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Genetic Relationship of Gestation Length with Birth and Weaning Weight in Hanwoo (Bos Taurus Coreanae)

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ABSTRACT : The genetic relationship of gestation length (GL) with birth and weaning weight (BW, WW) was investigated using data collected from the Hanwoo Experiment Station, National Institute of Animal Science, RDA, Republic of Korea. Analytical mixed models including birth year-season, sex of calf, linear and quadratic covariates of age of dam (days) and linear covariate of age at weaning (days) as fixed effects were used. Corresponding restricted maximum likelihood (REML) and Bayesian estimates of variance components and heritability were obtained with two models; Model 1 included only direct genetic effect and Model 2 included direct genetic, maternal genetic and permanent environmental effect. All the genetic parameter estimates from REML were corresponding to the Bayesian estimates. Direct heritability estimates for GL, BW, and WW were 0.48, 0.33 and 0.25 by Model 1. From Model 2, direct and maternal heritability estimates were 0.38 and 0.03 for GL, 0.14 and 0.05 for BW, and 0.08 and 0.05 for WW. Genetic correlation estimates between direct and maternal effects were 0.05 for GL, 0.59 for BW, and 0.52 for WW. Estimates of direct genetic correlation between GL and BW (WW) were 0.44 (0.21). Positive genetic correlation of GL with BW and WW imply that selection for greater BW or WW would lead to prolonged gestation length. (**Key Words :** Gestation Length, Birth Weight, Weaning Weight, Heritability, Genetic Correlation, Hanwoo)

INTRODUCTION

Hanwoo (*Bos Taurus Coreanae*) is a major beef cattle breed in Korea. This breed has been raised mostly in the Korean Peninsula and some northeastern areas of China. Hanwoo has been known to be superior in ability to reproduce, but inferior in production of meat because of low milking ability and slow growth (Kim and Lee, 2000). The Korean government has set goals to enhance meat productivity of Hanwoo and the goals have been amended several times as market demand has changed. A recently revised breeding goal for Hanwoo improvement was to enhance marbling score without changes in subcutaneous fat thickness (MAF, 2007), and currently intensive studies are conducted for marbling score (Lee et al., 2006; Cheong

et al., 2008). Another goal was to increase live body weight, carcass weight and eye-muscle area. Growth traits of beef cattle have been known to be correlated with reproduction traits. Especially, gestation length was reported to be positively correlated with birth weight (Reynolds et al., 1990; Bennett and Gregory, 2001; Hansen et al., 2004). Therefore selection on body weight could increase length of gestation. There have been, however, no studies on genetic parameters affecting the relationship of gestation length with pre-weaning growth traits in Hanwoo.

The objectives of this study were to examine the genetic relationship between gestation length and pre-weaning growth traits in Hanwoo. The frequentist approach and Bayesian approach were compared for analyzing such a relationship.

MATERIALS AND METHODS

Data

Data on birth weight (BW), weaning weight (WW) and gestation length (GL) of Hanwoo calves born from 1970 to 2006 were obtained from the Hanwoo Experiment Station, National Institute of Animal Science, RDA, in Korea. Hanwoo Experiment Station is located at an elevation of

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approximately 800 m above sea level. Annual rainfall averages 187 cm; summer is short and winter is long. The majority of cows and heifers produce calves from March to May and from August to October by artificial insemination (AI) and the parentages of animals are identified through AI information. The calves were weighed within 24 h after delivery for determination of BW and raised with their mother cows until 90-150 days of age. The WW was measured when the calves were 90 to 150 days old. The GL was defined as the number of days between the date of last insemination and calving date.

We excluded data for WW measured outside the range between 90 and 150 days of weaning age or for GL measured outside the range between 265 and 305 days. The range for GL (265 to 305 days) was determined by the results of Kim and Lee (2000) where means of GL in Hanwoo were 285.83 d for heifers and 286.86 d for cows, and their standard deviations were 5.43 d and 5.21 d.

The final data set for statistical analyses included 4,566 BW, 3,271 WW and 3,106 GL records from 4,844 Hanwoo calves. Pedigree information was additionally included for 950 animals, and the total of 5,794 animals, of which 219 were sires and 1,697 were dams, were included in the genetic parameter estimation.

Statistical analyses

Before genetic parameter estimation, preliminary analyses were conducted to determine how sex of calf and age of dam affected the traits using a simple linear model which included birth year-season and sex of calf as fixed effects and linear and quadratic age of dam effects as covariates for GL and BW, and a linear effect of calf age at weaning as a covariate for WW. Birth seasons were partitioned into four seasons as follows: Spring (Mar.-May), Summer (June-July), Fall (Sep.-Nov.), and Winter (Dec., Jan. and Feb. of subsequent year). Least square solutions for sex of calf and regression coefficients on age of dam were estimated using the GLM procedure in SAS Package (version 9.1).

Variance and covariance components were estimated with the following two models; Model 1 included direct genetic effect and residual effects and Model 2 included direct genetic, maternal genetic, direct×maternal genetic, permanent environmental effects and residual effects as random effects. Preweaning traits have been known to be influenced by maternal factors, and thus the terms are generally included in the analytical models. Nevertheless, parameter estimation was conducted also by the Model 1 to see how much the lack of maternal factors in the analytical model influenced other parameters. Fixed effects in these analytical models were the same as those used for preliminary analyses.

The analytical models are presented in matrix notation as following:

Model 1:
$$y = X\beta + Z_d u_d + e$$

Model 2:
$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_{\mathbf{d}}\mathbf{u}_{\mathbf{d}} + \mathbf{Z}_{\mathbf{m}}\mathbf{u}_{\mathbf{m}} + \mathbf{Z}_{\mathbf{p}e}\mathbf{u}_{\mathbf{p}e} + \mathbf{e}$$

Where, y is the vector of observations, X is an incidence matrix relating a vector of fixed effects (β) including birth year-season and sex of calf, linear and quadratic effects of dam age (days), and weaning age (days) of calf. We excluded parity effects because preliminary analysis showed their confusion with the dam age effects. Z_d , Z_m , and Z_{pe} are incidence matrices corresponding to additive genetic effect (u_d), maternal genetic effect (u_m) and permanent environmental effect (u_{pe}), respectively. e is the vector of residuals. The variance-covariance structures of the random variables are:

$$\mathbf{Var} \begin{bmatrix} \mathbf{u}_{d} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A} \mathbf{\sigma}_{d}^{2} & \mathbf{0} \\ \mathbf{0} & \mathbf{I}_{e} \mathbf{\sigma}_{e}^{2} \end{bmatrix} \text{ for Model 1 and,}$$

Where, σ_d^2 is direct genetic variance, σ_m^2 is maternal genetic variance, σ_{dm} is covariance between direct and maternal genetic effect, σ_{pe}^2 is permanent environmental variance, and σ_e^2 is random residual variance. A is a numerator relationship matrix among all animals, and I_{pe} is an identity matrix of order equal to the number of dams. I_e is an identity matrix of order equal to the number of animals.

Two-trait analyses with Model 2 were performed to obtain genetic, phenotypic and residual correlation coefficients of GL with BW and WW. MTDFREML program (Boldman et al., 1995) was used for the (co)variance components estimation. The program was run with a convergence criterion of simplex variance less than 10^{-11} . Direct (h_d^2) and maternal (h_m^2) heritability was obtained as the proportion of direct and maternal genetic variance to the phenotypic variance (σ_p^2) , respectively, and also the proportion of maternal permanent component to the phenotypic variance (c) was obtained. Genetic correlation between direct and maternal effect (r_{dm}) was obtained as follows:

$$r_{dm} = \sigma_{dm} / \text{SQRT}(\sigma_d^2 \times \sigma_m^2)$$

Genetic parameter estimates were continuously obtained

Table 1. Summary statistics of traits studied

Traits ¹	N	Mean	SD	Min	Max
Dam age (days)	4,801	1,959.90	1,008.70	538	6,881
Wage (days)	3,271	122.36	11.69	90	150
GL (days)	3,106	285.35	6.13	260	305
BW (kg)	4,566	24.35	3.73	10	40
WW (kg)	3,271	91.77	20.22	26	179

¹ Wage = Age at weaning, BW = Birth weight; WW = Weaning weight; GL = Gestation length.

Table 2. Genetic parameters estimated from single trait analysis for gestation length (GL), birth weight (BW) and weaning weight (WW) by DF-REML, AI-REML and GS

Method	Item -		Model 1			Model 2			
		GL	BW	WW	GL	BW	WW		
DF-REML	h_a^2	0.48	0.33	0.25	0.38	0.14	0.08		
	h_m^{-2}				0.03	0.05	0.05		
	r_{am}				0.05	0.59	0.52		
	c^2				0.06	0.02	0.06		
AI-REML	h_a^2	0.48 ± 0.04	0.34 ± 0.03	0.25 ± 0.04	0.38 ± 0.03	0.15 ± 0.02	0.08 ± 0.01		
	h_m^{2}				0.03 ± 0.01	0.05 ± 0.01	0.04 ± 0.01		
	r_{am}				0.05 ± 0.02	0.61 ± 0.05	0.62 ± 0.06		
	c^2				0.03 ± 0.01	0.05 ± 0.01	0.06 ± 0.01		
GS	h_a^2	0.48 ± 0.03	0.32 ± 0.02	0.25 ± 0.03	0.38 ± 0.03	0.15 ± 0.02	0.06 ± 0.01		
	h_m^{2}				0.03 ± 0.01	0.06 ± 0.01	0.05 ± 0.01		
	r_{am}				0.04 ± 0.01	0.62 ± 0.04	0.58 ± 0.05		
	c^2				0.05 ± 0.01	0.03 ± 0.01	0.04 ± 0.01		

 h_a^2 = Direct heritability, h_m^2 = Maternal heritability, r_{am} = Direct×maternal genetic correlation, c^2 = The proportion of maternal permanent component to the phenotypic variance.

with WOMBAT and MTGSAM packages to compare different methods. The WOMBAT (Meyer, 2006) was used for obtaining AI-REML estimates with their standard errors, and MTGSAM (Van Tassel and Van Vleck, 1996) was utilized for Baysian estimates through Gibbs sampling procedure. The Gibbs sampler with MTGSAM was run 60,000 rounds, and the first 10,000 rounds were discarded as a warming-up period. A thinning interval of 50 rounds was used to retain sampled values that reduced lag correlation among thinned samples. The posterior mean estimate of the genetic parameters was calculated as the mean of its conditional expected values in the post warming-up rounds from Gibbs sampling.

RESULTS AND DISCUSSION

Simple statistics for traits and covariates

Summary statistics for each variable utilized in this study are shown in Table 1. Average weaning age of calf was 122.36 d and average dam age at calving was 1,959.90 d with a range of 538 to 6,881 d and the averages of GL, BW and WW were 285.35 d, 24.35 kg and 91.77 kg, respectively. The average of GL in this study was similar to those for Canadian Charolais (285.2 d; Crews Jr. et al., 2006) and for Simmental (284.3 d; Wray et al., 1987). On the other hand, Danish Holstein had a smaller GL (278.5 d; Hansen et al., 2004). Average GL for Balck and White,

Braunvieh and Simmental in Swiss were 281.9, 288.5 and 286.6 d, respectively (Hagger and Hoffer, 1990). The GL of eight European breed sires ranged from 283.2 to 287.8 d and GL of calves produced by a Nellore sire which belongs to the Zebu breed was 293.0 d which is longer than those of European breeds (Cundiff et al., 1998). The average GL of Hanwoo tends to be closer to the averages of European beef breeds rather than to those of Zebu breeds.

The average BW of Hanwoo in this study was approximately 5 to 25 kg smaller than the averages for European breeds or Zebu breeds (Nugent 3rd et al., 1991; Paschal et al., 1991; Phocas and Laloë, 2004; Crews Jr. et al., 2006). Even BW of Japanese Black cattle was about 12% heavier than that of Hanwoo (27.45 kg; Aziz et al., 1991). The average WW of Hanwoo was 91.77±20.22. The small body weight of Hanwoo becomes more serious when it comes to WW comparing with other breeds. Average WW estimates were 202.5±30 kg for Hereford (Ferreira et al., 1999), and 306.8±11.11 kg for Charolais (Crews, Jr., 2006). The small body weight at weaning may be a characteristic of Hanwoo. One of the reasons was the short suckling period due to the low milk yield and milking persistency of Hanwoo cows (Kim and Lee, 2000). Most research on average WW has been conducted at 205 d or 180 d weaning ages (Ferreira et al., 1999; Crews Jr. et al., 2006), while the weaning age of Hanwoo was around 120 d in the current study.

Table 3. Genetic parameter estimates from two-trait analysis for gestation length (GL), birth weight (BW), and weaning weight (WW) by DF-REML, AI-REML, and GS algorithms

	DF-REML			AI-REML			GS		
Trait 1	GL	GL	BW	GL	GL	BW	GL	GL	BW
Trait 2	BW	WW	WW	\mathbf{BW}	WW	WW	BW	WW	WW
h_{dl}^{2}	0.36	0.39	0.14	0.36	0.40	0.16	0.38	0.39	0.16
				± 0.07	± 0.07	±0.03	±0.06	± 0.06	± 0.03
h_{d2}^{2}	2 0.15	0.09	0.08	0.15	0.09	0.09	0.17	0.09	0.08
				±0.03	±0.03	±0.03	±0.03	± 0.02	± 0.02
h_{mI}^{2}	$_{ml}^{2}$ 0.03	0.03	0.05	0.03	0.03	0.05	0.04	0.04	0.06
				± 0.01	± 0.01	± 0.02	± 0.01	± 0.01	± 0.02
h_{m2}^{2}	0.05	0.05	0.03	0.04	0.05	0.03	0.05	0.04	0.04
				± 0.02	± 0.02	± 0.01	± 0.02	± 0.01	± 0.01
r_{d1d2}	0.44 0.2	0.21	0.96	0.45	0.22	0.97	0.42	0.21	0.95
				±0.13	±0.11	±0.10	± 0.11	± 0.09	± 0.09
r_{m1m2}	0.64 -0.41	-0.41	11 0.38	0.65	-0.42	0.41	0.66	-0.38	0.41
				± 0.27	±0.23	± 0.18	±0.23	±0.20	± 0.18
r_{dlml}	0.12	0.04	0.52	0.12	0.03	0.53	0.13	0.04	0.56
				± 0.10	±0.11	± 0.20	± 0.09	± 0.09	± 0.17
r_{d1m2}	d_{lm2} 0.08	0.22	0.62	0.10	0.23	0.57	0.11	0.26	0.59
				± 0.11	±0.12	± 0.18	± 0.09	± 0.11	± 0.16
r_{d2m1}	0.69	0.61	0.38	0.68	0.61	0.40	0.66	0.59	0.38
				±0.19	± 0.20	±0.15	± 0.17	± 0.18	±0.14
r_{d2m2}	0.60	0.47	0.77	0.62	0.46	0.72	0.63	0.46	0.75
				±0.15	±0.22	±0.30	±0.13	±0.20	±0.26

 h_{dl}^2 ; direct heritability of trait 1 (2), h_{ml}^2 ; maternal heritability of trait 1 (2), r_{dld2} ; direct genetic correlation coefficient between traits 1 and 2, r_{mlm2} ; maternal genetic correlation coefficient between traits 1 and 2, r_{dl} (2) r_{mlm2} ; correlation coefficient between direct genetic effect of trait 1 (2) and maternal genetic effect of trait 1 (2), r_{dl} (2) r_{ml} (2); correlation coefficient between direct genetic effect of trait 1 (2) and maternal genetic effect of trait 2 (1).

Direct and maternal genetic parameters

Direct heritability estimate for GL was 0.48 using the Model 1 and 0.38 using the Model 2 (Table 2). This difference might be due to a more orthogonal design in Model 2. The maternal heritability (0.03) was not negligible, but smaller than those estimated by Hansen et al. (2004, 0.07 for Danish Holstein), Bennet and Gregory (2001, 0.08 for 12 beef cattle breeds) and Wray et al. (1987, 0.09).

We obtained 0.33 and 0.25 as the direct heritability estimate for BW and WW using Model 1, which was smaller than those of any other major studies in which direct heritability ranged from 0.35 to 0.50 for BW and from 0.21 to 0.35 for WW (Waldron et al., 1993; Cundiff et al., 1998; Ferreira et al., 1999). When we included maternal effects in the analytical model, direct and maternal heritability were 0.14 and 0.05 for BW and 0.08 and 0.05 for WW. These estimates were also smaller than the corresponding estimates reported by Meyer (1992), Robinson (1996), Dodenhoff et al. (1998), Crews Jr. (2006), Ferreira et al. (1999), Splan et al. (2002), and Phocas and Laloë (2004). The direct heritability estimates using Model 1 were smaller than those using Model 2 for BW and WW as shown for GL. Ignoring maternal genetic effect might lead to an overestimation of direct genetic effect as observed for growth traits by other groups (Ferreira et al., 1999; Waldron et al., 1993).

Direct heritability estimates for BW were larger than those for WW using both Models 1 and 2 while their maternal heritability estimates did not differ between BW and WW. The smaller direct heritability for WW than for BW might be partially due to the associations of preweaning environmental conditions, including maternal ability, with reduced genetic variabilities of the calves. This scenario might be persuasive because of low milk level of the Hanwoo dam. Low milk level tends to reduce the direct genetic variance of 200-d weight with non-significant reduction of maternal genetic variance in beef cattle (Bennet and Greory, 1996). French Limousine, a famous breed for large growth rate after birth, had similar BW (0.40) and WW (0.30) direct heritability to those of Hanwoo (Phocas and Laloe, 2004). Considering optimal selection criterion to be under a constraint of large BW, genetic improvement would be required for Hanwoo to have high growth rate similar to the Limousine breed.

Genetic correlation estimates between direct and maternal effects were all positive, 0.05 for GL, 0.59 for BW, and 0.52 for WW. The strong positive estimates for BW and WW suggested that maternal genetic effect for BW and WW might positively interact with direct genetic effect during the selection process. The weak positive estimate for GL in this study was quite different to the negative estimates (-0.37, -0.13 and -0.18) reported by Crews Jr.

Coefficients Residual Phenotypic Method BW WW BW WW DF-REML GL 0.23 0.04 0.31 0.10 BW 0.25 0.34 AI-REML GL 0.23 ± 0.04 0.04 ± 0.01 0.30 ± 0.02 0.08 ± 0.02 BW 0.24 ± 0.03 0.34 ± 0.03 GS GL 0.21±0.02 0.03 ± 0.01 0.29±0.02 0.08 ± 0.01 BW 0.25 ± 0.03 0.34 ± 0.02

Table 4. Residual and phenotypic correlation coefficients among GL, BW and WW by DF-REML, AI-REML and GS algorithm

GL = Gestation length, BW = Birth weight, WW = Weaning weight.

(2006), Hansen et al. (2004) and Bennet and Gregory (2001). Negative correlation was also obtained for BW and WW by Crews Jr. (2006) for Charolais, by de Mattos et al. (2000) for Herefords, by Dodenhoff et al. (1999) for Angus, by Duangjinda et al. (2001) for Hereford, Gelbvieh, and Charolais, by Ferreira et al. (1999) for Hereford, by Gutierrez et al. (2007) for Austriana de los Valles beef cattle, by Koch et al. (1994) for Hereford cattle, by Lee et al. (1997) for Simmental, by Robinson (1996) for Australian Angus, by Splan et al. (2002) for crossbred cattle and by Groeneveld et al. (1998) for Africander cattle.

Genetic correlation between traits

Direct genetic correlation coefficients between GL and growth traits were all positive (Table 3). This might be because of prolonged GL caused by selection for BW or WW. A moderate and positive correlation estimate between direct genetic effects of GL and BW concurred with the findings from Crews Jr. (0.34, 2006), Bennet and Gregory (0.36, 2001), Hagger and Hofer (0.49-0.59, 1990), Gregory et al. (0.30, 1995b), Bourdon and Brinks (0.25 and 0.22, 1982), Wray et al. (0.26, 1987) and Larsley et al. (0.41, 1961). However, direct genetic correlation of 0.21 between GL and WW in the current study was larger than obtained by Crews Jr. (0.11, 2006), Bennet and Gregory (0.16, 2001), Gregory et al. (-0.15, 1995a), Gregory et al. (-0.23, 1995b) and Wray et al. (0.13, 1987). Maternal correlation estimates between GL and BW were generally large; 0.64 in the current study, 0.62 in Crews Jr. (2006) and 0.41 in Bennet and Gregory (2001).

Direct genetic correlation coefficient between BW and WW was 0.96 (Table 3), and this value was quite larger than for other breeds, especially compared to the correlation for Austuriana de los Valles beef cattle breed (0.37, Gutierrez et al., 2007) and for French breeds (0.26-0.44, Phocas and Laloe, 2004). Short interval (approximately 122 days) from birth to weaning in our data might be a potential reason for a high genetic correlation coefficient. Such high correlation might suggest a genetic merit of WW could be largely predicted by that of BW. This might be a weak point for genetic improvement of Hanwoo. Consider the French

Limousine that had a small direct genetic correlation between BW and WW (Phocas and Laloe, 2004) and similar BW (0.40) and WW (0.30) direct heritability to Hanwoo. Considering optimal selection criterion to be under a constraint of large BW, genetic improvement would be required for Hanwoo to have high growth rate similar to the Limousine breed.

Estimated genetic and phenotypic correlation coefficients between GL and BW in this study implied that longer gestation might be a way to increase BW of the calf. Further studies are required for understanding the relationship of GL with dystocia in the Hanwoo population.

Comparisons of estimates by different methods

We compared genetic parameter estimates obtained by the following three different methods: derivative free restricted maximum likelihood (DF-REML) by Simplex procedure, average information restricted maximum likelihood (AI-REML) and Bayesian inference via Gibbs sampling (GS). From both single- and two-trait analyses, heritability estimates and genetic and environmental correlation estimates for GL, BW, and WW were all similar by the three methods (Tables 2, 3, and 4). These results concurred with the study of Van Tassell and Van Vleck (1996). Their standard error estimates were also similar, and the estimates obtained using GS tended to be smaller than those using REML (Tables 2 and 3). The small dispersion parameter estimates might be because Bayesian estimates incorporated prior distribution.

IMPLICATION

Longer gestation length was associated with heavier calves at birth. Heavier calves at birth might grow faster during the sucking period, but be a partial reason for higher probability of dystocia and prolonged calving interval for cow-calf operators. Therefore, appropriate level of calf birth weight should be targeted rather than heavier BW in terms of economic efficiency. Optimal selection criterion should be stressed under a constraint of large BW. Instead, genetic improvement would be required for Hanwoo to have a high

growth rate like the Limousine breed. We need to improve genetic merits of milk production in Hanwoo cows to meet the objective.

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