = A\sigma_{am} \tag{4}$$

$$y = Xb + Z_a a + Z_m m + Z_c c + e \text{ with } \mathrm{Cov}(a, m) = 0 \tag{5}$$

$$y = Xb + Z_a a + Z_m m + Z_c c + e \text{ with } \mathrm{Cov}(a, m) = A\sigma_{am} \tag{6}$$

where y is a vector of observations for each trait; b, a, m, c and e are vectors of fixed effects (birth year, season of birth, parity of dam and sex of lambs), direct additive genetic effects, maternal additive genetic effects, permanent environmental effects of dam and the residual effects, respectively; X, Z_a, Z_m, Z_c are the incidence matrices of fixed effects, direct additive genetic effects, maternal genetic effects and permanent environmental effect of the dam; A is the numerator relationship matrix between animals; and

Table 1 Characteristics of data structure for growth traits of Chokla sheep

Item		Weight at:				
		Birth	Weaning (3 months)	6 months	9 months	12 months
No. of records		2030	1688	1470	1260	1040
No. of animals in the pedigree		2307	1973	1760	1561	1338
No. of sires[a]	(i)	150	149	142	137	131
	(ii)	116	113	103	96	84
	(iii)	1320	1102	920	801	603
	(iv)	12.29	10.48	9.70	8.80	7.63
No. of dams[a]	(i)	616	552	520	473	422
	(ii)	439	385	360	311	272
	(iii)	1298	1028	880	686	526
	(iv)	3.18	2.91	2.66	2.47	2.23
	(v)	317	293	274	248	213
Average weight (kg)		2.72	11.64	16.82	18.07	21.26
SD (kg)		0.53	3.01	3.35	3.54	4.02

[a](i) With progeny in data; (ii) with own record as well; (iii) number of sire-offspring record pairs (for sire) and dam-offspring record pairs (for dam); (iv) average number of progeny per sire (dam); (v) no. of dams, themselves recorded and with grand-offspring with records.

σ_{am} is the covariance between additive direct and maternal genetic effects. The (co)variance structure for the model was:

$$V(a) = A\sigma_a^2, V(m) = A\sigma_m^2, V(c) = I_P\sigma_c^2,$$
$$V(e) = I_R\sigma_c^2 \quad \text{and} \quad \text{Cov}(a, m) = A\sigma_{am}$$

where I_P and I_R are identity matrices with orders equal to the number of dams and the number of lambs, respectively and σ_a^2, σ_m^2, σ_c^2 and σ_e^2 are direct additive genetic variance, maternal additive genetic variance, maternal permanent environmental variance and residual variance, respectively. Convergence of REML solutions was assumed when variance in the log of the likelihood function among rounds of iterations was less than 10^{-8}. The analyses were restarted for additional rounds of iterations using results from the previous round as starting values to ensure that a global maximum was reached. When estimates did not change, convergence was confirmed. Estimates of heritability (h^2), maternal heritability (m^2) and permanent maternal environmental effects (c^2) were calculated as ratios of estimates of σ_a^2, σ_m^2 and σ_c^2, respectively, to the phenotypic variance (σ_p^2). The direct maternal correlation (r_{am}) was computed as the ratio of the estimates of direct maternal covariance (σ_{am}) to the product of the square roots of estimates of σ_a^2 and σ_m^2. SE were calculated for the estimated parameters as a part of the DFREML program (Meyer 2000). The total maternal effect, $t_m = \frac{1}{4}h^2 + m^2 + c^2 + m r_{am} h$ was calculated to estimate repeatability of ewe performance. The heritability of the total genetic component was estimated (Willham 1972) as $h_t^2 = h^2 + 0.5m^2 + 1.5 m r_{am} h$, and predicts the expected response to phenotypic selection.

Log-likelihood values (log L) for different models were compared using the test statistic $D = 2(\log L_f - \log L_s)$ where log L_f is log L for a more complete model and log L_s is log L for a simpler model. A chi-square distribution with number of degrees of freedom equal to the difference in number of parameters (random effects) fit for the two models was used to determine the associated significance level. Level of significance was set at $p < 0.05$. Comparisons generally involved progressively more complex models that differed by only one degree of freedom.

Results and discussion

Number of observations, phenotypic means and SD for body weights of Chokla sheep at birth, weaning, and 6, 9 and 12 months of age are shown in Table 1.

Coefficients of variation for body weights ranged from 18.9% to 25.9% and were within the range of reported values for other sheep breeds (Al-Shorepy & Notter 1998; Ligda *et al.* 2000; Matika *et al.* 2003; Mandal *et al.* 2006b; Behzadi Bahreini *et al.* 2007).

Birth weight

Estimates of (co)variance components and genetic parameters for birth weight and likelihood values for each of the six models are summarized in Table 2. Model 1, which ignored maternal effects, overestimated direct additive genetic effects compared with the other models. Introducing either a permanent environmental maternal effect (model 2) or a maternal additive effect (model 3) decreased the estimate of additive heritability by approximately one half. Models 2 and 3 yielded estimates of c^2 and m^2 that explained 19% and 20% of phenotypic variance, respectively. Model 5, which included both additive maternal and maternal permanent environmental effects was clearly superior to model 3 ($p < 0.05$) and tended to also be superior to model 2 ($p < 0.10$). The estimate of c^2 from model 5 was approximately one-third larger than the estimate of m^2. Models 4 and 6 also included the direct maternal additive covariance but did not significantly improve goodness of fit. The estimate of the direct maternal additive correlation was only –0.11. Hence, model 5, which included both additive maternal and maternal permanent environmental effects, was the most appropriate model to describe birth weight.

The estimate of direct heritability of birth weight of 0.20 from model 5 was both similar to the average value from the literature for other wool breeds summarized by Safari *et al.* (2005) and well within the range of values estimated by other workers (Ligda *et al.* 2000; Matika *et al.* 2003; Maxa *et al.* 2007). The direct heritability estimate of 0.31 reported by Kumar *et al.* (2005) for birth weight in this breed using model 1 was similar to the estimate of 0.39 from model 1 in the present study. These model 1 estimates of h^2 are inflated by failure to properly account for maternal effects and overestimate the potential for improvement of additive breeding values for birth weight in this population. Heritability estimates of Solomon *et al.* (2007)) and Miraei-Ashtiani *et al.* (2007) for birth weight in other sheep breeds were higher than those obtained in the present study, but lower estimates were reported by Boujenane & Kansari (2002) in Timahdite sheep (0.05), Ekiz *et al.* (2004) in Turkish Merino (0.11), Mandal *et al.* (2006a,b) in Muzaffarnagari sheep

Table 2 Estimates of variance components and genetic parameters for birth weight of Chokla sheep

Item[a]	Model 1	Model 2	Model 3	Model 4	Model 5[b]	Model 6
σ^2_a	0.091	0.053	0.044	0.048	**0.046**	0.049
σ^2_m	–	–	0.046	0.050	**0.020**	0.022
σ_{am}	–	–	–	–0.005	–	–0.003
σ^2_c	–	0.042	–	–	**0.026**	0.026
σ^2_e	0.141	0.131	0.140	0.138	**0.135**	0.133
σ^2_p	0.232	0.227	0.231	0.231	**0.227**	0.227
h^2	0.39	0.23	0.19	0.21	**0.20 (0.05)**	0.22
m^2	–	–	0.20	0.22	**0.09(0.04)**	0.09
r_{am}	–	–	–	–0.11	–	–0.11
c^2	–	0.19	–	–	**0.12 (0.04)**	0.12
h^2_t	0.39	0.23	0.29	0.28	**0.25**	0.24
t_m	0.10	0.25	0.25	0.25	**0.26**	0.25
log L	–34.41	–3.05	–4.66	–4.53	**–0.08**	0

[a]σ^2_a is the direct additive genetic variance; σ^2_m is the maternal additive genetic variance; σ_{am} is the additive direct maternal genetic covariance; σ^2_c is the maternal permanent environmental variance; σ^2_e is the environmental variance; σ^2_p is the phenotypic variance; h^2 is the heritability; m^2 is the maternal heritability; r_{am} is the additive direct maternal genetic correlation; $c^2 = \sigma^2_c/\sigma^2_p$; h^2_t is the total heritability; t_m is the repeatability of the ewe performance and log L is the log-likelihood expressed as a deviation from the model with highest likelihood.
[b]The model in bold represents the most appropriate model. Values in parentheses are SE of estimates from this model.

(0.08), Behzadi Bahreini *et al.* (2007) in Kermani sheep (0.10) and Rashidi *et al.* (2008) in Kermani sheep (0.04).

The maternal heritability estimate for birth weight (0.09) was lower than the average of the literature values (Safari *et al.* 2005) but similar to estimates reported by Matika *et al.* (2003) and Ekiz *et al.* (2004). Mandal *et al.* (2006a,b) also obtained low estimates for additive maternal heritability of birth weight (0.07–0.08) from model 5 in Muzaffarnagari sheep. However, estimates of Behzadi Bahreini *et al.* (2007), Maxa *et al.* (2007) and Rashidi *et al.* (2008) for maternal heritability of birth weight in different sheep breeds were higher than those obtained in the present study. The estimate of the permanent environmental maternal effect for birth weight (0.12) was in accord with the results of several studies (Safari *et al.* 2005; Mandal *et al.* 2006a; b). However, other authors (Ligda *et al.* 2000; Ekiz *et al.* 2004) reported higher estimates of permanent environment effects.

The estimate of 0.25 for total heritability (h^2_t) for birth weight (Table 2) was substantial, suggesting that mass selection would be effective in improving this trait. Mandal *et al.* (2006b) calculated the total heritability and repeatability of ewe performance for birth weight from published estimates of h^2, m^2, c^2

and r_{am} from various studies where h^2_t and t_m were not explicitly calculated. With regard to those published estimates, the total heritability for birth weight observed in this study was comparable with the results of several studies (Bromley *et al.* 2000; Neser *et al.* 2001; Safari *et al.* 2005), although higher estimates of total heritability were obtained by Assan *et al.* (2002), Matika *et al.* (2003) and Behzadi Bahreini *et al.* (2007) in different breeds of sheep. Estimates reported by Boujenane & Kansari (2002) in Timahdite sheep (0.03), Ekiz *et al.* (2004) in Turkish Merino sheep (0.08) and Mandal *et al.* (2006a) in Muzaffarnagari sheep (0.12) were lower than those observed in our study.

Estimates of the repeatability of ewe performance are normally much less variable that the component estimates of m^2 and c^2. Our maternal repeatability estimates for birth weight (Table 2) were comparable with the values reported by Mandal *et al.* (2006b) except for that of Boujenane & Kansari (2002) ($t_m = 0.03$). Estimates of t_m for birth weight were essentially the same for all models (Table 2), suggesting that the repeatability of ewe performance was estimated consistently across the different maternal effects models.

Weaning weight

(Co)variance components and genetic parameter estimates for weaning weight are presented in Table 3. Estimates of direct heritability ranged from 0.18 to 0.28 depending on the model used. Inclusion of either a permanent environmental maternal effect (model 2) or a maternal additive effect (model 3) produced a significant improvement in likelihood compared with model 1. However, the inclusion of both additive and permanent environmental maternal effects in model 5 did not significantly improve the likelihood compared with either model 2 or model 3. Inclusion of the direct maternal covariance in models 4 and 6 yielded estimates for σ_{am} ranged from –0.25 to –0.30 with corresponding estimates of r_{am} of –0.27 to –0.29, but did not produce significant improvements in likelihoods. In comparison with model 1, the estimate of t_m was approximately doubled in models that included various combinations of maternal effects, and the heritability estimate was reduced by 21–36%.

The direct heritability estimate (0.18 from model 3) for weaning weight in this study was in accord with the average value of 0.21 reported by Safari *et al.* (2005) from various wool sheep breeds. Behzadi Bahreini *et al.* (2007) obtained a similar direct

Table 3 Estimates of variance components and genetic parameters for weaning weight of Chokla sheep

Item[a]	Model 1	Model 2	Model 3[b]	Model 4	Model 5	Model 6
σ^2_a	1.800	1.428	**1.123**	1.498	1.158	1.476
σ^2_m	–	–	**0.541**	0.733	0.402	0.562
σ_{am}	–	–	–	–0.300	–	–0.248
σ^2_c	–	0.467	–	–	0.174	0.168
σ^2_e	4.599	4.449	**4.661**	4.429	4.587	4.393
σ^2_p	6.399	6.344	**6.325**	6.361	6.322	6.352
h^2	0.28	0.22	**0.18 (0.06)**	0.24	0.18	0.23
m^2	–	–	**0.08 (0.03)**	0.11	0.06	0.09
r_{am}	–	–	–	–0.29	–	–0.27
c^2	–	0.07	–	–	0.03	0.03
h^2_t	0.28	0.22	**0.18**	0.24	0.18	0.23
t_m	0.07	0.13	**0.13**	0.12	0.14	0.14
log L	–6.47	–2.00	**–0.46**	–0.27	–0.14	0

[a]σ^2_a is the direct additive genetic variance; σ^2_m is the maternal additive genetic variance; σ_{am} is the additive direct maternal genetic covariance; σ^2_c is the maternal permanent environmental variance; σ^2_e is the environmental variance; σ^2_p is the phenotypic variance; h^2 is the heritability; m^2 is the maternal heritability; r_{am} is the additive direct maternal genetic correlation; $c^2 = \sigma^2_c/\sigma^2_p$; h^2_t is the total heritability; t_m is the repeatability of the ewe performance and log L is the log-likelihood expressed as a deviation from the model with highest likelihood.
[b]The model in bold represents the most appropriate model. Values in parentheses are SE of estimates from this model.

heritability estimate (0.22 from model 3) in Kermani sheep. A larger paternal half-sib estimate of heritability for weaning weight (0.24) was reported by Kushwaha *et al.* (1996) in Chokla sheep, but similar heritability estimates (0.20–0.22) were obtained in this breed by Kumar *et al.* (2005) from univariate and multivariate analyses using a simple animal model. However, much higher heritability estimates for weaning weight were reported by El Fadili *et al.* (2000) in Timahdit sheep (0.50), Assan *et al.* (2002) in Sabi sheep (0.38) and Rashidi *et al.* (2008) in Kermani sheep (0.27). Vatankhah & Talebi (2008) reported a lower direct heritability estimate (0.11) than that obtained in our study.

The estimate of the permanent environmental maternal effect (c^2) from this analysis ranged from 0.03 to 0.07 across models and was similar to the average value of 0.06 summarized by Safari *et al.* (2005) for various wool breeds. However, a slightly higher estimate ($c^2 = 0.13$) was reported by Rashidi *et al.* (2008) in Kermani sheep. The maternal heritability for weaning weight in this study (0.06–0.11) was likewise within the range of published values (Larsgard & Olesen 1998; Hanford *et al.* 2003; Ekiz *et al.* 2004; Ozcan *et al.* 2005; Mandal *et al.* 2006b; Behzadi Bahreini *et al.* 2007). A decline in the

relative importance of maternal effects from birth to weaning was also observed by Snyman *et al.* (1995), Näsholm & Danell (1996), Yazdi *et al.* (1997), El Fadili *et al.* (2000), Safari *et al.* (2005) and Mandal *et al.* (2006b).

Estimated correlations between additive direct and maternal effects for weaning weight (Table 3) in different models were not significant but of reasonable magnitude (–0.25 to –0.29), in contrast with the very large negative estimates of this correlation reported in a number of other studies (María *et al.* 1993; Notter 1998; El Fadili *et al.* 2000; Ozcan *et al.* 2005; Mandal *et al.* 2006b).

Estimates of total heritability (h^2_t) for weaning weight in the current study (0.18–0.22) were comparable with the published estimates in other sheep breeds (Larsgard & Olesen 1998; Notter 1998; Hanford *et al.* 2003). The estimate of maternal repeatability (t_m) of 0.13–0.14 was comparable with estimates reported by Ekiz *et al.* (2004) and Mandal *et al.* (2006b) but larger than the estimate of 0.04 reported by El Fadili *et al.* (2000) for Timahdit sheep.

Postweaning weights

Evidence for the importance of maternal effects on weights at 6, 9 and 12 months of age was equivocal. Heritability estimates from model 1, which considered only additive direct effects were 0.22, 0.31 and 0.32 at 6, 9 and 12 months, respectively (Table 4). Model 5, which included both additive and permanent environmental effects, did not produce a significant improvement in likelihood when compared with models 1 with 2 additional degrees of freedom (p < 0.25). However, when models containing a single maternal effect (models 2 and 3) were compared with Model 1 with only one degree of freedom, model 2 was the best-fitting model at 6 months ($h^2 = 0.16$, $c^2 = 0.08$, p < 0.10) and model 3 was the best-fitting model at 9 months ($h^2 = 0.22$, $m^2 = 0.07$, p = 0.10) and 12 months ($h^2 = 0.23$, $m^2 = 0.08$, p < 0.10). Estimates of t_m were consistent across models 2, 3 and 5 (0.10–0.11 at 6 months, 0.12–0.13 at 9 months and 0.14–0.15 at 12 months) and were 50–100% larger than the estimates of $t_m = \frac{1}{4}h^2$ associated with additive effects alone from model 1. Addition of the additive direct maternal covariance (results not shown) led to essentially no improvement in likelihood and in some cases produced unreasonable results (e.g. $r_{am} = 1.00$ at 6 and 9 months).

These analyses suggest that the direct heritability estimate for body weight at 6 months in Chokla sheep (0.15 from model 5) was similar to the value

of 0.18 observed at weaning, but that the heritability subsequently increased to 0.22 at 9 months and 0.24 at 12 months. Other studies (Fossceco & Notter 1995; Näsholm & Danell 1996; Safari et al. 2005; Mandal et al. 2006b) also confirmed that the importance of additive direct effects on body weight increased with increasing age. Direct heritability estimates for postweaning weights in our study were comparable with estimates reported in other sheep breeds (Abegaz et al. 2002; Ozcan et al. 2005; Safari et al. 2005; Behzadi Bahreini et al. 2007; Bosso et al. 2007). Kumar et al. (2005) estimated the heritability of 6-month weight by both paternal half-sib method and REML and reported values ranging from 0.16 to 0.26 in Chokla sheep. A higher heritability estimate for postweaning weight at 6 months of age was obtained by Miraei-Ashtiani et al. (2007) in Sangsari sheep (0.49). A higher estimate of heritability (0.37) for 6-month body weight was also reported by Kushwaha et al. (1996) in Chokla sheep using the paternal half-sib method, but this estimate is likely inflated by failure to consider maternal effects. However, Mandal et al. (2006b) estimated direct heritabilities for body weights at 6 ($h^2 = 0.06$; model 2), 9 ($h^2 = 0.06$; model 2) and 12 months ($h^2 = 0.14$; model 1) of age in Muzaffarnagari sheep, which were much lower than the present values. Lower heritability estimates for 9- and 12-month weight was also reported by Miraei-Ashtiani et al. (2007) in Sangsari sheep. Our estimates of the proportion of variance associated with additive and (or) permanent environmental maternal effects on postweaning weights were lower than those observed at birth but similar to those observed at weaning and consistent with averages of other reported estimates in various wool breeds (Safari et al. 2005).

Estimates of total heritability for postweaning weights were within the range of other estimates made at similar ages (Abegaz et al. 2002; Ozcan et al. 2005). However, both higher (Safari et al. 2005) and lower estimates (Mandal et al. 2006b) of h^2_t for postweaning weights have been reported. Estimates of t_m for postweaning weights ranged from 0.12 to 0.15 and agree with published results from other sheep breeds (Abegaz et al. 2002; Safari et al. 2005). Only Ozcan et al. (2005) in Turkish Merino sheep and Mandal et al. (2006b) in Muzaffarnagari sheep reported lower estimates of t_m at 12 months.

Conclusions

Results of this study demonstrate potential for genetic improvement of body weights from birth through 12 months of age in Chokla sheep. Across ages, estimates of total heritability (h^2_t) ranged from 0.16 to 0.27, and indicate that simple mass selection based on phenotypes would generate substantial selection responses. However, more sophisticated methods based on BLUP breeding value estimates that incorporate records of relatives and consider both direct and maternal effects would be expected to enhance selection response.

Additive maternal effects were important at birth, presumably reflecting differences in the quality of the uterine environment, and at weaning, presumably reflecting differences in milk production and, perhaps, other behavioural aspects of mothering ability. Non-additive maternal effects, including both permanent environmental and non-additive genetic effects of the dam, were also important for birth weight but could not be clearly distinguished from additive maternal effects at weaning. Overall (additive plus permanent environmental) maternal effects approached significance for postweaning weights but could not be adequately partitioned into additive and non-additive components. The total maternal variances ($\sigma^2_m + \sigma^2_c$) at 6 and 9 months were similar to that at weaning, suggesting a simple carry-over effect of maternal effects present at weaning. However, the total maternal variance component then inexplicably increased from 0.51 kg^2 at 9 months to 0.84 kg^2 at 12 months.

Both heritability estimates and repeatabilities of ewe effects (t_m) were relatively consistent for all weights between models 2, 3 and 5. Thus, relatively consistent estimates of additive animal and total maternal effects could be anticipated for any of the maternal effects models, but the most appropriate value for m^2 could not be clearly determined. The t_m predicts future performance of the ewe and can be used to identify and cull less-productive ewes, but accurate separation of additive and non-additive maternal effects is necessary to implement selection to improve maternal performance. We thus conclude that model 1 is not appropriate because it fails to consider the important maternal effects; models 4 and 6 are unnecessary because there is no evidence of significant additive direct maternal covariance; and models 2, 3 and 5 are essentially equivalent and should, at a minimum, improve accuracy of additive breeding value prediction relative to model 1.

Implementation of more general models to describe the impact of direct and maternal additive effects on body weights across the entire range of ages represented in these data would be desirable. Now that the pattern of change in maternal

Table 4 Estimates of variance components and genetic parameters for postweaning weights of Chokla sheep from Models 1, 2, 3 and 5

Item[a]	Model 1	Model 2[b]	Model 3[b]	Model 5
6-month weight				
σ^2_a	1.706	**1.263**	1.136	1.139
σ^2_m	–	**–**	0.506	0.217
σ^2_c	–	**0.587**	–	0.422
σ^2_e	6.043	**5.841**	6.058	5.907
σ^2_p	7.749	**7.691**	7.700	7.685
h^2	0.22	**0.16 (0.06)**	0.15	0.15
m^2	–	**–**	0.07	0.03
c^2	–	**0.08 (0.03)**	–	0.05
h^2_t	0.22	**0.16**	0.18	0.16
t_m	0.06	**0.12**	0.11	0.12
log L	–3.51	**–0.33**	–0.92	0
9-month weight				
σ^2_a	2.302	1.944	**1.669**	1.665
σ^2_m	–	–	**0.506**	0.497
σ^2_c	–	0.396	**–**	0.011
σ^2_e	5.222	5.121	**5.269**	5.269
σ^2_p	7.524	7.462	**7.443**	7.441
h^2	0.31	0.26	**0.22 (0.07)**	0.22
m^2	–	–	**0.07 (0.03)**	0.07
c^2	–	0.05	**–**	0.002
h^2_t	0.31	0.26	**0.26**	0.26
t_m	0.08	0.12	**0.13**	0.13
log L	–2.68	–1.26	**0**	0
12-month weight				
σ^2_a	2.848	2.407	**2.026**	2.107
σ^2_m	–	–	**0.744**	0.473
σ^2_c	–	0.726	**–**	0.365
σ^2_e	6.087	5.744	**6.074**	5.902
σ^2_p	8.935	8.877	**8.844**	8.847
h^2	0.32	0.27	**0.23 (0.07)**	0.24
m^2	–	–	**0.08 (0.04)**	0.05
c^2	–	0.08	**–**	0.04
h^2_t	0.32	0.27	**0.27**	0.26
t_m	0.08	0.15	**0.14**	0.15
log L	–3.32	–0.69	**–0.33**	0

[a]σ^2_a is the direct additive genetic variance; σ^2_m is the maternal additive genetic variance; σ^2_c is the maternal permanent environmental variance; σ^2_e is the environmental variance; σ^2_p is the phenotypic variance; h^2 is the heritability; m^2 is the maternal heritability; $c^2 = \sigma^2_c/\sigma^2_p$; h^2_t is the total heritability; t_m is the repeatability of the ewe performance and log L is the log-likelihood expressed as a deviation from the model with highest likelihood.
[b]The model in bold represents the most appropriate model. Values in parentheses are SE of estimates from this model.

components of variance has been determined for the recorded body weights, estimation of genetic, permanent environmental and residual covariances among weights using appropriate statistical models for each age should follow. Incorporation of these covariances into a comprehensive system of genetic evaluation of growth will permit greater accuracy of evaluation and allow us to account for animals that do not have records at all ages. Random regression procedures (Lewis & Brotherstone 2002; Schaeffer 2004) also have potential to achieve such a comprehensive synthesis, but are not particularly well suited to the current data. Most random regression applications have utilized very large data sets with relatively large numbers of measurements on each individual recorded across a range of time points and with a similar underlying model assumed at all times. In contrast, our data had only a modest number of subjects; all animals were weighed on the day of the target ages, resulting in relatively large and consistent gaps between time points; and the apparent pattern of change in maternal variances following weaning was not particularly consistent with the polynomial models commonly used to describe changes in variance components over time in random regression models. We believe that results in Tables 2, 3 and 4 are thus adequate to portray changes in genetic parameters over time and, when extended using multitrait analyses to incorporate genetic relationships among the different weights, will provide a solid basis for genetic evaluation of growth in this population. However, we acknowledge the potential benefits from application of more holistic random regression models in larger data sets with a greater range and larger number of measurement times.

Acknowledgements

References

Abegaz S., Negussie E., Duguma G., Rege J.E.O. (2002) Genetic parameter estimates for growth traits in Horro sheep. *J. Anim. Breed. Genet.*, **119**, 35–45.

Al-Shorepy S.A., Notter D.R. (1998) Genetic parameters for lamb birth weight in spring and autumn lambing. *Anim. Sci.*, **67**, 327–332.

Assan N., Makuza S., Mhlanga F., Mabuku O. (2002) Genetic evaluation and selection response of birth weight and weaning weight in indigenous Sabi sheep. *Asian-Aust. J. Anim. Sci.*, **15**, 1690–1694.

Behzadi Bahreini M.R., Shahroudi F.E., Van Vleck L.D. (2007) Estimates of genetic parameters for growth traits in Kermani sheep. *J. Anim. Breed. Genet.*, **124**, 296–301.

Bosso N.A., Cisse M.F., van der Waaij E.H., Fall A., van Arendonk J.A.M. (2007) Genetic and phenotypic parameters of body weight in West African Dwarf goat and Djallonke sheep. *Small Rumin. Res.*, **67**, 271–278.

Boujenane I., Kansari J. (2002) Estimates of (co)variances due to direct and maternal effects for body weights in Timahdite sheep. *Anim. Sci.*, **74**, 409–414.

Bromley C.M., Snowder G.D., Van Vleck L.D. (2000) Genetic parameters among weight, prolificacy and wool traits of Columbia, Polypay, Rambouillet and Targhee sheep. *J. Anim. Sci.*, **78**, 846–858.

Ekiz B., Özcan M., Yilmaz A., 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 J. Vet. Anim. Sci.*, **28**, 383–389.

El Fadili M., Michaux C., Detilleux J., Leroy P.L. (2000) Genetic parameters for growth traits of the Moroccan Timahdit breed of sheep. *Small Rumin. Res.*, **37**, 203–208.

Fossceco S.L., Notter D.R. (1995) Heritabilities and genetic correlations of body weight, testis growth and ewe lamb reproductive traits in crossbred sheep. *Anim. Sci.*, **60**, 185–195.

Hanford K.J., Van Vleck L.D., Snowder G.D. (2003) Estimates of genetic parameters and genetic change for reproduction, weight and wool characteristics of Targhee sheep. *J. Anim. Sci.*, **81**, 630–640.

Harvey W.R. (1990) User's Guide for LSMLMW MIX-MDL, PC-2 Version. Columbus, OH, USA.

Kumar Ravindra., Singh C.V., Mehta B.S. (2005) Genetic parameter estimates for the weight and fleece traits in Chokla sheep. *Indian J. Anim. Sci.*, **75**, 1073–1079.

Kushwaha B.P., Singh G., Arora A.L., Bohra S.D.J. (1996) Selection indices in Chokla sheep. *Indian J. Anim. Sci.*, **66**, 296–297.

Kushwaha B.P., Kumar S., Kumar R., Mehta B.S. (1997) The Chokla sheep in India. *Anim. Genet. Resour. Inform., Rome, Food Agricult. Organi.*, **22**, 19–27.

Larsgard A.G., Olesen I. (1998) Genetic parameters for direct and maternal effects on weights and ultrasonic muscle and fat depth of lambs. *Livest. Prod. Sci.*, **55**, 273–278.

Lewis R.M., Brotherstone S. (2002) A genetic evaluation of growth in sheep using random regression techniques. *Anim. Sci.*, **74**, 63–70.

Ligda Ch., Gabriilidis G., Papadopoulos Th., Georgoudis A. (2000) Investigation of direct and maternal genetic effects on birth and weaning weight of Chios lambs. *Livest. Prod. Sci.*, **67**, 75–80.

Mandal A., Neser F.W.C., Rout P.K., Roy R., Notter D.R. (2006a) Estimation of direct and maternal (co)variance components for pre-weaning growth traits in Muzaffarnagari sheep. *Livest. Sci.*, **99**, 79–89.

Mandal A., Neser F.W.C., Rout P.K., Roy R., Notter D.R. (2006b) Genetic parameters for direct and maternal effects on body weights of Muzaffarnagari sheep. *Anim. Sci.*, **82**, 133–140.

María G.A., Boldman K.G., Van Vleck L.D. (1993) Estimates of variances due to direct and maternal effects for growth traits of Romanov sheep. *J. Anim. Sci.*, **71**, 845–849.

Matika O., van Wyk J.B., Erasmus G.J., Baker R.L. (2003) Genetic parameter estimates in Sabi sheep. *Livest. Prod. Sci.*, **79**, 17–28.

Maxa J., Norberg E., Berg P., Pedersen J. (2007) Genetic parameters for growth traits and litter size in Danish Texel, Shropshire, Oxford Down and Suffolk. *Small Rumin. Res.*, **68**, 312–317.

Meyer K. (1997) Estimates of genetic parameters for weaning weight of beef cattle accounting for direct-maternal environmental covariances. *Livest. Prod. Sci.*, **52**, 187–199.

Meyer K. (2000) DFREML Programs to Estimate Variance Components by Restricted Maximum Likelihood Using a Derivative-Free Algorithm – User Notes, Version 3.0 *β*., Mimeograph, Animal Genetics and Breeding Unit, University of New England, Armidale, NSW, Australia.

Miraei-Ashtiani S.R., Seyedalian S.A.R., Shahrbabak M.M. (2007) Variance components and heritabilities for body weights traits in Sangsari sheep using univariate and multivariate animal models. *Small Rumin. Res.*, **73**, 109–114.

Näsholm A., Danell Ö. (1994) Maternal genetic effects on lamb weights. Proceedings of the Fifth World Congress on Genetics Applied to Livestock Production, Guelph, Canada, vol. **18**, pp. 163–166.

Näsholm A., Danell Ö. (1996) Genetic relationships of lamb weight, maternal ability, and mature ewe weight in Swedish finewool sheep. *J. Anim. Sci.*, **74**, 329–339.

Neser F.W.C., Erasmus G.J., van Wyk J.B. (2001) Genetic parameter estimates for pre-weaning weight traits in Dorper sheep. *Small Rumin. Res.*, **40**, 197–202.

Notter D.R. (1998) Genetic parameters for growth traits in Suffolk and Polypay sheep. *Livest. Prod. Sci.*, **55**, 205–213.

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 Rumin. Res.*, **56**, 215–222.

Parthasarthy S., Kushwaha B.P. (1996) Luster in Chokla wool from an organized farm. *Wool Woolens India*, **33** Jan–Mar, pp. 27–28.

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 Rumin. Res.*, **74**, 165–171.

Robison O.W. (1981) The influence of maternal effects on the efficiency of selection – a review. *Livest. Prod. Sci.*, **8**, 121–137.

Safari E., Fogarty N.M., Gilmour A.R. (2005) A review of genetic parameter estimates for wool, growth, meat and reproduction traits in sheep. *Livest. Prod. Sci.*, **92**, 271–289.

Schaeffer L.R. (2004) Application of random regression models in animal breeding. *Livest. Prod. Sci.*, **86**, 35–45.

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. *Livest. Prod. Sci.*, **44**, 229–235.

Solomon Gizaw., Lemma Sisay., Komen Hans., Van Arendonk J.A.M. (2007) Estimates of genetic parameters and genetic trends for live weight and fleece traits in Menz sheep. *Small Rumin. Res.*, **70**, 145–153.

Vatankhah M., Talebi M.A. (2008) Genetic parameters of body weight and fat-tail measurements in lambs. *Small Rumin. Res.*, **75**, 1–6.

Willham R.L. (1972) The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. *J. Anim. Sci.*, **35**, 1288–1293.

Yazdi M.H., Engström G., Näsholm A., Johansson K., Jorjani H., Liljedahl L.E. (1997) Genetic parameters for lamb weight at different ages and wool production in Baluchi sheep. *Anim. Sci.*, **65**, 247–255.