Estimates of Direct and Maternal Effects on Growth Traits in Angora Rabbits

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ABSTRACT : Genetic parameters of growth traits were estimated in the German Angora rabbit reared in the sub-temperate region of India. Estimates of (co)variance components were obtained for body weights at weaning (42 days) and post-weaning at 84, 126 and 168 days. A total of 8,324 animal records were used for the analysis of these traits. The data were analyzed by restricted maximum likelihood (REML) fitting six animal models with various combinations of direct and maternal effects. A log likelihood ratio test was used to select the most appropriate univariate model for each trait. Direct heritability estimates were observed to be moderate for the traits under study. Heritability estimates for weaning (42 d), 84, 126 and 168 d weights obtained from the best models were 0.25±0.05, 0.17±0.05, 0.21±0.06 and 0.12±0.05. Maternal effects had higher importance at weaning, and declined with the advancement of age. Significant maternal permanent environmental effect on weaning and post-weaning weights was a carryover effect of maternal influences during pre-weaning age. The estimated repeatabilities of doe effects on body weights were 0.37, 0.22, 0.18 and 0.28 at weaning, 84, 126 and 168 d body weight, respectively. Results indicated that modest rate of genetic progress is possible for body weight traits of Angora rabbit through selection. Similarly, these growth traits could be included in selection criteria along with wool traits for early selection of the animals. (**Key Words :** Angora Rabbit, Animal Model, Growth Traits, Heritability, Maternal Effect)

INTRODUCTION

Selection at an early age, for breeding and higher production, is a prerequisite under intensive livestock production system, through out the world. It holds true for Angora rabbit as well, where the farmers concern primarily for growth and wool production; as the body weight is directly correlated to the wool yield of the animals (Jelinek et al., 1980; Garcia and Magofke, 1982; Singh et al., 2006). In most of the rabbit breeding programmes, post weaning growth had been considered very effective criteria for selection (Piles et al., 2004) and evident that live body weight increased significantly after selection for fleece yield in Angora rabbits (Rafat et al., 2007, 2008). A strong positive correlation between the body weight and wool production dictate growth as desirable trait for early selection in Angora rabbits aimed to increase wool production (Qinyu, 1992). Studies in rabbit had revealed that both direct and maternal influences are important for

animal growth (Ferraz et al., 1992; Lukefahr et al., 1993; Lukefahr et al., 1996) and affects the phenotypic expression of the young through her genotype for maternal effects and direct additive genes for growth. The best method to estimate genetic parameters is animal model (Henderson, 1988). Animal models using Restricted Maximum Likelihood (REML) procedure had been widely used, in meat rabbits, to estimate the genetic and environmental parameters for different traits including growth (Ferraz et al., 1992; Lukefahr et al., 1993; Lukefahr et al., 1996). However, use of such animal model procedure for estimates of direct and maternal effects on growth traits of Angora rabbit is limited. The objective of this study was, therefore, to estimate genetic (co)variance components for growth traits using REML procedure with various combinations of direct and maternal effects for German Angora flock raised in sub temperate Himalayan region.

MATERIALS AND METHODS

The body weight records of German Angora rabbit at weaning (42 d) and post weaning (84, 126 and 168 d) were obtained for a period of seven years from 2002 to 2008. A total of 8,324 animal records were taken for the analysis of

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these traits and the characteristics of the data structure are summarized in Table 1. The flock was a closed type where 40 to 60 breeding females were maintained every year with male to female ratio of 1:5. Animals after weaning at 42 d of age were kept individually in all wire cages of standard dimensions under similar housing and management conditions and sheared manually with scissors. Rabbits were fed concentrate, containing 15 to 20% crude protein, in graded quantity from 30 to 140 g at different ages and seasonal grasses *ad libitum* (Bhatt and Sharma, 2009). All the animals were weighed and sheared exactly on the target age(s).

Data were arranged and subjected to the statistical analysis. Different fixed effects to be included in the model(s) were identified by least squares analysis of variance (SPSS, 2005) and only those fixed effects, which were significant ($p<0.05$) for the growth traits were included in the model(s). These fixed effects were sex (2 levels), year of birth (7 levels) and season of birth (4 levels: January-March, April-June, July-September, October-December). Further, (Co)variance components were estimated by DFREML (Meyer, 2000). The variance of less than 10^{-8} for the function values (-2logL) in the model(s) was assumed for the convergence. The convergence was confirmed when no further change in the estimates was observed after restart of analysis ensured at a global maximum. Six different single-trait linear models which accounts for the direct and maternal effects were initially fitted for each trait.

$$y = X\beta+Z_a a+\varepsilon \tag{1}$$

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

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

$$y = X\beta+Z_a a+Z_{pe}pe+\varepsilon \tag{4}$$

$$y = X\beta+Z_a a+Z_m m+Z_{pe}pe+\varepsilon \text{ with Cov } (a_m, m_o) = 0 \tag{5}$$

$$y = X\beta+Z_a a+Z_m m+Z_{pe}pe+\varepsilon$$
$$\text{with Cov } (a_m, m_o) = A\sigma_{am} \tag{6}$$

Where, y, β, a, m, pe and ε denotes vectors of records,

fixed effect, direct additive genetic effect, maternal additive genetic effect, permanent environmental effect of dam and residual effect, respectively. X, Z_a, Z_m and Z_{pe} are association matrices and A is the numerator relationship matrix between animals. σ_{am} denotes the covariance between direct additive genetic and maternal genetic effects. Assumptions for variance (V) and covariance (Cov) matrices involving random effects were

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

where, I is an identity matrix and σ^2_a, σ^2_m, σ^2_c and σ^2_e are additive direct, additive maternal, maternal permanent environmental and residual variances, respectively. 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^2_a and σ^2_m. Maternal across year repeatability for doe performance ($t_m = (1/4) h^2+m^2+c^2+mr_{am}h$) was calculated; where, m^2 is σ^2_m/σ^2_p and c^2 is σ^2_c/σ^2_p. The total heritability (h^2_t), was calculated using the formula $h^2_t= (\sigma^2_a+0.5\sigma^2_m+1.5\sigma_{am})/\sigma^2_p$, (Willham, 1972).

The most appropriate univariate model selected for each trait was based on likelihood ratio test-LRT (Meyer, 1992). An effect, causing significant ($p<0.05$) increase in the log likelihood value for a model compared to other models where it was ignored was considered significant. Differences in log-likelihoods for the two models were compared for significance level ($p<0.05$) by chi square distribution and the degree of freedom considered was equal to the difference in the number of (co)variance components of these models.

RESULTS AND DISCUSSION

Least squares means along with the standard deviation (SD) and percent coefficient of variation for growth traits under study are given in Table 1. (Co)variance components and genetic parameters estimated by different models for growth traits are presented in Table 2 and 3. The most appropriate model, which included direct additive and permanent environmental effects of the dam for traits under

Table 1. Characteristics of data structure for growth traits of German Angora

Trait	42 d BW	84 d BW	126 d BW	168 d BW
No. of records	2,184	2,098	2,058	1,984
No. of sires	117	116	116	116
No. of dams	292	291	291	289
Least squares mean(s) of body weight (g)	727.35	1,588.47	2,187.34	2,592.05
Standard deviation	163.41	260.96	255.44	261.80
CV%	22.47	16.43	11.68	10.10

Table 2. Estimates of (co)variance components (in gm^2) and genetic parameters for the weaning weight (42 d BW)

Items[x]	Model 1	Model 2	Model 3	**Model 4**	Model 5	Model 6
σ^2_a	11,078.43	7,224.16	10,402.85	**7,063.62**	7,062.31	10,400.12
σ^2_m	-	15,252.26	19,311.75	**-**	133.64	2,562.07
σ_{am}	-	-	-6,299.46	**-**	-	-4,858.44
σ^2_c	-	-	-	**8,974.21**	8,854.21	9,343.26
σ^2_e	15,697.71	12,864.40	11,202.88	**12,797.25**	12,798.84	11,038.86
σ^2_p	26,776.14	35,340.83	34,618.02	**28,835.07**	28,848.99	28,485.87
h^2	0.41 (0.04)	0.20 (0.04)	0.30[y]	**0.25 (0.05)**	0.24 (0.05)	0.37[y]
m^2	-	0.43 (0.03)	0.56[y]	**-**	0.005 (0.032)	0.09[y]
r_{am}	-	-	-0.44[y]	**-**	-	-0.94[y]
c^2	-	-	-	**0.31 (0.03)**	0.31 (0.04)	0.33
h^2_t	0.41	0.42	0.31	**0.25**	0.25	0.16
t_m	0.10	0.48	0.45	**0.37**	0.37	0.34
log L	-12,341.45	-12,555.61	-12,551.65	**-12,219.27[z]**	-12,533.81	-12,528.12

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

[x] $\sigma^2_a, \sigma^2_c, \sigma^2_e$ and σ^2_p are additive direct, maternal permanent environmental, residual variance and phenotypic variance, respectively; h^2 is heritability; c^2 is σ^2_c/σ^2_p; t_m is maternal across year repeatability for doe performance; h^2_t is total heritability and log L is log likelihood for the model obtained from DFREML (Meyer, 2000).

[y] Indicates that the approximation used to define standard errors of parameter estimates failed.

[z] Indicates that log L of the model is significantly (p<0.05) different from rest of the models.

study, was model-4 according to likelihood ratio test.

Weaning weight

In the present study, the heritability and additive genetic variance for the weaning weight (42 d BW), for the best model 4, were 0.25 and 7,063.62, respectively (Table 2) and were moderate. This indicates further scope for genetic improvement in the weaning weight through selection. Our finding was lower than the estimated h^2 for weaning weight (0.66) in NZW rabbits using BLUP method (Panella et al., 1992). Very high (Castellini and Panella, 1988) and very low (Ferraz et al., 1992) h^2 estimates had also been reported for weaning weights in rabbits. Similarly, the maternal permanent environment effect (c^2 = 0.31±0.03), the repeatability of doe performance (t_m = 0.37) and the estimate of total heritability (h^2_t = 0.25) for 42 d BW were moderate in the model 4. The maternal permanent environment effect indicates the importance of maternal care from birth to weaning, as kit remain for more time with their dams. The moderate repeatability of doe performance and total heritability estimates for the weaning weight reflects the consistency of the maternal performance. In addition, moderate t_m estimate indicate that selection for higher weaning weight is possible by culling of less productive dams. Estimates were consistent over models 2 to 6.

The model 4, which includes direct additive and maternal permanent environment effect, was sufficient to explain the variation in the weaning weight. In the model 1, h^2 estimate for 42 d BW was 0.41±0.04. Addition of maternal genetic effect (m^2 = 0.43) reduced h^2 estimate to 0.20 in model 2. Addition of covariance between direct and maternal effect has shown negative estimate of r_{am} in models 3 and 6. In model 5, which is more inclusive, the estimates for h^2, m^2 and c^2 were 0.24±0.05, 0.005±0.032 and 0.31±0.04, respectively. All these models, however, did not increase the likelihood. Addition of c^2 to direct genetic effect (model 4) increased the likelihood over other models significantly (p<0.05) as per LRT. Partitioning of the maternal effect into the additive and permanent environment effects seems difficult, as it requires large amount of repeated records on individual dam and related dams in the data (Notter and Hough, 1997). In the present study, no evidence of the maternal genetic effect on the weaning weight could be recorded.

Post weaning weights

Analysis for the (co)variance components estimates of the post weaning weights (84, 126 and 168 d) is presented in the Table 3. The direct heritability (h^2) estimates for post weaning weights at 84, 126 and 168 d, from the most appropriate model 4 in this study, were 0.17±0.05, 0.21±0.06 and 0.12±0.05, respectively (Table 3). There was overall decrease in heritability estimates as the age

Table 3. Estimates of (co)variance components (in gm^2) and genetic parameters for post weaning weights

Post weaning wt	Items[x]	Model 1	Model 2	Model 3	**Model 4**	Model 5	Model 6
84 d BW	σ^2_a	23,997.89	13,723.65	13,967.96	**11,388.87**	11,357.78	12,611.05
	σ^2_m	-	17,221.36	17,468.17	**-**	0.9368E-03	273.82
	σ_{am}	-	-	-439.15	**-**	-	-1,858.28
	σ^2_c	-	-	-	**12,223.49**	12,274.46	12,965.38
	σ^2_e	43,373.74	42,413.15	42,288.52	**42,901.76**	42,904.23	42,220.01
	σ^2_p	67,371.63	73,358.16	73,285.51	**66,514.12**	66,536.46	66,211.98
	h^2	0.36 (0.05)	0.19 (0.05)	0.19[y]	**0.17 (0.05)**	0.17[y]	0.19[y]
	m^2	-	0.23 (0.03)	0.24[y]	**-**	0.00[y]	0.004[y]
	r_{am}	-	-	-0.03[y]	**-**	-	-1.00[y]
	c^2	-	-	-	**0.18 (0.02)**	0.18[y]	0.20[y]
	h^2_t	0.36	0.30	0.30	**0.17**	0.17	0.15
	t_m	0.09	0.28	0.28	**0.22**	0.22	0.22
	log L	-12,772.47	-13,024.32	-13,024.32	**-12,739.62[z]**	-12,994.34	-12,993.33
126 d BW	σ^2_a	23,536.93	12,629.10	13,184.98	**13,521.08**	13,087.78	14,154.08
	σ^2_m	-	11,252.17	12,037.06	**-**	1,208.85	1,921.02
	σ_{am}	-	-	-1,145.66	**-**	-	-1,579.02
	σ^2_c	-	-	-	**8,359.56**	7,496.40	7,799.41
	σ^2_e	43,277.78	44,695.16	44,384.82	**43,737.36**	43,940.55	43,334.48
	σ^2_p	66,814.71	68,576.42	68,461.19	**65,617.99**	65,733.58	65,629.96
	h^2	0.35 (0.05)	0.18 (0.06)	0.19[y]	**0.21 (0.06)**	0.20 (0.05)	0.22[y]
	m^2	-	0.16 (0.03)	0.18[y]	**-**	0.02 (0.03)	0.03[y]
	r_{am}	-	-	-0.09[y]	**-**	-	-0.30[y]
	c^2	-	-	-	**0.13 (0.02)**	0.11 (0.03)	0.12[y]
	h^2_t	0.35	0.27	0.26	**0.21**	0.21	0.20
	t_m	0.09	0.21	0.21	**0.18**	0.18	0.18
	log L	-12,544.46	-12,758.22	-12,758.18	**-12,516.99[z]**	-12,755.47	-12,755.33
168 d BW	σ^2_a	25,924.37	6,989.98	8,027.84	**6,884.62**	6,753.80	8,351.83
	σ^2_m	-	20,552.90	22,478.41	**-**	2,602.54	3,987.71
	σ_{am}	-	-	-2,767.74	**-**	-	-2,916.25
	σ^2_c	-	-	-	**14,038.01**	11,931.14	12,499.92
	σ^2_e	33,422.55	36,229.39	35,668.20	**36,195.30**	36,237.81	35,361.83
	σ^2_p	59,346.93	63,772.28	63,406.71	**57,117.93**	57,525.28	57,285.03
	h^2	0.44 (0.05)	0.11 (0.05)	0.13[y]	**0.12 (0.05)**	0.12 (0.0)	0.15[y]
	m^2	-	0.32 (0.04)	0.35[y]	**-**	0.05 (0.0)	0.07[y]
	r_{am}	-	-	-0.21[y]	**-**	-	-0.51[y]
	c^2	-	-	-	**0.25 (0.03)**	0.21 (0.02)	0.22[y]
	h^2_t	0.44	0.27	0.24	**0.12**	0.14	0.11
	t_m	0.11	0.35	0.34	**0.28**	0.29	0.28
	log L	-11,938.88	-12,127.20	-12,126.93	**-11,882.17[z]**	-12,122.90	-12,122.39

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

[x, y, z] As indicated for Table 2.

advanced indicating declination in genetic variability for body weight as animals grow older. These findings were collaborative to the estimated h^2 for 52 d BW (0.29) and 73 d BW (0.20) in NZW rabbits using BLUP method (Panella et al., 1992). Similarly, Lukefahr et al. (1992) also reported medium values of heritability for 90 d BW in domestic rabbit breeds using animal model by REML method. On the contrary, high (Castellini and Panella, 1988) and low (Ferraz et al., 1992) h^2 estimates had also been reported for post weaning weights in rabbits. Under sub-temperate conditions, moderate heritability (0.29) for body weight at 168 d in NZW rabbits had been reported (Mahajan and Lahiri, 1983).

Maternal permanent environmental effect was an important source of variation on post-weaning weights. Estimates of maternal permanent environment (c^2) varied across the age and reduced from 31% at 42 d BW (weaning) to 18% at 84 d BW and 13% at 126 d BW and corresponds with the decline in the m^2. In general, maternal effect was observed maximum at weaning stage and then declined as the age advanced. It was expected as weaners became more independent of doe with the advancement of the age. These observations were consistent to the higher maternal genetic heritability and permanent environment effect for growth traits at initial stage which decreased in latter stage (Ferraz et al., 1992). Further, models 5 and 6, which included maternal genetic and permanent environmental components with and without interaction, revealed that maternal environment was major component responsible for maternal effect than maternal heritability for all the growth traits. Results indicated the importance of the maternal genetic effect, as it accounts for significant portion of the total genetic variance. Higher importance of maternal effect over additive genetic effect on the post weaning growth traits in rabbits had also been documented earlier (Ferraz et al., 1992; Lukefahr et al., 1993). Maternal effects cannot be compared with the other studies due to differences in the models fitted, as suggested by Meyer (1992). No evidence for the additive maternal effect was observed on post weaning weights at any age. This indicates the impact of animal's own genotype for body weight at post weaning stage. As discussed earlier, partitioning of the total maternal effect in to its direct and permanent environmental components was difficult for post weaning weights. At 84 d BW, model 2 yielded estimate of h^2 and m^2 as 0.19 and 0.23, respectively. Estimates of h^2, m^2 and c^2 from inclusive model 5 were 0.17, 0.00 and 0.18, respectively. At 126 d BW, model 2 yielded estimate of h^2 and m^2 as 0.18 and 0.16, respectively. Similar results were also found in model 5 (h^2 = 0.20, m^2 = 0.02 and c^2 = 0.11). For 168 d BW, results from the model 2 for h^2 and m^2 were 0.11 and 0.32, respectively, whereas the comprehensive model 5 yielded h^2 = 0.12, m^2 = 0.05 and c^2 = 0.21. However as per LRT, model 4 was superior to all other models significantly (p<0.05) for all the post weaning weight traits. Estimates of r_{am} were high and negative for all the traits under consideration. Strong negative σ_{am} may arise from genes having antagonistic pleiotropic effects on maternal performance and offspring trait; thus by limiting an evolutionary response, it may act to maintain genetic variance after natural selection for an intermediate optimum (Roff, 2002; Wilson et al., 2006).

Total heritability estimates were also moderate in magnitude for post weaning weights, indicating scope for further genetic improvement in the trait. Similarly, estimates for t_m were 0.22 for 84 d BW, 0.18 for 126 d BW and 0.28 for 168 d BW in the Angora rabbit, indicating moderate repeatability for the doe performance and hence, further scope for improvement in the trait through maternal selection.

CONCLUSIONS

The additive genetic variability for all the growth traits in Angora rabbits was moderate. Maternal heritability was not evident for the body weight traits, whereas the permanent environment effects due to dam on live weights was evident. Considerably higher estimate of h^2 for body weight at 126 d could make it as a suitable criterion for selection of the Angora rabbits under sub-temperate conditions.

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