

## Heterogeneity of Variance by Sex in Postweaning Gain of Angus Calves under Different Environment Levels

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**ABSTRACT** : Angus postweaning daily gain (PWDG) were analyzed to investigate heterogeneous variance by sex. A set of data (16,239 records) was divided into six sub-data sets according to level of environment. REML estimation was conducted by a multitrait model, where PWDG in each sex was treated as a separate trait. Estimates showed diversity among environmental levels, where the heritability for heifers was high in good environment but low in poor environment. The bull's estimates varied among environmental levels. The largest heterogeneity of phenotypic variance between sexes was estimated in a data set of the poor environment level. The genetic correlations between the heifer's PWDG and the bull's PWDG were high in the good environment and low in the poor environment (-0.17). The results suggest existence of genotype by sex interaction in the poor environment. (*Asian-Aus. J. Anim. Sci.* 1999. Vol. 12, No. 6 : 846-849)

**Key Words** : Genotype-Environment Interaction, Variance Components, Growth, Beef Cattle, Sex

### INTRODUCTION

Sex effect is mostly treated as a fixed effect for the analysis of animal breeding, where variances are assumed to be same between the sexes. The invalidity of this assumption is a classical problem in animal breeding. Often, the prediction of EBVs may be different if heterogeneity of variance exists. However this heterogeneous variance is no longer a serious problem if genetic correlation is assumed to be unity. Models which are feasible to work with were developed by Henderson (1984), Gianola (1986) and Quaas et al. (1989).

The genetic correlations between two sexes were estimated by Tong et al. (1976) as 0.85, 0.83 and 0.76 for weaning weight, yearling weight and postweaning gains. Garrick et al. (1989) reported heterogeneous variance by sex and percent purebred in Simmental, and concluded that the growth traits in both sexes were genetically the same traits. For detecting heterogeneity of variance, Lee and Pollak (1997) suggested that use of the multiple-trait model, treating male records as one trait and female records as the other, is necessary. The objectives of this study were to examine the heterogeneity of variance components and genotype by sex interaction under different levels of environment by use of the multiple-trait animal model.

### MATERIALS AND METHODS

Data studied were Angus records of the Group

Breed Plan (Nicol et al., 1985) collected from 1972 to 1989. The number of postweaning daily gain (PWDG, kg) was 20,103. After the basic data validation, records of unconnected herds and records of herds with less than 100 records were excluded. Records of steers were also eliminated because of the small number of steers (690). The total number of records was 16,239 after editing the data. The effect of selection before weaning on PWDG was assumed to be negligible. Selection after weaning was examined by calculating proportion of selected animals and selection intensities. Weaning weight (WW) was adjusted to 200 days, and yearling weight (YW) was adjusted to 400 days of age previously. PWDG was calculated from these two adjusted weights. Weight records between 100 days and 299 days of age were used for WW, and likewise weights between 300 days and 499 days for YW. The age adjustment was done by the intercept method (Raymond, 1982) for each sex.

The whole data were divided into six sub-data sets by environmental levels estimated separately for the bulls and heifers. Unconnected herds within the data sets were discarded. To infer the environment level of herds, the best linear unbiased estimator (BLUE) of the cohort was preliminarily estimated by the mixed model procedure. The model included simpler herd-year-season-sex effect as a cohort instead of herd-year-season-sex-management group.

The herds were categorized into three environment levels; high, medium and low in each sex according to the average BLUEs of the cohort. These herd averages are presented in table 1. Pairs of the environment levels for each sex are as follows:

1. HH : High in both bulls and heifers
2. HM : High in bulls and medium in heifers
3. MH : Medium in bulls and high in heifers

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- 4. MM : Medium in both heifer and bull
- 5. ML : Medium in bulls and low in heifers
- 6. LL : Low in both bulls and heifers

**Table 1.** Average BLUEs for the postweaning gain (kg) of the cohort (herd-year-season)

Data set <sup>a</sup>	Bull	Heifer
HH	0.58	0.35
HM	0.54	0.25
MH	0.44	0.31
MM	0.44	0.26
ML	0.41	0.18
LL	0.28	0.18

<sup>a</sup> H, M and L refer to high, medium and low environment level. The first letter indicates the bull's level, and the second letter indicates the heifer's level. (e.g. HM is high in the bulls and medium in the heifers).

LM data set was eliminated because of small number of records. There was no extreme pairs of herds such as HL and LH.

Variance and covariance components were estimated separately for the data sets using a multitrait animal model; PWDGs of the bulls and the heifers were treated as separate traits.

The model was:

$$y_{ijk} = \text{hysmg}_{ij} + a_{ik} + e_{ijk}$$

for  $i = M(\text{male})$  and  $F(\text{female})$ , where:

- $y_{ijk}$  = PWDG of animal  $k$  in herd-year-season-management group  $j$  in sex  $i$ ;
- $\text{hysmg}_{ij}$  = fixed effect of herd-year-season-management group  $j$  in sex  $i$ ;
- $a_{ik}$  = random additive genetic effect of animal  $k$  in sex  $i$ ;
- $e_{ijk}$  = random residual of animal  $k$  in herd-year-season-management group  $j$  in sex  $i$ ;

A management group comprised of animals raised together through weaning to yearling and weighed on the same date. In matrix notation, the model would be

$$y = Xb + Za + e,$$

where  $y$  is a vector of observations,  $b$  is a vector of the fixed effect,  $X$  is an incidence matrix relating elements of  $b$  to elements of  $y$ ,  $a$  is a vector of random additive genetic effects,  $Z$  is a known incidence matrix relating the elements of  $a$  to  $y$ , and  $e$  is the vector of residual effects.

Then

$$E \begin{bmatrix} Y \\ a \\ e \end{bmatrix} = E \begin{bmatrix} Xb \\ 0 \\ 0 \end{bmatrix}$$

$$\text{Var}(a) = \begin{bmatrix} \sigma_{aM}^2 & \sigma_{aMF} \\ \sigma_{aMF} & \sigma_{aF}^2 \end{bmatrix} \# A, \text{ and}$$

$$\text{Var}(e) = \begin{bmatrix} \sigma_{eM}^2 & 0 \\ 0 & \sigma_{eF}^2 \end{bmatrix} \# I$$

where “#” is the Kronecker product operation of matrix,  $A$  is the numerator relationship matrix among animals,  $I$  is the identity matrix,  $\sigma_{aM}^2$ ,  $\sigma_{aF}^2$  and  $\sigma_{aMF}^2$  are additive genetic variance of PWDG in female, male and additive genetic covariance between male and female;  $\sigma_{eM}^2$  and  $\sigma_{eF}^2$  are residual variance of male and female animals, respectively.

REML estimation for variance components was conducted by the multivariate DFREML program (Meyer, 1990). Initial starting values of the variance components were averages of the estimates by preliminary univariate analyses. Then other starting values were used to examine the global maximum. Likelihood ratio tests (Kendall and Stuart, 1979) were carried out to estimate significant range of the genetic correlation.

### RESULTS AND DISCUSSION

The statistical description of the data is presented in table 2. The numbers of herds included in the data sets varied from two in MH to ten in HH. The other data sets had five or six herds within them. The means of PWDG reflected the difference of the environment level. The largest CV was found on the bulls of LL. In the heifers, no tendency was observed about their CVs.

The estimates of the variance components and the heritabilities are presented in table 3. The genetic variances of PWDG were in the range of 0.0011 and 0.0035 kg<sup>2</sup> for the heifers and showed the tendency of the small variance in the data set of the poor environment effect. The bull's genetic variance varied from 0.0005 to 0.0104 kg<sup>2</sup>. Larger difference of the genetic variance was observed in the bulls than in the heifers. The residual variances of the heifers were relatively consistent and in the range of 0.0036 and 0.0063 kg<sup>2</sup>. The residual variance was small in the poor environment for the heifers. The residual variances of the bulls were larger than those of the heifers.

The heritabilities for the heifers showed a similar tendency to the genetic variance; less variable among the data sets than those for the bulls and tended to be small in the poor environment. No clear tendency was observed for the heritability of the bulls.

Environment factors may affect the estimates for each sex in a different manner. A possible source of variation is a sexual difference of sensitivity to

**Table 2.** Summary of data sets of post weaning daily gain (PWDG)

	Data set <sup>a</sup>					
	HH	HM	MH	MM	ML	LL
No. of herds	10	6	2	5	6	5
No. of HYSM <sup>b</sup>	200	121	46	79	63	129
	184	105	42	78	68	144
No. of records <sup>c</sup>	1249	840	927	745	653	1188
	1452	1110	1591	866	837	1832
PWDG <sup>c</sup> (kg)						
Mean	0.85	0.85	0.67	0.68	0.63	0.45
	0.57	0.43	0.44	0.43	0.32	0.30
SD	0.21	0.27	0.25	0.21	0.18	0.21
	0.18	0.17	0.18	0.15	0.17	0.13
CV	0.24	0.31	0.38	0.31	0.28	0.46
	0.31	0.40	0.40	0.35	0.52	0.43

<sup>a</sup> H, M and L refer to high, medium and low environment level. The first letter indicates the bull's level, and the second letter indicates the heifer's level.

<sup>b</sup> Herd-year-season-management group. <sup>c</sup> The first row in each item is for the bulls, and the second row is for the heifers.

**Table 3.** Estimates of (co)variances and genetic parameters of postweaning daily gain

Parameter <sup>bc</sup>	Data set <sup>a</sup>					
	HH	HM	MH	MM	ML	LL
$V_g$ ( $\times 10^2$ kg)	0.38	0.58	0.54	0.05	0.26	1.04
	0.35	0.32	0.35	0.23	0.22	0.11
Cov ( $\times 10^2$ kg)	0.36	0.27	0.22	0.07	0.11	-0.06
$V_r$ ( $\times 10^2$ kg)	0.92	0.65	1.02	1.16	0.55	0.56
	0.48	0.63	0.50	0.50	0.36	0.39
$h^2$	0.29	0.48	0.35	0.04	0.32	0.65
	0.42	0.34	0.41	0.32	0.38	0.22
$r_g^d$	1.00	0.63	0.52*	0.64	0.48*	-0.17*

<sup>a</sup> H, M and L refer to high, medium and low environment level. The first letter indicates the bull's level, and the second letter indicates the heifer's level.

<sup>b</sup>  $V_g$ , Cov,  $V_r$ ,  $h^2$  and  $r_g$  are genetic variance, genetic covariance between sex specific postweaning daily gain, residual variance, heritability and genetic correlation, respectively.

<sup>c</sup> The first row in each item is for the bulls, and the second row is for the heifers.

<sup>d</sup>  $r_g$  with "\*" indicated significant difference ( $p < 0.05$ ) from unity.

environment effect. The bull's genetic variances showed large difference among the data sets. The largest genetic variance in LL may be related to competition among the bulls under the poor environment. The bull's residual variances also had larger difference than the heifer's.

Results in laboratory animals showed that large phenotypic variance exists for male mice selected for high aggression if they were housed in high

population density (Oikawa et al., 1998). However, male mice of low aggression or female mice of the both lines showed small phenotypic variance whether they were housed in high or low population density. Falconer (1989) suggested that competition among animals can be an additional source of variation for growth rate under limited resource. In the bulls of LL, the competition induced by the poor environment may increase the genetic variance and the residual variance.

The genetic variances of the heifers seem to be dependent on the level of the environment; the large variance in the good environment level and vice versa in the poor environment level. The residual variances of the heifers were affected by the environment levels less than the genetic variances.

The estimated heritabilities of PWDG varied in both sexes, but the averages were moderate and agreed with average values in review papers (Woldehawariat et al., 1977; Koots et al., 1994). The heifer's heritability was the same as the estimates (0.32) by Garrick et al. (1989). The bull's heritability was higher than their estimate (0.26).

The highest genetic correlation was unity in HH data set, whereas the lowest was below zero in LL. The correlations in the other data sets were moderate and showed a slight downward tendency according to the decrease of the environment level. The genetic correlations in LL, ML and MH were significantly different from correlations of unity by the likelihood ratio test.

The average genetic correlation was close to the value (0.71) reported by Tong et al. (1976), but lower than the perfect correlation suggested by Garrick et al. (1989). In this study, the correlation of unity was estimated in the good environment for both sexes. On the contrary, the low correlation was found in the

poor environment. This result suggests that the genotype by sex interaction under the poor environment may be caused by additional factors in the bulls such as their aggression.

The genotype by sex interaction was suggested to exist in some of the data sets. Moreover the estimates of the variance components were different between the sexes in all the data sets. However this result does not necessarily require the inclusion of the heterogeneity of variance into the prediction model for the breeding values. An additional study needs to be conducted to compare prediction models for data sets with the heterogeneous variance and the genotype by sex interaction.

Table 4 presents proportions selected, selection differentials and selection intensity when selection is assumed to be conducted after the weaning. The proportion selected was low in the bulls of MH and LL, and in the heifers of HH and MM. The selection intensities were high for the heifers of HH and for the bulls of HM. A moderate intensity was found for bulls of LL, and low intensities were in the other sub-data sets.

**Table 4.** Proportion selected (P), selection differential (S) and selection intensity (i), under an assumption of selection after weaning (200 days of age)

Item <sup>b</sup>	Data set <sup>a</sup>					
	HH	HM	MH	MM	ML	LL
P (%)	82	71	41	91	70	34
	44	89	96	53	95	61
S	6	5	18	3	1	10
	16	3	4	5	3	5
i (%)	17	15	53	9	3	29
	46	11	13	19	12	17

<sup>a</sup> H, M and L refer to high, medium and low environment level. The first letter indicates the bull's level, and the second letter indicates the heifer's level.

<sup>b</sup> The first row in each item is for the bulls, and the second row is for the heifers.

Under the assumption of the selection in which animals are selected by weight gain or a trait closely related to growth, no clear relationship was observed between the intensity of selection and the estimates of the genetic parameters. Thus this simple assumption seems to be inadequate. A number of traits may influence the selection after the weaning, such as susceptibility to disease, maternal effect, robustness to new environment etc. Thus the effect of the selection based only on the postweaning growth seems to have no effect on the estimates of the genetic parameters.

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**REFERENCES**

Falconer, D. S. 1989. Introduction to quantitative genetics. 3rd ed. Longman Scientific International and John Wiley and Sons, Essex, UK and New York.

Garrick, D. J., E. J. Pollak, R. L. Quaas and L. D. Van Vleck. 1989. Variance heterogeneity in direct and maternal weight traits by sex and percent purebred for Simmental-sired calves. *J. Anim. Sci.* 67:2515.

Gianola, D. 1986. On selection criteria and estimation of parameters when the variance is heterogeneous. *Theor. Appl. Genet.* 72:671.

Henderson, C. R. 1984. Applications of Linear Models in Animal Breeding. Univ. of Guelph, Guelph, Ontario, Canada.

Kendall, M. G. and A. Stuart. 1979. The advanced theory of statistics, vol. II :inference and relationship. 4th Ed. Charles Griffin.

Koots, K. R., J. P. Gibson, C. Smith and J. W. Wilton. 1994. Analyses of published genetic parameter estimates for beef production traits. 1. Heritability. *Anim. Breed. Abstr.* 62:309.

Lee, C. and E. J. Pollak. 1997. Influence of partitioning data by sexon genetic variance and covariance components for weaning weight in beef cattle. *J. Anim. Sci.* 75:61.

Meyer, K. 1991. Estimating variances and covariances for multivariate animal models by restricted maximum likelihood. *Genet. Sel. Eval.* 23:67.

Nicol, D. C., H. U. Graser, B. Tier and K. Hammond. 1985. BREEDPLAN - A new within-herd evaluation system for the national beef recording scheme. Proc. 5th Conf. Aust. Assoc. Anim. Breed. Genet. Sydney: 151-153.

Oikawa, T., Y. Kawamoto, H. Matsui, S. Nakamura, T. Fujiki, T. Morimasa and K. Sato. 1998. Effect of population density on growth of mice selected for high and low aggression. Proc. 6th World Cong. Genet. Appl. Livest. Prod. 27:169.

Quaas, R. L., D. J. Garrick and W. H. McElhenney. 1989. Multiple trait prediction for a type of model with heterogeneous genetic and residual covariance structures. *J. Anim. Sci.* 67:2529.

Raymond, C. A. 1982. Systematic environmental effects on beef cattle growth. M. Rur. Sci. Thesis. University of New England, Armidale.

Tong, A. K. W., J. W. Wilton and L. R. Schaeffer. 1976. Simultaneous estimations of variance and covariance components between male and female growth traits in beef cattle. *Can. J. Anim. Sci.* 56:830.

Woldehawariat, G., R. R. Talamantes, R. R. Petty, Jr. and T. C. Cartwright. 1977. A summary of genetic and environmental statistics for growth and conformation characters of young beef cattle. Texas A&M Dept. of Anim. Sci. Tech. Rep. 103.