Genetic parameter estimates for birth and weaning weights in Raeini goats

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ABSTRACT: The aim of the present study was to estimate variance components and genetic parameters for birth and weaning weights in Raeini goats. The data were collected from the Breeding Centre of Raeini (BCR) cashmere goats in Kerman province of Iran from 1986 to 2008. Random effects included direct and maternal additive genetic effects, maternal permanent environmental effects with direct-maternal genetic covariance and random residual effects. Variance and covariance components and genetic parameters were estimated using the DFREML program by fitting six single-trait animal models. Depending on the model, h_d^2 varied from 0.057 to 0.323 for birth weight and from 0.043 to 0.229 for weaning weight. Estimates of m^2 ranged from 0.016 to 0.289 for birth weight and from 0.01 to 0.184 for weaning weight. The maternal permanent environmental effect was significant for both traits and ignoring maternal effects in the model caused the overestimation of direct heritability.

Keywords: body weight; growth; heritability; maternal effects; goat

Nowadays, body weight is one of the major selection traits in a goat population. Animals follow different growth patterns (Krejčová et al., 2008) due to different environments, management restrictions, and compensation from changing environments. Animals with high growth potential are negatively affected by unfavourable environmental factors more than animals with poor growth capability (Přibyl et al., 2008). Estimates of genetic and environmental parameters of different component traits related to growth are needed to develop a proper selection program. In addition, these parameters are necessary for the prediction of a response to selection. Studies of various breeds have shown that growth traits, particularly at early ages, are influenced not only by the genes of the individual for growth and by the environment in which it is raised, but also by the maternal genetic composition and environment provided by the dam (Ghafouri et al., 2008). Maternal effects in animals have been studied intensively in recent years both because of their economic importance in domestic mammals and because of their theoretical interest (Willham, 1972). From the mother's perspective, maternal effects on progeny performance result from maternal traits controlled by her genotype and associated environmental factors. Therefore, these effects are divided into genetic and environmental components. However, from the side of the offspring, maternal effects are reflected as environmental. So, there are indirect genetic and environmental effects. In consequence, maternal genetic effects are defined as any influence from dam to progeny, excluding the effects of directly transmitted genes (Szwaczkowski et al., 2006). To take advantage of different schemes for breed utilization, the genetic parameters for the traits of importance should be known (Boujenane and Bradford, 1991). The aim of this study was to estimate genetic parameters for birth and weaning weights in Raeini goats by fitting 6 animal models, attempting to separate direct genetic, maternal genetic and maternal permanent environmental effects. In addition, the genetic correlation between additive direct and additive maternal effects was estimated.

MATERIAL AND METHODS

The data used in the present study were collected from the Breeding Centre of Raeini (BCR) cashmere goats in Kerman province of Iran from 1986 to 2008. The traits analyzed were birth and weaning weights. The characteristics of the data structure are shown in Table 1. Generally, animals were managed following conventional industrial practices. Natural pasture is the main source of feed. The quantity and quality of the pasture vary considerably during the year. With the dry season, the quantity and quality of the pasture decreases and supplemental feeding has to be provided. In the Raeini breed, the does were bred once a year in summer (July–August) and kids were born in January. During the kidding season, the does were indoors and carefully managed. The kids were weighed and ear tagged within early of birth. The identities of newborns and of their parents, date of birth, sex, birth type and birth weight were recorded. The kids were weaned at about 3 months of age; accordingly, individual weaning weight was adjusted to 90 days of age.

Variance and covariance components and genetic parameters were estimated using the DFREML program (Meyer, 1998) by fitting six single-trait animal models. To identify the fixed effects to be included in the models, the GLM procedure in the SPSS 11.5 program (SPSS, 2002) was used. The analysis showed that fixed effects of year of birth, sex, type of birth (single and multiple) and age of dam were significant for birth and weaning weights. Consequently, those effects were included in the models. The random effects in used mixed models are summarized in Table 2. All models included an additive direct effect, and this was the only random factor in Model 1. Model 2 included the maternal permanent environmental effect, fitted as an additional random effect, uncorrelated with all other effects in the model. Model 3 included an additive maternal effect fitted as a second random effect. Model 4 was the same as Model 3, but allowed for a direct maternal covariance (Cov (a,m)). Model 5 and Model 6 included additive maternal and maternal permanent environmental effects, ignoring and fitting, respectively, direct-maternal covariance. The models were as follows:

Model 1: $Y = Xb + Z_a a + e$
Model 2: $Y = Xb + Z_a a + Z_c c + e$
Model 3: $Y = Xb + Z_a a + Z_m m + e$ with $\text{Cov}(a,m) = 0$
Model 4: $Y = Xb + Z_a a + Z_m m + e$ with $\text{Cov}(a,m) = \text{A}\sigma_{am}$
Model 5: $Y = Xb + Z_a a + Z_m m + Z_c c + e$ with $\text{Cov}(a,m) = 0$
Model 6: $Y = Xb + Z_a a + Z_m m + Z_c c + e$ with $\text{Cov}(a,m) = A\sigma_{am}$

where:
Y = vector of observations
b vector contained year of birth, sex, type of birth (single and multiple) and age of dam as fixed effects
a, m, c, e = vectors of direct additive genetic effects, maternal genetic effects, permanent environmental effect of dam and the residual, respectively
X, Z_a, Z_m, Z_c = incidence matrices relating observations to b, a, m and c, respectively
A = numerator relationship matrix
σ_{am} = covariance between direct and maternal genetic effects

The (co)variance structure of the random effects in the analysis can be described as:

$$V(a) = A\sigma^2_a;\ V(m) = A\sigma^2_m;\ V(c) = I_d\sigma^2_c;\ V(e) = I_n\sigma^2_e;\ \text{Cov}(a,m) = A\sigma_{am}$$

where:
A = numerator relationship matrix
σ^2_a = direct additive genetic variance
σ^2_m = maternal additive genetic variance
σ_{am} = direct-maternal additive genetic covariance
σ^2_c = maternal permanent environmental variance
σ^2_e = residual variance
I_d, I_n = identity matrices of an order equal to the number of dams and records, respectively (Ekiz et al., 2004).

Total heritability $(\sigma^2_a + 0.5\ \sigma^2_m + 1.5\ \sigma_{am})/\sigma^2_p$ is as defined by Willham (1972). The principles of derivative-free restricted maximum likelihood (DFREML) wee previously described by Meyer (1989). Convergence was assumed when the variance of likelihood values in the simplex was less

Table 1. Characteristics of the data structure for birth and weaning weights

	Birth weight	Weaning weight
Mean (kg)	2.40	14.80
Standard deviation (kg)	0.42	3.12
Coefficient of variation (%)	17.50	21.05
Number of records	3 733	2 625
Number of sires	158	136
Number of dams	695	658
Number of grand-sires	98	89
Number of grand-dams	242	226

than 10^{-8}. In addition, a restart of each analysis was performed with different starting values to avoid convergence to local maxima. To determine the most appropriate model, likelihood ratio tests were used for each trait. The effect was considered to have a significant influence when its addition caused a significant increase in log likelihood, in comparison with the model in which it was ignored. When log likelihoods did not differ significantly ($P > 0.05$), the model that had fewer parameters was selected as the most appropriate. Parameters were considered to be different from zero when the estimate divided by its standard error was greater than the corresponding values of the standard normal distribution (Tosh and Kemp, 1994).

RESULTS AND DISCUSSION

As seen in Table 1, the coefficient of variation for birth weight is much lower than that for the other trait, which indicates the smaller effect of environment on birth weight than on the weaning weight.

Estimates of (co)variance components and genetic parameters regarding birth and weaning weights are presented in Tables 3 and 4, respectively. The results showed that fitting either additive or permanent environmental maternal effect in models increased the log likelihood values significantly ($P < 0.05$) in comparison with Model 1. Model 1, which ignored maternal effects, resulted in higher estimates for σ_a^2 and h_d^2 than did the other models. In Model 2, the addition of the maternal environmental effect reduced the values of both σ_a^2 and h_d^2 compared to Model 1. Models 3 and 4, which included the additive maternal effect but not the maternal environmental effect, yielded smaller estimates of $\sigma_a{}^2$ and $h^2{}_d$ than did Models 1 and 2. The same result was found in previous reports which compared models for various goat and sheep breeds (Saatci et al., 1999; Ligda et al., 2000; Szwaczkowski et al., 2006; Roy et al., 2008). Meyer (1992) showed that models not accounting for maternal genetic effects could result in substantially higher estimates of additive direct genetic variance and, therefore, higher estimates of h_d^2. If maternal effects are present but not considered, the estimate of additive genetic variance will include at least a part of the maternal variance. Therefore, estimates of direct heritability will decrease when maternal effects are included. It should be remembered that the estimation of maternal effects is dependent on key pedigree relationships and data structure.

Table 2. Description of animal models fitted

Model	(Co)Variance components estimated
1	σ_a^2, σ_e^2
2	σ_a^2, σ_c^2, σ_e^2
3	σ_a^2, σ_m^2, σ_e^2
4	σ_a^2, σ_m^2, σ_{am}, σ_e^2
5	σ_a^2, σ_m^2, σ_c^2, σ_e^2
6	σ_a^2, σ_m^2, σ_{am}, σ_c^2, σ_e^2

σ_a^2 = direct additive genetic variance; $\sigma_m{}^2$ = maternal additive genetic variance; σ_{am} = direct-maternal genetic covariance; σ_c^2 = maternal environmental variance; σ_e^2 = error variance

The impact of data structure on separating maternal genetic and maternal environmental effects from combined and direct effects was demonstrated by Maniatis and Pollott (2003). The authors showed that the accuracy of estimation of maternal effects depends on the family structure and demonstrated that both the number of progeny per dam and the proportion of dams having their own record in the data considerably affect the variance component estimation. When the additive maternal effect was included in the models, m^2 was higher than h^2_d. The addition of the permanent maternal environmental effect with the additive maternal effect already fitted reduced σ_m^2 and m^2 for birth and weaning weights. Models 2, 5 and 6 had the highest log likelihood values and the differences between these models were not significant ($P > 0.05$). On the basis of the log likelihood ratio test results and number of parameters used, Model 2 was determined to be the most appropriate model for these traits, hence the permanent environmental effect of the dam was determined to be more important than the additive maternal effect for birth and weaning weights. Naeemipour-Younesi et al. (2008) reported that Models 2 and 1 were the most appropriate models for the birth and weaning weight of goat, respectively, in southern Khorasan. Roy et al. (2008) suggested that maternal additive effects are important only in the early stages of growth, whereas the permanent environmental maternal effect existed from weaning to 9 months of age in Jamunapari goats. Direct heritability estimates in this study for birth and weaning weights are higher than those of some authors for various breeds (Al-Shorepy et al., 2002; Naeemipour-Younesi et al., 2007; Roy et al., 2008), but they are lower than those (0.48 and 0.68) obtained by Unalan and Cebeci (2001) for birth and weaning weights, respectively. Heritabilities obtained by used models 2–6 are low. In general, the addition of additive maternal and/or maternal permanent environmental effects to the models reduces the values of both σ_a^2 and h^2_d compared to Model 1. The same result was found in previous reports (Yazdi et al., 1997; Ligda et al., 2000; Ekiz et al., 2004; Bahreini Behzadi et al., 2007). Revelle and Robison (1973) also showed that heritability of a trait may be low due to small additive genetic variance, excessive environmental variability, negative correlations between direct genetic and maternal effects or negative genetic correlations between components of the trait.

Table 3. Estimates of (co)variance components and genetic parameters for birth weight

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_a	0.068	0.017	0.014	0.012	0.016	0.015
σ^2_m			0.055	0.052	0.011	0.0031
σ_{am}				0.0004		0.006
σ^2_c		0.057			0.04	0.048
σ^2_e	0.12	0.11	0.12	0.11	0.11	0.12
σ^2_p	0.21	0.21	0.21	0.21	0.21	0.21
h^2_d	0.323	0.081	0.066	0.057	0.076	0.071
m^2			0.289	0.265	0.0574	0.0164
C_{am}				0.002		0.029
r_{am}				0.01843		0.31
C^2		0.271			0.191	0.228
h^2_T	0.323	0.081	0.198	0.183	0.102	0.121
−2 logl	1 225.5341	1 274.8089	1 269.2411	1 269.3349	1 274.0708	1 274.3131

σ^2_a = direct additive genetic variance; σ^2_m = maternal additive genetic variance; σ_{am} = direct-maternal genetic covariance; σ^2_c = maternal environmental variance; σ^2_e = error variance; σ^2_p = phenotypic variance; h^2_d = direct heritability; m^2 = maternal heritability; $C_{am} = \sigma_{am}/\sigma^2_p$; r_{am} = genetic correlation between direct and maternal effects; $C^2 = \sigma^2_c/\sigma^2_p$ maternal permanent environmental variance as a proportion of phenotypic variance; h^2_T = total heritability = $(\sigma^2_a + 0.5\sigma^2_m + 1.5\sigma_{am})/\sigma^2_p$

Table 4. Estimates of (co)variance components and genetic parameters for weaning weight

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ_a^2	1.421	0.32	0.262	0.29	0.31	0.38
σ_m^2			1.41	1.89	0.001	0.049
σ_{am}				–0.501		–0.13
σ_c^2		0.53			0.46	0.625
σ_e^2	2.58	2.18	2.36	2.31	2.17	2.14
σ_p^2	6.201	6.02	6.03	6.03	6.02	6.02
h_d^2	0.229	0.053	0.043	0.048	0.051	0.063
m^2			0.184	0.162	0.01	0.012
C_{am}				–0.083		–0.021
r_{am}				–0.634		–0.651
C^2		0.088			0.076	0.103
h_T^2	0.229	0.053	0.161	0.081	0.052	0.034
–2 log L	–4 440.2633	–4 354.6145	–4 374.012	–4 371.482	–4 354.61	–4 354.44

σ_a^2 = direct additive genetic variance; σ_m^2 = maternal additive genetic variance; σ_{am} = direct-maternal genetic covariance; σ_c^2= maternal environmental variance; σ_e^2 = error variance; σ_p^2 = phenotypic variance; h_d^2 = direct heritability; m^2 = maternal heritability; $C_{am} = \sigma_{am}/\sigma_p^2$; r_{am} = genetic correlation between direct and maternal effects; $C^2 = \sigma_c^2/\sigma_p^2$ maternal permanent environmental variance as a proportion of phenotypic variance; h_T^2 = total heritability = $(\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am})/\sigma_p^2$

Maternal permanent environment variance as a proportion of phenotypic variance (C^2) ranged from 0.191 to 0.271 for birth weight and from 0.076 to 0.103 for weaning weight. Ghafouri Kesbi et al. (2008) reported that estimates of c^2 are high at birth, when direct effects are the least important, but they decrease sharply after weaning and at the highest age this effect is negligible. The same result was found in other reports (Zhou et al., 2002; Ekiz et al., 2004; McManus et al., 2008). However, Al-Shorepy et al. (2002) found opposing results and related that although the permanent environmental effects had a higher influence on weaning weight than on birth weight, the genetic basis for these effects could not be interpreted. In addition, Meyer (2001) reported that breed differences in the importance of maternal environmental effects are important and in some breeds lower c^2 is due to an earlier decline of the lactation curve than in other breeds. Depending on the model, m^2 ranged from 0.016 to 0.289 for birth weight and from 0.01 to 0.184 for weaning weight in this study. The higher estimate of maternal heritability for birth weight compared with the estimate for weaning weight supports the conclusion of Robinson (1981) that maternal genetic effects generally are important for weight at younger ages and diminish with an increasing age. The tendency of m^2 to decline from birth to later ages, as obtained here, is in agreement with other literature (Tosh and Kemp, 1994; Ligda et al., 2000; Ekiz et al., 2004; Ghafouri Kesbi et al., 2008)

Correlations between direct and maternal genetic effects (r_{am}) ranged from 0.018 to 0.31 and –0.651 to –0.634 for birth weight and weaning weight, respectively. Numerous studies have found a negative correlation between additive direct and additive maternal effects (ram) for birth and weaning weights of various breeds (Maria et al., 1993; Tosh and Kemp, 1994; Ligda et al., 2000). However, positive relationships have also been reported (Nasholm and Danell, 1996; Yazdi et al., 1997). Nasholm and Danell (1996) concluded that selection for increased weights will also improve the maternal ability in the case of a positive correlation between direct and maternal genetic effects. The reasons for the negative estimates obtained could not be explained conclusively by these authors. It may be due to natural selection for an intermediate optimum (Tosh and Kemp, 1994). It is generally assumed that the covariance between direct and maternal genetic effects on body weight is negative (Maria et al., 1993; Tosh and Kemp, 1994). However, a positive relationship was also found (Nasholm and Danell, 1996; Yazdi et al., 1997). In this study we found different covariances between direct and maternal genetic effects. For weaning weight a negative covariance between direct and maternal genetic effects was registered. This influenced the magnitude of total heritabilities, which ranged between 0.034 and 0.229. Szwaczkowski et al. (2006) showed that the negative covariance between direct and maternal genetic effects indicates different rankings of individuals when the maternal contribution is omitted in the evaluation procedure. Furthermore, Swalve (1993) suggested that the negative covariance between direct and maternal genetic effects may be the result of management system. However, an investigation conducted by Dodenhoff et al. (1999) on several breeds of beef cattle indicates that dependences between direct and maternal effects are determined by breed. Moreover, Přibyl et al. (2008) showed that editing the database plays a role in estimating genetic parameters and includes a more complex pedigree as well as produces slightly different results. In the case of birth weight a positive covariance between direct and maternal genetic effects was registered.

In conclusion, maternal effects on birth and weaning weights in Raeini goats were significant and may be taken into consideration in any selection program on this breed.

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