

Estimation of Genetic Parameters for Direct, Maternal and Grandmaternal Genetic Effects for Birth, Weaning and Six Month Weights of Hanwoo (Korean Cattle)

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ABSTRACT : The objectives of this study of Hanwoo (Korean Cattle) were 1) to estimate genetic parameters for direct and maternal genetic effects for birth weight, weaning weight, and six months weight which can be used for genetic evaluations and 2) to compare models with and without grandmaternal effects. Data were obtained from the National Livestock Research Institute in Rural Development Administration (RDA) of Korea and were used to estimate genetic parameters for birth weight (BW, n=10,889), weaning weight at 120-d (WW, n=8,637), and six month weight (W6, n=8,478) in Hanwoo. Total number of animals in pedigrees was 14,949. A single-trait animal model was initially used to obtain starting values for multiple-trait animal models. Estimates of genetic parameters were obtained with MTDFREML using animal models and derivative-free REML (Boldman et al., 1995). Estimates of direct heritability for BW, WW, and W6 analyzed as single-traits were 0.09, 0.03, and 0.02 from Model 3 which included direct and maternal genetic, maternal permanent environmental effects, and effects due to sire \times region \times year-season interaction, respectively. Ignoring sire \times region \times year-season interaction effect in the model (Model 2) resulted in larger estimates for direct heritability than for Model 3. Estimates of maternal heritability for BW, WW and W6 were 0.04, 0.05, and 0.07 from Model 3, respectively. The estimates of direct-maternal genetic correlation were positive for BW, WW, and W6 with Model 3 but were negative with Model 2 for WW and W6. Estimates of direct genetic correlations between BW and WW, BW and W6, and WW and W6 were large: 0.52, 0.45, and 0.90, respectively. Genetic correlations were also large and positive for maternal effects for BW with maternal effects for WW and W6 (0.69 and 0.74), and even larger for WW with W6 (0.97). The log likelihood values were the same for models including grandmaternal effects as for models including maternal effects for all traits. These results indicate that grandmaternal effects are not important for these traits for Hanwoo or that the data structure was not adequate for estimating parameters for a grandmaternal model. (*Asian-Aus. J. Anim. Sci.* 2000. Vol. 13, No. 2 : 149-154)

Key Words : Hanwoo, Genetic Parameters, Maternal, Model

INTRODUCTION

Genetic parameters for weight traits at birth and weaning for Korean Cattle which is called Hanwoo using models including maternal effects have not been previously reported extensively. Maternal effects may be important to offspring for some traits. Improvement in weaning weights of beef calves has been found to depend on increased preweaning growth potential of calves and maternal ability of cows (e.g., Mangus and Brinks, 1971). Birth weight and growth rate have been shown to be influenced by an animal's genetic potential and by the maternal environment (Meyer, 1992). Numerous studies of preweaning growth of beef cattle have reported a genetic correlation between direct and maternal genetic effects (Bertrand and Benyshek, 1987; Brown and Galvez, 1969; Burfening

et al., 1981; Garrick et al., 1989; Koch, 1972; Kriese et al., 1991; Nelsen et al., 1984; Yokoi et al., 1997).

Willham (1963) suggested that the maternal effect of the granddam may influence the maternal effect of the dam. He (1972) developed principles for biometrical analyses of direct and maternal effects and again proposed the possible influence of a grandmaternal effect. Dodenhoff et al. (1998) reported that grandmaternal effects were not important for birth weight but seemed to be important for weaning weight in Herefords. They suggested that when the model did not include grandmaternal effects, maternal heritability may be underestimated.

Models which include the effects of sire \times herd \times year interaction (Dodenhoff et al., 1999) and of sire \times year interaction (Lee and Pollak, 1997; Robinson, 1994) in beef cattle have been investigated. Lee and Pollak (1997) and Robinson (1994) reported that the direct-maternal genetic correlation increased when the effects of sire \times year interaction were included in the model.

The objectives of this study of Hanwoo were 1) to estimate genetic parameters for direct and maternal genetic effects with and without effects in the model for effects of sire \times region \times year-season interaction, 2) to compare models with and without grandmaternal

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effects, and 3) to estimate genetic correlations among the traits.

MATERIALS AND METHODS

The materials and methods section is divided into two parts. The first part is a description of direct and maternal genetic effects included in the model. The second part is a description of grandmaternal genetic effects included in the model. Only records with maternal granddam known were used in the second part.

Section I. Model with direct and maternal genetic effects

Data were collected from 1974 through 1995 by the National Livestock Research Institute in Rural Development Administration (RDA) of Korea and were used to estimate genetic parameters for birth weight (BW, $n=10,889$), 120-d weaning weight (WW, $n=8,637$), and 180-d six month weight (W6, $n=8,478$). Total number of animals in pedigrees was 14,949. Numbers of records, overall means, and standard deviations by trait and by sex are in table 1. Adjusted weaning weight at 120-d was calculated as:

$$\text{Adjusted 120-day weight} = \frac{\text{actual weaning weight} - \text{birth weight}}{\text{age in days at weaning}} \times 120 + \text{birth weight}$$

Three single-trait animal models were initially used for this analysis. Then estimates from the most

appropriate single trait model were used as starting values for two-trait analyses. Region \times year-season and age of dam \times sex of calf were fitted as fixed effects for all models. The spring season is centered on April and the fall season is centered on October. Two recording regions were involved. Herd identification was unavailable. Animals were intact males and females. Thus, steers were not included in these data. Table 2 presents genetic parameters to be estimated with the three models.

Table 2. Parameters estimated with the three models

Model	Parameters ^a					
	σ_a^2	σ_m^2	σ_{am}	σ_p^2	σ_q^2	σ_e^2
1	✓	✓	✓	✓		✓
2 ^b	✓	✓	✓	✓		✓
3 ^b	✓	✓	✓	✓	✓	✓

^a σ_a^2 = direct genetic variance, σ_m^2 = maternal genetic variance, σ_{am} = covariance between direct and maternal genetic effects, σ_p^2 = variance of maternal permanent environmental effects, σ_q^2 = variance of sire \times region \times year-season interaction effects, and σ_e^2 = variance of temporary environmental effects.

^b If sire identification was missing then the record was deleted.

Model 1 included direct and maternal genetic, maternal permanent environmental and residual environmental effects,

$$y = X\beta + Z_1a + Z_2m + W_1p + e,$$

where

y = the $N \times 1$ vector of observations,

Table 1. Number of observations, overall means (kg)^a and standard deviations (SD) by trait including and not including progeny with missing sire identification

Trait ^b		No. of records	No. of sires	No. of dams	No. of SRYS ^c	mean \pm SD
Including missing sires						
BW		10,889	1,386	3,908	-	23.02 \pm 2.76
WW		8,637	1,300	3,423	-	95.39 \pm 20.55
W6		8,478	1,243	3,419	-	131.76 \pm 19.36
Not including missing sires						
BW	Overall	10,747	1,346	3,826	1,506	23.01 \pm 2.76
	Female	5,207	946	2,619	1,086	22.20 \pm 2.52
	Male	5,540	885	2,607	1,012	23.77 \pm 2.76
WW	Overall	8,528	1,263	3,355	1,396	95.41 \pm 20.49
	Female	3,929	852	2,244	965	91.03 \pm 18.88
	Male	4,599	858	2,300	969	99.15 \pm 21.07
W6	Overall	8,377	1,208	3,359	1,347	131.78 \pm 19.35
	Female	3,696	765	2,115	881	126.04 \pm 16.14
	Male	4,681	875	2,396	990	136.30 \pm 20.45

^a Records unadjusted for the model effects.

^b BW = birth weight (kg), WW = weaning weight (kg), and W6 = six month weight (kg).

^c SRYS = sire \times region \times year-season interaction.

β = vector of fixed effects (region \times year-season and age of dam \times sex combinations),
 a = vector of breeding values for direct genetic effects,
 m = vector of breeding values for maternal genetic effects,
 p = vector of maternal permanent environmental effects,
 e = vector of random residual effects, and X , Z_1 , Z_2 , and W_1 are known matrices relating observations in y to fixed and random effects.

Model 2 was based on Model 1 but if identification of a sire was missing then the record was deleted. Model 3 was based on Model 2 but was extended to include effects due to sire \times region \times year-season (SRYS) interaction,

$$y = X\beta + Z_1a + Z_2m + W_1p + W_2q + e,$$

where for the added part of the model q = vector of sire \times region \times year-season interaction effects, and W_2 is a known matrix relating observations in y to random effects in q .

For the model:

$$E[y] = X\beta,$$

and the (co)variance structure of the random effects for Model 3 is:

$$V \begin{bmatrix} a \\ m \\ p \\ q \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & A\sigma_{am} & 0 & 0 & 0 \\ A\sigma_{am} & A\sigma_m^2 & 0 & 0 & 0 \\ 0 & 0 & I_{N_d}\sigma_p^2 & 0 & 0 \\ 0 & 0 & 0 & I_N\sigma_q^2 & 0 \\ 0 & 0 & 0 & 0 & I_N\sigma_e^2 \end{bmatrix}$$

where

N_d = number of dams,

N_s = number of sire \times region \times year-season combinations,

N = number of records,

A = numerator relationship matrix among animals in the pedigree file, and

I = identity matrix of appropriate order.

Estimates of genetic parameters were obtained with MTDFREML which is a set of programs for estimating (co)variance components using animal models and derivative-free REML (Boldman et al., 1995).

Section II. Model with direct, maternal and grandmaternal genetic effects

Data were birth (BW, $n=5,023$), 120-d weaning (WW, $n=4,218$), and 180-d six month weights (W6, $n=4,040$). All animals with records were required to have a known granddam. Total number of animals in

pedigrees was 7,785. Three single-trait animal models were compared. Region \times year-season and age of dam \times sex combinations were fitted as fixed effects for all models. However, effects of sire \times region \times year-season (SRYS) interaction were not included in the model in this section.

Effects in Model 1 included direct and maternal genetic, maternal permanent environmental, and residual environmental effects.

Model 2 was based on Model 1 but was extended to include a vector of grandmaternal effects assumed to be uncorrelated.

Model 3 was based on Model 2 but was extended to include grandmaternal genetic effects.

Estimates of genetic parameters were obtained with REML using the average information method (AI-REML) (Johnson et al., 1995) with a program developed by Dodenhoff et al. (1998).

The results were inconclusive as estimates (and likelihoods) were the same as for the maternal effects model. The most likely reason is that the data structure was inadequate for estimating the six genetic (co)variance components and the three environmental (co)variance components. A less likely reason is that grandmaternal effects are nil for Hanwoo cattle.

RESULTS AND DISCUSSION

For all single trait analyses, estimates with Models 1 and 2 were essentially the same as only a few animals did not have an identified sire. Therefore this section will compare results with Models 2 and 3.

Birth weight

Parameter estimates for birth weight using the three models are shown in table 3 for single trait analyses. Estimates of direct and maternal heritability with Model 2, which ignored effects due to sire \times region \times year-season (SRYS) interaction were 0.14 and 0.04, respectively. Estimates of direct and maternal heritability with Model 3, which included effects due to sire \times region \times year-season (SRYS) interaction were 0.09 and 0.04, respectively. Failure to include sire \times region \times year-season interaction effects in the model (Model 2) resulted in a higher estimate for direct heritability than for Model 3. The direct-maternal genetic correlation with Model 3 was large and positive (0.61) but was only 0.23 with Model 2. This result agrees with Meyer (1992) who reported a positive direct-maternal genetic correlation of 0.29 in Australian beef cattle. Including effects due to sire \times region \times year-season interaction (Model 3) resulted in an improvement in the log likelihood compared to Model 2 and estimates of variance components with Model 3 were significantly different from those for Model 2. The estimate of direct heritability was less and direct-

Table 3. Estimates of variance components and genetic parameters (asymptotic standard errors) for birth, weaning and six month weights

Parameters ^a	Birth weight			Weaning weight			Six month weight		
	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3
-2log L	29336.74	28925.48	28920.37	54935.06	54198.86	54187.91	55632.92	54971.96	54956.57
σ_a^2	0.82	0.77	0.48	31.42	30.29	7.46	39.42	38.81	6.21
σ_m^2	0.25	0.25	0.23	17.04	16.95	11.88	28.30	29.09	20.99
σ_{am}	0.09	0.10	0.20	-10.31	-9.87	1.08	-11.60	-11.76	4.53
σ_b^2	0.16	0.14	0.13	25.72	24.85	25.02	29.54	28.68	29.04
σ_q^2			0.09			7.24			9.74
σ_e^2	4.29	4.32	4.44	163.91	164.04	173.67	196.65	197.65	211.46
h_a^2	0.25	0.14	0.09	0.14	0.13	0.03	0.14	0.13	0.03
	(0.02)	(0.02)	(0.03)	(0.03)	(0.03)	(0.04)	(0.03)	(0.03)	(0.04)
h_m^2	0.04	0.04	0.04	0.07	0.07	0.05	0.07	0.10	0.07
	(0.02)	(0.02)	(0.02)	(0.03)	(0.03)	(0.03)	(0.04)	(0.04)	(0.04)
r_{am}	0.20	0.23	0.61	-0.45	-0.44	0.11	-0.35	-0.35	0.40
	(0.19)	(0.26)	(0.48)	(0.34)	(0.17)	(0.72)	(0.29)	(0.18)	(0.48)
p^2	0.03	0.03	0.02	0.11	0.11	0.11	0.10	0.10	0.10
	(0.02)	(0.02)	(0.02)	(0.02)	(0.02)	(0.02)	(0.02)	(0.03)	(0.03)
q^2			0.02			0.03			0.04
			(0.01)			(0.01)			(0.01)
e^2	0.76	0.77	0.80	0.72	0.73	0.77	0.70	0.70	0.75
	(0.02)	(0.02)	(0.02)	(0.02)	(0.02)	(0.02)	(0.02)	(0.02)	(0.02)

^a σ_a^2 = direct genetic variance, σ_m^2 = maternal genetic variance, σ_{am} = covariance between direct and maternal effects, σ_b^2 = variance of maternal permanent environmental effects, σ_q^2 = variance of sire \times region \times year-season interaction effects, σ_e^2 = variance of temporary environmental effects, h_a^2 = direct heritability, h_m^2 = maternal heritability, r_{am} = genetic correlation between direct and maternal effects, p^2 = fraction of variance due to maternal permanent environmental effects, q^2 = fraction of variance due to sire \times region \times year-season interaction effects, and e^2 = fraction of variance due to temporary environmental effects.

maternal genetic correlation were greater with Model 3 than with Model 2. Earlier studies showed mostly negative correlations between direct and maternal effects for birth weight as reviewed by Mohiuddin (1993). This analysis indicates that inclusion of sire \times region \times year-season interaction effect in the model seems to be important for birth weight for Korean Cattle.

Weaning weight

Parameter estimates for weaning weight with the three models also are shown in table 3. The pattern for estimates for weaning weight is similar to the pattern for birth weight. Estimates of direct and maternal heritability with Model 3 were 0.03, and 0.05, respectively compared to 0.13 and 0.07 with Model 2. The direct-maternal genetic correlation from Model 3 was positive (0.11) but was negative (-0.44) with Model 2. The estimate of 0.11 agrees with Wright et al. (1987) who reported a positive direct-maternal genetic correlation of 0.16 in American Simmental cattle. Inclusion of effects due to sire \times region \times year-season interaction (Model 3) resulted in an improvement in the log likelihood compared to Model 2. Estimates of variance components for Model 3 were significantly different from those from Models

2 and 1 because including effects of sire \times region \times year-season interaction increased the direct-maternal genetic correlation from large negative (-0.44) to slightly positive (0.11) and also reduced the estimate of direct heritability. This pattern has been reported by Robinson (1994) and by Lee and Pollak (1997). Numerous studies of beef cattle have found mostly negative genetic correlation correlations between direct and maternal effects for weaning weight as reviewed by Mohiuddin (1993). Model 2 that ignored sire \times region \times year-season interaction for weaning weight resulted in a significantly poorer log likelihood. The results indicate that inclusion of sire \times region \times year-season interaction effects in the model for weaning weight seems to be important for Korean Cattle.

Six month weight

Parameter estimates for six month weight with the three models are presented in table 3. The pattern for estimates for six month weight is similar to the pattern for birth and weaning weights. Estimates of direct and maternal heritability with Model 3 for six month weight analyzed as single-traits were 0.02, and 0.07, respectively but were 0.13 and 0.10 with Model 2. Including effects of sire \times region \times year-season interaction also increased the direct-maternal genetic

correlation from large negative (-0.35) to positive (0.40) and also reduced the estimate of direct heritability compared to Model 2. The difference in log likelihoods between Models 2 and 3 was significant indicating including effects of sire \times region \times year-season interaction in the model is important. The differences in estimates between Models 2 and 3 follow the same pattern for W6 as for WW as would be expected. The results indicate that inclusion of effects of sire \times region \times year-season interaction for six month weight in the model also is important for analyses of six month weight in Hanwoo.

With these early-in-life traits, positive estimates of genetic correlation between direct and maternal genetic effects were found when sire \times region \times year-season interaction effects were included in the model (Model 3). The model ignoring effects of sire \times region \times year-season interaction resulted in negative genetic correlations between direct and maternal genetic effects except for birth weight. For all traits, including the interaction effects resulted in an increase in the direct-maternal genetic correlation and a decrease in direct heritability. These results agree with those of Robinson (1994) and Lee and Pollak (1997) who reported that estimates of direct-maternal correlations increased when sire \times year effects were included in the model.

Multiple trait analyses

Parameter estimates for two-trait analyses for birth, weaning, and six month weights are shown in table 4. Model 3, which included effects of sire \times region \times year-season (SRYS) interaction, was the best fitting model for single trait analyses of birth, weaning, and six month weights. Therefore, Model 3 was used for the two-trait analyses.

Estimates of direct genetic correlations between BW and WW, and between BW and W6 were 0.52 and 0.45, respectively which are moderate and positive, and between WW and W6 was large (0.90). Estimates of direct with maternal genetic correlations were similar to those from the single trait analyses with Model 3. Estimate of genetic correlation between direct genetic for BW and maternal effects for WW was near zero, -0.04. The estimate of the maternal genetic correlation between BW and WW was 0.66. Estimate of maternal permanent environmental correlation between BW and WW was 0.20 and between WW and W6 was large (0.99). Estimates of environmental correlations between BW and WW and between BW and W6 were 0.17 and 0.17, respectively, the estimate between WW and W6 was large (0.73). Nelsen and Kress (1979) reported an estimate of direct genetic correlation between BW and WW to be 0.53 for Angus in USA. Koots et al. (1994) in a review reported the average of estimates of direct genetic

Table 4. Parameter estimates from two-trait analyses for birth and weaning weight, birth and six month weights, and weaning and six month weights

Traits ^a	1	BW	BW	WW
	2	WW	W6	W6
$\sigma_{y_i}^2$		5.59	5.59	234.39
$\sigma_{y_j}^2$		227.81	283.73	312.50
$h_{a_i}^2$		0.08	0.08	0.06
$h_{a_j}^2$		0.04	0.03	0.05
$h_{m_i}^2$		0.05	0.05	0.05
$h_{m_j}^2$		0.06	0.09	0.07
$r_{a_i a_j}$		0.52	0.45	0.90
$r_{a_i m_i}$		0.59	0.54	0.11
$r_{a_i m_j}$		-0.04	0.21	0.19
$r_{a_j m_i}$		0.66	0.83	0.17
$r_{a_j m_j}$		0.03	0.26	0.32
$r_{m_i m_j}$		0.69	0.74	0.97
p_1^2		0.02	0.01	0.11
p_2^2		0.11	0.10	0.11
q_1^2		0.02	0.02	0.03
q_2^2		0.03	0.04	0.03
$r_{b_i b_j}$		0.20	0.00	0.99
$r_{a_i e_i}$		0.59	0.73	0.87
e_1^2		0.79	0.79	0.75
e_2^2		0.76	0.74	0.72
$r_{e_i e_j}$		0.17	0.69	0.73

^a BW= birth weight, WW= weaning weight, W6= six month weight, $\sigma_{y_i}^2$ = phenotypic variance for trait i , $h_{a_i}^2$ = direct heritability for trait i , $h_{m_i}^2$ = maternal heritability for trait i , $r_{a_i a_j}$ = genetic correlation between direct effects for trait i and j , $r_{a_i m_i}$ = genetic correlation between direct and maternal effects for trait i , $r_{a_i m_j}$ = genetic correlation between direct effects for trait i and maternal effects for trait j , $r_{a_j m_i}$ = genetic correlation between direct and maternal effects for trait j , and 2, p_i^2 = fraction of variance due to maternal permanent environmental effects for trait i , q_i^2 = fraction of variance due to sire \times region \times year-season interaction effects for trait i , $r_{b_i b_j}$ = correlation between maternal permanent environmental effects for trait i and j , $r_{a_i e_i}$ = correlation between sire \times region \times year-season interaction effects for trait i and j , and e_i^2 = fraction of variance due to temporary environmental effects for trait i , and $r_{e_i e_j}$ = correlation between temporary environmental effects for traits i and j .

genetic correlation between BW and WW to be 0.50, the average of estimates of correlation between direct genetic for BW and maternal effects for WW to be -0.14, the average of estimates of correlations between direct genetic for WW and maternal effects for BW to be -0.05, and the average of estimates of maternal genetic correlations between BW and WW to be 0.39.

CONCLUSIONS

Results of this study suggest that maternal effects are important for Hanwoo (Korean Native Cattle) for birth, weaning, and six month weights. Including sire \times region \times year-season interaction effects in the model for genetic analysis of birth, weaning, and six month weight may be important because interaction effects seem to influence variance and covariance components associated with direct and maternal genetic effects. The data structure was not sufficient to determine whether grandmaternal effects are important for birth, weaning, and six month weight for Hanwoo. The large genetic correlations between weights at weaning (about four months) and at six months and similar estimates of heritability indicate little reason to maintain or analyse both weaning and six-month weights in Hanwoo.

REFERENCES

- Bertrand, J. K. and L. L. Benyshek. 1987. Variance and covariance estimates for maternally influenced beef growth traits. *J. Anim. Sci.* 64:728-734.
- Boldman, K. G., L. A. Kriese, L. D. Van Vleck, C. P. Van Tassell and S. D. Kachman. 1995. A manual for use of MTDFREML. A set of programs to obtain estimates of variances and covariances. USDA, ARS.
- Brown, C. J. and V. Galvez. 1969. Maternal and other effects on birth weight of beef calves. *J. Anim. Sci.* 28:162-167.
- Burfening, P. J., D. D. Kress and R. L. Friedrich. 1981. Calving ease and growth rate of Simmental sired calves. III. Direct and maternal effects. *J. Anim. Sci.* 53:1210-1216.
- Dodenhoff, J., L. D. Van Vleck and D. E. Wilson. 1999. Comparison of models to estimate genetic effects for weaning weight of Angus cattle. *J. Anim. Sci.* (in press).
- Dodenhoff, J., L. D. Van Vleck, S. D. Kachman and R. M. Koch. 1998. Parameter estimates for direct, maternal, and grandmaternal genetic effects for birth weight and weaning weight in Hereford cattle. *J. Anim. Sci.* 76:2521-2527.
- 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.* 67:2515-2528.
- Johnson, D. L. and R. Thompson. 1995. Restricted maximum likelihood estimation of variance components for univariate animal models using sparse matrix techniques and average information. *J. Dairy Sci.* 78:449-456.
- Koch, R. M. 1972. The role of maternal effects in animal breeding. VI. Maternal effects in beef cattle. *J. Anim. Sci.* 35:1316-1323.
- Koots, K. R., J. P. Gibson and J. W. Wilton. 1994. Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. *Anim. Breed. Abst.* 62:825-853.
- Kriese, L. A., J. K. Bertrand and L. L. Benyshek. 1991. Genetic and environmental growth trait parameter estimates for Brahman and Brahman-derivative cattle. *J. Anim. Sci.* 69:2362-2370.
- Lee, C. and E. J. Pollak. 1997. Relationship between sire \times year interactions and direct-maternal genetic correlation for weaning weight of Simmental cattle. *J. Anim. Sci.* 75:68-75.
- Mangus, W. L. and J. S. Brink. 1971. Relationships between direct and maternal effects on growth in Herefords. I. Environmental factors during preweaning growth. *J. Anim. Sci.* 32:17-25.
- Nelsen, T. C. and D. D. Kress. 1979. Estimates of heritabilities and correlations for production characters of Angus and Hereford calves. *J. Anim. Sci.* 48:286-292.
- Nelsen, T. C., R. E. Short, J. J. Urlick and W. L. Reynolds. 1984. Genetic variance components of birth weight in a herd of unselected cattle. *J. Anim. Sci.* 59:1459-1466.
- Meyer, K. 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. *Livest. Prod. Sci.* 31:179-204.
- Mohiuddin, G. 1993. Estimates of genetic and phenotypic parameters of some performance traits in beef cattle. *Anim. Breed. Abst.* 61:495-522.
- Robinson, D. L. 1994. Models which might explain negative correlations between direct and maternal genetic effects. 5th World Congr. Genet. Appl. Livest. Prod. 18:378-380.
- Willham, R. L. 1963. The covariance between relatives for characters composed of components contributed by related individuals. *Biometrics.* 19:18-27.
- 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.
- Wright, H. B., E. J. Pollak and R. L. Quaas. 1987. Estimation of variance and covariance components to determine heritabilities and repeatability of weaning weight in American Simmental cattle. *J. Anim. Sci.* 65:975-981.
- Yokoi, N., K. Moriya and Y. Sasaki. 1997. A measure for predicting genetic merit for milking and nursing ability in beef cattle. *Anim. Sci.* 65:39-43.