Estimation of Covariance Functions for Growth of Angora Goats

Liu Wenzhong*, Zhang Yuan[1] and Zhou Zhongxiao

College of Animal Science and Technology, Shanxi Agricultural University, Taigu 030801, China

ABSTRACT : Body weights of 862 Angora goats between birth and 36 months of age, recorded on a semiyearly basis from 1988 to 2000, were used to estimate genetic, permanent environmental and phenotypic covariance functions. These functions were estimated by fitting a random regression model with 6th order polynomial for direct additive genetic and animal permanent environmental effects and 4th and 5th order polynomial for maternal genetic and permanent environmental effects, respectively. A phenotypic covariance function was estimated by modelling overall animal and maternal effects. The results showed that the most variable coefficient was the intercept for both direct and maternal additive genetic effects. The direct additive genetic (co)variances increased with age and reached a maximum at about 30 months, whereas the maternal additive genetic (co)variances increased rapidly from birth and reached a maximum at weaning, and then decreased with age. Animal permanent environmental (co)variances increased with age from birth to 30 months with lower rate before 12 months and higher rate between 12 and 30 months. Maternal permanent environmental (co)variances changed little before 6 months but then increased slowly and reached a maximum at about 30 months. These results suggested that the contribution of maternal additive genetic and permanent environmental effects to growth variation differed from those of direct additive genetic and animal permanent environmental effects not only in expression time, but also in action magnitude. The phenotypic (co)variance estimates increased with age from birth to 36 months of age. (**Key Words :** Angora Goats, Growth, Covariance Function, Estimation, Random Regression Model)

INTRODUCTION

Growth is one of the important traits in animal production. Animal breeders are concerned with growth trajectories because of the potential to increase the economic value of domesticated species by altering growth patterns through artificial selection (Fitzhugh, 1976). Though the main product of Angora goats is mohair, which is chiefly used in the upholstery and apparel trades, growth is still important for mohair production and reproduction. Body weights and/or average daily gain had been included in breeding objectives in several countries (Stapleton, 1987; Lupton and Shelton, 1989; Snyman and Olivier, 1996).

Growth is a continuous process and can be recorded repeatedly during the animal life, i.e., longitudinal data. Covariance functions (CFs) (Kirkpatrick and Heckman, 1989; Kirkpatrick et al., 1990; 1994) and random regression model (RRM) (Schaeffer and Dekkers, 1994) have been proposed as an alternative to model longitudinal traits and

have been used for growth traits in beef cattle (Meyer and Hill, 1997; Meyer, 1998a; 1999; 2001; Xu et al., 2004), Zebu cattle (Albuquerque and Meyer, 2001) and swine (Liu Wenzhong et al., 2001; 2002), for test-day records in dairy cattle (Jamrozik and Schaeffer, 1997; Van der Werf et al., 1998; Park and Lee, 2006), and for reproductive traits in swine (Lukovic et al., 2007; Oh and See, 2008).

The objective of this paper was to estimate genetic, permanent environmental and phenotypic covariance functions for weights from birth to 36 months of age in Angora goats.

MATERIALS AND METHODS

Materials

Data of body weight of Angora goats at birth, 6, 12, 18, 24, 30 and 36 months of age were collected from the Qinshui Demonstration Farm, Shanxi province, China. For the natural ecological conditions, feeding and management methods on the farm, see Jin Zongli et al. (1992) and Liu Wenzhong et al. (1996). Animals with vague or missing pedigree were discarded, so that 5,166 records of 862 animals born from 1988 to 2000 were used to estimate the CFs. The description of the dataset is listed in Table 1.

* Corresponding Author: Liu Wenzhong. Tel: +86-354-6289036, Fax: +86-354-6285986, E-mail: tglwzyc@yahoo.com.cn
[1] College of Animal Science and Technology, China Agricultural University, Beijing 100094, China.

Table 1. Description of the dataset

Total records	5,166
Animals in analysis	925
Number of sires with progeny records	51
Number of dams with progeny records	257
Number of animals with records	862
With 2 records	84
With 4 records	109
With 6 records	121
With 7 records	548
Number of fixed effects	6
Mean (kg)	23.38
SD (kg)	12.74

Methods

Covariance functions were estimated by fitting a random regression model (Meyer, 1998a) and using the program DXMRR (Meyer, 1998b). The general model can be presented by (Albuquerque and Meyer, 2001):

$$y_{ij} = F_{ij} + \sum_{m=0}^{k_A-1} \alpha_{im} \phi_m (a_{ij}^*) + \sum_{m=0}^{k_m-1} \beta_{im} \phi_m (a_{ij}^*)$$
$$+ \sum_{m=0}^{k_c-1} \gamma_{im} \phi_m (a_{ij}^*) + \sum_{m=0}^{k_Q-1} \rho_{im} \phi_m (a_{ij}^*) + \varepsilon_{ij} \quad (1)$$

where y_{ij} is the j-th record from the i-th animal, a_{ij}^* is the standardized (-1 to 1) age at recording, $\phi_m(a_{ij}^*)$ is the m-th Legendre polynomial of age. α_{im}, β_{im}, γ_{im} and ρ_{im} are the random regression coefficients for direct additive genetic, maternal additive genetic, animal and maternal permanent environmental effects, respectively, and k_A, k_M, k_C and k_Q denote the corresponding orders of polynomial fit. F_{ij} is a set of fixed effects including birth year, birth month, age of dam, birth type (single vs. twin), and birth date (birth time relative to the first kid born within the kidding season, i.e., early: ≤15 days; middle: >15 and ≤30 days; late: >30 days). ε_{ij} is the temporary environmental effect (measurement error).

Assume the animal has n records, and define Legendre polynomials for the range of $[u, v] = [-1, 1]$, the j-th standardised age a_{ij}^* can be computed as (Kirkpatrick et al., 1994):

$$a_j^* = u + \frac{(v-u)(a_j - a_1)}{a_n - a_1} \quad (2)$$

where a_1 and a_n are the ages at the first and n-th recording respectively. Then the r-th polynomial of j-th standardised age a_j^* is given as:

$$\phi(a_j^*)_r = \frac{1}{2^r} \sqrt{\frac{2r+1}{2}} \sum_{m=0}^{[r/2]} (-1)^m$$
$$\binom{r}{m}\binom{2r-2m}{r}(a_j^*)^{r-2m} \quad (3)$$

where $[r/2]$ indicates that fractional values are rounded down to the nearest integer.

In matrix notation, equation (1) can be represented as:

$$y = Xb + Z_1\alpha + Z_2\beta + W_1\gamma + W_2\rho + \varepsilon \quad (4)$$

and

$$V\begin{bmatrix} \alpha \\ \beta \\ \gamma \\ \rho \\ \varepsilon \end{bmatrix} = \begin{bmatrix} K_A \otimes A & 0 & 0 & 0 & 0 \\ 0 & K_M \otimes A & 0 & 0 & 0 \\ 0 & 0 & K_C \otimes I & 0 & 0 \\ 0 & 0 & 0 & K_Q \otimes I & 0 \\ 0 & 0 & 0 & 0 & R \end{bmatrix} \quad (5)$$

where y is the vector of observations, b is the vector of fixed effects, α, β, γ and ρ are the vectors of direct additive genetic, maternal additive genetic, animal and maternal permanent environmental effects, respectively, X, Z_1, Z_2, W_1 and W_2 are the corresponding incidence matrices, and ε is the vector of residuals. K_A, K_M, K_C and K_Q are the matrices of coefficients of the covariance function for direct and maternal additive genetic effects and animal and maternal permanent environmental effects, respectively. A is the numerator relationship matrix, I is an identity matrix and R is the residual (co)variance matrix. $\otimes$ denotes the direct product operator. Independent distribution for temporary environmental effect and zero (co)variances between random effects were assumed.

Based on the model and order of fit selection (Liu Wenzhong et al., unpublished), a model with 6 orders of fit for direct additive genetic and animal permanent environmental effects, and 4 and 5 orders of fit for maternal additive genetic and permanent environmental effects, respectively, was used to estimate corresponding CFs. For phenotypic covariance function estimation, as Meyer (2001) suggested, only overall animal and dam effects were considered in the model rather than splitting them into their genetic and permanent environmental components. Further, any relationship between animals was ignored. Four orders of polynomial were fitted for animal and maternal effects based on previous order of fit selection.

RESULTS

Additive genetic covariance functions

Estimates of (co)variances and correlations between random regression coefficients are presented in Table 2. The

Table 2. Estimates of additive genetic and permanent environment variances (diagonal), (co)variances (lower triangular) and correlations (upper triangular) among random regression coefficients[a]

	0	1	2	3	4	5
Direct additive genetic effect						
0	3.93	0.76	-0.72	-0.44	0.31	0.11
1	2.15	2.05	-0.43	-0.84	0.22	-0.33
2	-0.62	-0.27	0.19	0.12	-0.78	-0.18
3	-0.34	-0.46	0.02	0.15	-0.26	0.10
4	0.19	0.10	-0.11	-0.03	0.10	0.42
5	0.03	-0.06	-0.01	0.00	0.02	0.01
Maternal additive genetic effect						
0	0.07	-1.00	-1.00	1.00		
1	-0.02	0.01	1.00	-1.00		
2	-0.02	0.01	0.01	-1.00		
3	0.03	-0.01	-0.01	0.01		
Animal permanent environmental effect						
0	21.28	0.82	-0.44	-0.40	0.06	0.34
1	9.75	6.66	0.14	-0.65	-0.40	0.30
2	-2.11	0.38	1.07	-0.37	-0.71	-0.06
3	-2.71	-2.48	-0.57	2.21	-0.00	-0.84
4	0.17	-0.62	-0.45	-0.00	0.37	0.54
5	2.08	1.03	-0.09	-1.65	0.44	1.78
Maternal permanent environmental effect						
0	7.44	0.40	-0.31	-0.99	-0.82	
1	1.89	2.95	0.50	-0.50	-0.54	
2	-1.65	1.70	3.85	0.32	-0.25	
3	-3.51	-1.11	0.81	1.70	0.76	
4	-3.33	-1.38	-0.73	1.48	2.22	

[a] 0: intercept, 1: linear, 2: quadratic, 3: cubic, 4: quartic and 5: quintic coefficient.

most variable coefficient was the intercept for both direct and maternal additive genetic effects. Correlations between the intercept and the linear coefficient were high positive (0.76) and negative (-1) for direct and maternal genetic effects respectively. Though, comparatively, the maternal additive genetic (co)variances between random regression coefficients were small, high correlations were obtained (positive or negative unity).

The resulting coefficients of covariance functions are summarized in Table 3. For example, let t_i and t_j be the j-th standardised age of the i-th animal, the direct additive genetic CF can be represented by:

$$A_{i,j} = \begin{bmatrix} 1 & t_i & t_i^2 & t_i^3 & t_i^4 & t_i^5 \end{bmatrix} \begin{bmatrix} 3.19 & 3.16 & -3.95 & -2.08 & 2.74 & 0.70 \\ 3.16 & 6.98 & -3.23 & -4.14 & 2.57 & -0.33 \\ -3.95 & -3.23 & 11.11 & 4.42 & -9.38 & -2.73 \\ -2.08 & -4.14 & 4.42 & 8.61 & -4.35 & -5.21 \\ 2.74 & 2.57 & -9.38 & -4.35 & 8.23 & 2.71 \\ 0.70 & -0.33 & -2.73 & -5.21 & 2.71 & 5.04 \end{bmatrix} \begin{bmatrix} 1 \\ t_j \\ t_j^2 \\ t_j^3 \\ t_j^4 \\ t_j^5 \end{bmatrix}$$

Table 3. Coefficients of covariance functions

	0	1	2	3	4	5
Additive genetic effects[a]						
0	3.19		0.07	-0.10	-0.06	0.13
1	3.16	6.98		0.15	0.09	-0.19
2	-3.95	-3.23	11.11		0.05	-0.11
3	-2.08	-4.14	4.42	8.61		0.24
4	2.74	2.57	-9.38	-4.35	8.23	
5	0.70	-0.33	-2.73	-5.21	2.71	5.04
Permanent environmental effects[b]						
0	14.64		6.55	4.09	-11.22	-9.07	-0.18
1	19.91	130.70		25.47	46.11	-28.71	-54.32
2	-12.46	-5.36	46.10		189.23	-46.25	-179.51
3	-45.66	-358.66	69.49	1114.31		37.23	64.42
4	7.10	10.88	-36.94	-83.54	31.62		190.80
5	34.90	253.31	-68.11	-816.55	75.10	606.31	

[a] Coefficients of direct (lower triangular) and maternal (upper triangular) additive genetic CFs.
[b] Coefficients of animal (lower triangular) and maternal (upper triangular) permanent environmental CFs.
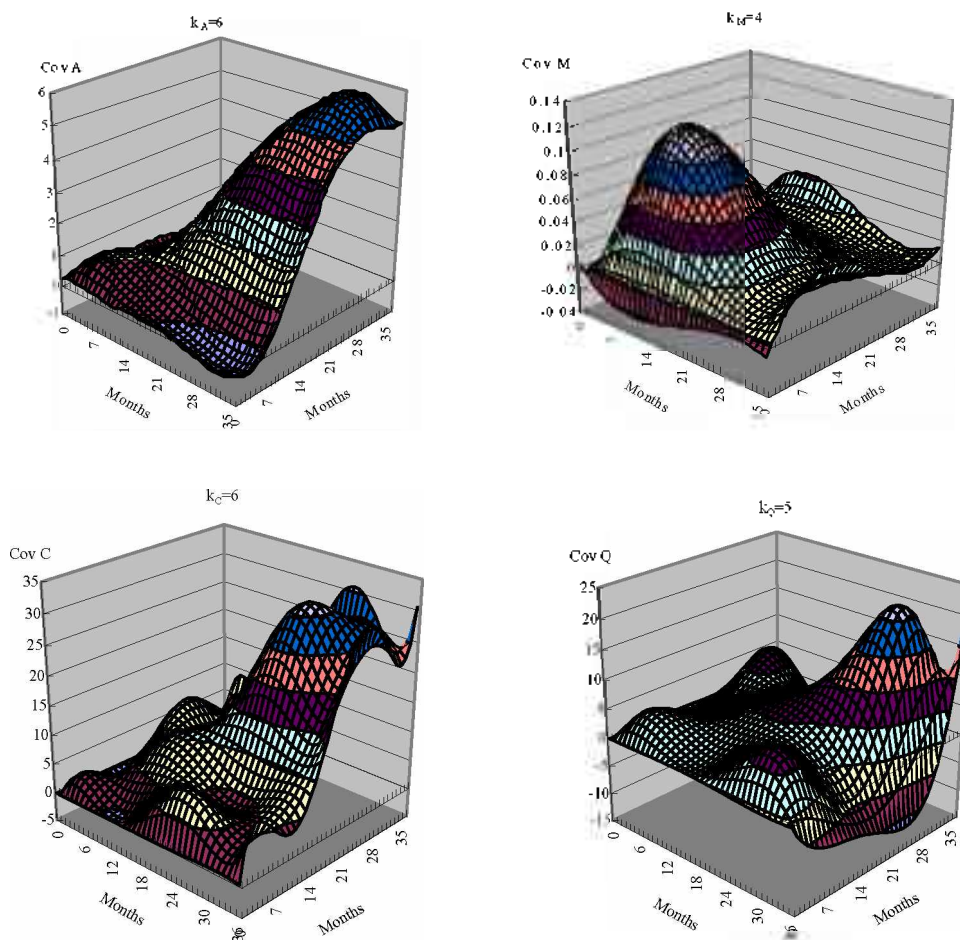
Figure 1. Estimates of direct (upper left) and maternal (upper right) additive genetic, animal (lower left) and maternal (lower right) permanent environmental (co)variances with increasing age.

Likewise, the maternal genetic CF can be written in the same way.

The (co)variance estimates for weight from birth to 36 months of age, obtained from these CFs, are presented in Figure 1 (top). The direct additive genetic (co)variances increased with age and reached a maximum at about 30 months, whereas the maternal additive genetic (co)variances increased rapidly from birth and reached a maximum at about 6 months of age, i.e., around weaning, and then decreased with age. There was almost no maternal genetic effect during 24-30 months of age.

Permanent environmental covariance functions

Intercepts of the polynomial regressions were more variable for the two sources of permanent environmental effects (Table 2). Correlations between the intercept and the linear regression coefficients were consistently positive, moderate (0.40) for maternal but high (0.82) for animal permanent environmental effects. Conversely, correlations between the intercepts and the quadratic coefficients were moderately negative. Besides, for maternal permanent

environmental effect, all correlations between the adjacent coefficients were positive but those between the separating coefficients negative.

The coefficients of CFs are also presented in Table 3 and the corresponding (co)variance estimates are plotted in Figure 1 (bottom). The animal permanent environmental (co)variances increased with age from birth to 30 months at a lower rate before 12 months and at a higher rate between 12 and 30 months. The maternal permanent environmental (co)variances changed little before 6 months, then increased slowly and reached a maximum at about 30 months.

Phenotypic covariance functions

Estimates of (co)variances and correlations between random regression coefficients for overall animal and maternal effects are listed in Table 4 and the resulting covariance functions are summarised in Table 5. The intercept for the animal effect and the linear coefficient for the maternal effect were the most variable among the random regression coefficients. This seems that the two kinds of effects influence the growth in different ways.

Table 4. Estimates of variances (diagonal), (co)variances (lower triangular) and correlations (upper triangular) between random regression coefficients[a] for overall animal and maternal effects

	Animal effect				Maternal effect			
	0	1	2	3	0	1	2	3
0	24.27	0.88	-0.43	-0.69	0.93	0.55	-0.50	-0.23
1	13.93	10.38	-0.01	-0.59	0.57	1.23	-0.28	-0.92
2	-3.20	-0.05	2.31	0.64	-0.09	-0.06	0.04	0.35
3	-2.80	-1.57	0.80	0.68	-0.12	-0.58	0.04	0.33

[a] 0: intercept, 1: linear, 2: quadratic and 3: cubic.

Table 5. Coefficients of covariance functions for overall animal and maternal effects

	Animal effect				Maternal effect			
	0	1	2	3	0	1	2	3
0	17.16				0.59			
1	19.45	31.70			0.89	8.42		
2	-9.71	-5.50	13.01		-0.23	-0.44	0.21	
3	-12.23	-17.90	8.91	14.87	-0.56	-7.63	0.43	7.17

Phenotypic covariance estimates were obtained by computing animal and maternal (co)variances between weights at different ages, based on animal and maternal CFs and combined with the estimated error variances. The results are given in Figure 2. The phenotypic (co)variance estimates also increased with age from birth to 36 months of age.

DISCUSSION

For estimation of genetic and permanent environmental CFs, the intercepts of the polynomial regressions were most variable. Correlations between intercepts and linear coefficients were positive (except that for maternal additive genetic effect) and those between intercepts and quadratic coefficients were negative. Similar results were also obtained by Meyer (2001) and Albuquerque and Meyer

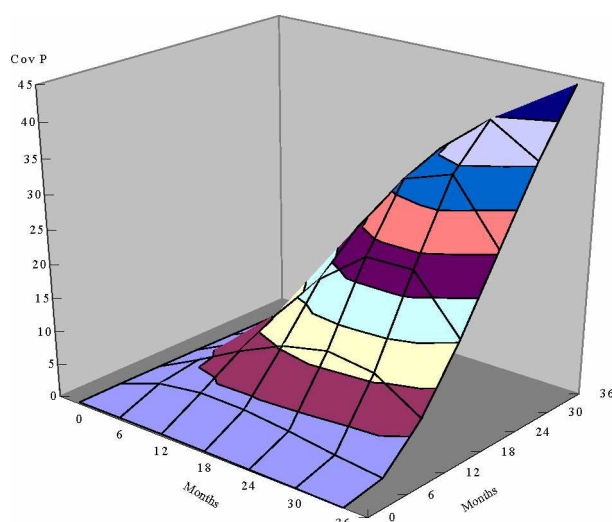**Figure 2.** Estimates of phenotypic (co)variances with increasing age.

(2001) in the estimation of CFs for growth of beef cattle and Zebu cattle, respectively.

Maternal effects are important for growth traits until weaning, although significant effects remain and have been identified for later weights as well (Meyer, 1992; Eler et al., 1995). From the present study, the remainder of maternal effects seems to be a maternal permanent environmental effect. The difference between the action of the two kinds of effects is chiefly in expression time with maternal genetic effects before weaning and maternal environmental effects after weaning. Comparatively, contributions of the animal direct genetic and permanent environmental effects to growth variation are more lasting. The two sources of permanent environmental effects differ both in expression time and in action magnitude. Besides the action time, the permanent environmental effect of animal origin contributes more variations to growth than those of maternal origin.

Covariance functions and the random regression model provide an effective and parsimonious way to accommodate longitudinal data. Albuquerque and Meyer (2001) suggested that random regression models were expected to give more accurate estimates of genetic parameters and predictions of breeding values than the conventional multi-trait model. However, with a complex model, some problems are still existed in e.g., separating different sources of random effects and computational highly demanding when fitting high order polynomials and estimating a large number of highly correlated parameters (Meyer, 2001) etc. Future research should thus be aimed at the feasibility of the approaches in routine genetic evaluation.

CONCLUSION

Analyses of continuous growth variation by using covariance functions and random regression models are feasible. Usually, correlations between the intercept and

linear coefficients are positive and those between the intercept and quadratic coefficients negative. The contribution of maternal additive genetic and permanent environmental effects to growth variation differed from those of direct additive genetic and animal permanent environmental effects in not only expression time, but also action magnitude. In the estimation of variance components and the resulting genetic parameters of growth traits, it is necessary to consider the maternal effects rationally.

ACKNOWLEDGMENTS

REFERENCES

Albuquerque, L. G. and K. Meyer. 2001. Estimates of covariance functions for growth from birth to 630 days of age in Nelore cattle. J. Anim. Sci. 79:2776-2789.

Fitzhugh, H. A. 1976. Analysis of growth curves and strategies for altering their shapes. J. Anim. Sci. 33:1036-1051.

Eler, J. P., L. D. Van Vleck, J. B. S. Ferraz and R. B. Lobo. 1995. Estimation of variances due to direct and maternal effects for growth traits in Nelore cattle. J. Anim. Sci. 72:3253-3258.

Jamrozik, J. and L. R. Schaeffer. 1997. Estimates of genetic parameters for a test day model with random regression for production of first lactation Holsteins. J. Dairy Sci. 80:762-770.

Jin Zongli, Ai Laizeng, Li Mengzhao and Dong Shangde. 1992. The grazing characters of Angora goats pastured in the native grassland of bunch grass and bush-wood on the Loess Plateau (in Chinese). J. Shanxi Agric. Univ, Special Issue, 25-30.

Kirkpatrick, M. and N. Heckman. 1989. A quantitative genetic model for growth, shape, and other infinite dimensional characters. J. Math. Biol. 27:429-450.

Kirkpatrick, M., D. Lofsvold and M. Bulmer. 1990. Analysis of the inheritance, selection and evolution of growth trajectories. Genetics 24:979-993.

Kirkpatrick, M., W. G. Hill and R. Thompson. 1994. Estimating the covariance structure of traits during growth and aging, illustrated with lactation in dairy cattle. Genet. Res. 64:57-69.

Liu Wenzhong, Li Mengzhao and Ai Laizeng. 1996. Studies on acclimatization of Angora goats in Shanxi province and recommended management practices. In: Proceedings of 6th International Conference on Goats, Beijing, China, 1:454-457.

Liu Wenzhong, Zhang Yuan and Zhou Zhongxiao. 2001. Influences of different additional random effects on estimating covariance functions (in Chinese). Hereditas (Beijing), 23:317-320.

Liu Wenzhong, Cao Guoqing, Zhou Zhongxiao and Zhang Guixian. 2002. Estimation of genetic and phenotypic covariance functions for body weight as longitudinal data of SD-II Swine Line. Asian-Aust. J. Anim. Sci. 15:622-626.

Lukovic, Z., M. Uremovic, M. Konjacic, Z. Uremovic and D. Vincek. 2007. Genetic parameters for litter size in pigs using a random regression model. Asian-Aust. J. Anim. Sci. 20:160-165.

Lupton, C. J. and M. Shelton. 1989. The 1989 Angora performance test. Ranch Magazine, 71(10):38-43.

Meyer, K. 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. Livest. Prod. Sci. 31:179-204.

Meyer, K. 1998a. Estimating covariance functions for longitudinal data using a random regression model. Genet. Sel. Evol. 30:221-240.

Meyer, K. 1998b. "DXMRR"-A program to estimate covariance functions for longitudinal data by restricted maximum likelihood. Proc. 6th World Congr. Genet. Appl. Livest. Prod. Armidale, Australia. 27:465-466.

Meyer, K. 1999. Estimates of genetic and phenotypic covariance functions for post-weaning growth and mature weight of beef cows. J. Anim. Breed. Genet. 116:181-205.

Meyer, K. 2001. Estimates of direct and maternal covariance functions for growth of Australian beef calves from birth to weaning. Genet. Sel. Evol. 33:487-514.

Meyer, K. and W. G. Hill. 1997. Estimation of genetic and phenotypic covariance functions for longitudinal or 'repeated' records by restricted maximum likelihood. Livest. Prod. Sci. 47:185-200.

Oh, S.-H. and M. T. See. 2008. Comparison of genetic parameter estimates of total sperm cells of boars between random regression and multiple trait animal models. Asian-Aust. J. Anim. Sci. 21:923-927.

Park, B. and D. Lee. 2006. Prediction of future milk yield with random regression model using test-day records in Holstein cows. Asian-Aust. J. Anim. Sci. 19:915-921.

Schaeffer, L. R. and J. C. M. Dekkers. 1994. Random regressions in animal models for test-day production in dairy cattle. Proc. 5th World Congr. Genet. Appl. Livest. Prod. Guelph, Canada. 18:443-446.

Snyman, M. A. and J. J. Olivier. 1999. Repeatability and heritability of objective and subjective fleece traits and body weight in South African Angora goats. Small Rumin. Res. 34:103-109.

Stapleton, D. L. 1987. Breeding objectives for goats. Proc. 6th Conf. Assoc. Anim. Breed. Genet. pp. 9-11.

Van der Werf, J., M. Goddard and K. Meyer. 1998. The use of covariance functions and random regression for genetic evaluation of milk production based on test day records. J. Dairy Sci. 81:3300-3308.

Xu, S. Z., R. Q. Yang, H. Y. Ren and Y. C. Pan. 2004. Estimation of genetic parameters for body weight in Chinese Simmental cattle using random regression model. Asian-Aust. J. Anim. Sci. 17:914-918.