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Maternal and Direct Genetic Effects on Variance Components Estimation for Economic Traits in Japanese Black Cattle

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Summary

Variance components due to direct and maternal effects were estimated using data recorded on 740 Japanese Black cattle during the period from 1971-2003. Traits studied were feed intake (FI), feed conversion ratio (FCR), residual feed intake (RFI), average daily gain (ADG), metabolic body weight (MWT) at the mid point of the test period, and body weight (BWT) at the finish of the test (345 days). Data were analyzed using six alternative animal models (direct and including or excluding associated maternal effects). Direct heritability estimates from the model including direct and all the maternal effects were 0.21 ± 0.03 for FI, 0.16 ± 0.05 for FCR, 0.15 ± 0.05 for RFI, 0.18 ± 0.09 for ADG, 0.45 ± 0.03 for MWT and 0.36 ± 0.02 for BWT. Maternal heritability estimates were small and significantly different from zero for only RFI (0.03 ± 0.01), MWT (0.03 ± 0.01) and BWT (0.08 ± 0.04). Antagonistic relationships were observed between direct and maternal genetic effects for FCR and growth traits. The estimates of direct heritability for feed efficiency traits were reduced up to 37% when maternal genetic and maternal environmental effects were considered in the model. The results showed that an antagonistic relationship existed between direct and maternal genetic effect for FCR and growth traits, which indicates that maternal effects should be accounted for these traits in genetic evaluation system.

Key words : Genetic parameters, growth, feed efficiency, maternal effects.

Introduction

The accuracy of estimates of variance components and heritabilities depend

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on application of the appropriate model for traits of interest. Estimates may be biased by failure to account for appropriate genetic and environmental sources of variation, such as, maternal (environment and genetic) effects. Maternal effects arise from the ability of the mother to produce the milk needed for growth and other maternal behavior. Hence, to achieve optimum progress in a selection program for many traits both the direct and maternal component should be taken into account. Comparing dam-offspring correlations with expected values derived from paternal and maternal half-sib contrasts, Koch (1972) speculated that the correlation between direct and maternal additive effects was of the order of -0.10 to -0.19 for gain of beef calves from birth to weaning. Cantet et al. (1988) estimated this to be -0.15 and -0.25 for birth weight and weaning weight, respectively. Assessment of these effects is especially important if an antagonistic relationship between them exists (Baker 1980; Robinson 1981).

Estimates of genetic parameters are necessary for development of effective genetic selection programs. While direct genetic effects have received the most attention, maternal genetic effects can often be an important source of variation and may merit consideration in selection programs. Improvement in both direct and maternal effects can contribute to improve early growth performance in beef cattle (Meyer 1997). For this purpose, selection programs based on genetic evaluations require accurate estimates of genetic and environmental parameters. The estimations of direct and maternal genetic effects tend to be imprecise due to large sampling correlations between parameters (Meyer 1997).

Residual feed intake (RFI) represents the deviation of the actual feed eaten by an animal from that predicted from a combination of growth traits. The predicted feed intake is the amount of feed the animal is expected to consume on the basis of its body weight and growth performance. The RFI is relatively a new trait which can be used to identify animals for genetic improvement of beef cattle, where efficient animals have lower RFI. The presence of maternal effects in the models used for genetic evaluation reduces the variance of direct genetic effects (Meyer 1992). Part of this reduction is explained by maternal genetic and maternal environmental variances. Since antagonism has been observed between direct and maternal effects for growth traits, knowledge of the maternal influence on growth and feed efficiency, and the correlation between these effects, is fundamental for achieving unbiased heritability estimates. This paper presents estimates of genetic parameters for growth and feed efficiency in Japanese Black cattle fitting several animal models, attempting to separate direct genetic, maternal genetic, and maternal permanent environmental effects.

Materials and Methods

Animals and feed management

A total of 740 Japanese Black bulls were tested at the Okayama Prefecture Animal Industry Centre, Japan during the period from 1971–2003. Of these, 77 bulls were tested for 140 days and the other 663 bulls for 112 days. Feeding and management of animals throughout the test period were the same as those described by (Hoque *et al.* 2006). Briefly, each year, 20–30 bulls were selected on the basis of heavier body weight for performance test from approximately 200 bulls. The selected bulls were within the age limit of 7–8 months and body weight of 200–300 kg. They were introduced to the test station and housed in individual box stalls ($2.7 \times 3.6 \text{ m}^2$) with an adjacent 10 m^2 paddock for voluntary exercise. Cohort was defined as a group of bulls introduced to the test station on the same day and tested under a uniform environment during the same period. A total of 171 cohorts were used in the analyses. In order to estimate variance components for the traits measured, a pedigree file was constructed. The tested bulls were the progeny of 61 sires and 555 dams and the pedigrees of the tested bulls were traced back three generations giving a total of 4,897 cattle in the pedigree. After a 3-week adjustment period to the feed, the bulls were provided *ad libitum* access to roughage (green forage, silage or hay); however, feeding of concentrate was restricted to twice daily for 1 hour morning and evening. The concentrate consisted of 20 parts ground barley, 35 parts ground yellow corn, 20 parts wheat bran, 17 parts defatted rice bran, 6 parts soybean meal, 1 part NaCl and 1 part calcium carbonate with 15.5% of DCP and 73% of TDN. Water was supplied *ad libitum*. Sufficient feed was given to each animal according to its previous consumption. Records of roughage and concentrate consumption were maintained on a dry matter basis throughout the test. The weekly body weight of individual bulls during the test period was recorded and feed intake was measured daily by the difference between supplied and leftover feed.

Traits in study

The traits studied were average daily gain (ADG) during the test period, metabolic body weight (MWT) at the midpoint of the test period, final body weight (BWT), daily feed intake (FI), feed conversion ratio (FCR) and RFI. The ADG for each animal was calculated from the difference between the start and the end of test weights divided by the number of days. The mean weight (MBW) of an animal during the test period was computed as the average of the start and the end of test weights. MWT was calculated as MBW, raised to the power of 0.75 ($\text{MBW}^{0.75}$). FI was then combined with ADG and MWT to compute different measures of feed efficiency: FCR and RFI. FCR was calculated as FI divided by ADG. The RFI was calculated as the residual of the multiple regression of

animal's FI on MWT and ADG using SAS (1992) software.

$$\text{RFI was calculated as : } \text{RFI} = \text{FI} - \beta_w \times \text{MWT} - \beta_g \times \text{ADG}$$

where β_w and β_g were the multiple regression coefficients of animal's FI on MWT and ADG, respectively.

Statistical analysis

The (co) variance components and genetic parameters were estimated by the REML method using VCE-5 variance component estimation software (Kovac & Groeneveld 2003). The covariance structure for additive genetic effects of animals and residual effects is described below :

$$\begin{aligned} V(\mathbf{a}) &= \sigma_a^2 \mathbf{A} \\ V(\mathbf{m}) &= \sigma_m^2 \mathbf{A} \\ V(\mathbf{c}) &= \sigma_c^2 \mathbf{I} \\ V(\mathbf{e}) &= \sigma_e^2 \mathbf{I} \\ \text{Cov}(\mathbf{a}, \mathbf{m}) &= \sigma_{am} \mathbf{A} \end{aligned}$$

where \mathbf{a} and \mathbf{m} denote the vectors of animals' direct and maternal effects, respectively, and \mathbf{c} and \mathbf{e} the vectors of maternal environmental effects and residual errors. \mathbf{A} is the numerator relationship matrix between animals and the identity matrix (\mathbf{I}). σ_a^2 is the additive genetic variance, σ_m^2 the maternal genetic variance, σ_{am} the direct and maternal genetic covariance, σ_c^2 the maternal permanent environmental variances, and σ_e^2 the error variance.

The (co) variance components and genetic parameters for all the studied traits were estimated using six different models. The first model of analysis fitted, Model 1, was a simple animal model with animals' additive genetic effects as the only random effect. Model 2 allowed for a permanent environmental effect due to dam, fitting this as an additional random effect, uncorrelated with all other effects in the model. While Model 3 attributed maternal effects to the genotype of the dam, fitting the maternal genetic effect as a second random effect for each animal with the same covariance structure as the direct additive genetic effect. Model 3 assumed that direct and maternal effects were uncorrelated, i.e. $\sigma_{am} = 0$, Model 4 allowed for a covariance between them. Model 5 and 6 then included both a permanent environmental and a genetic maternal effect, ignoring and including a genetic correlation between direct and maternal effects, respectively. The six models were :

$$Y_{ij} = F_i + a_j + e_{ij} \dots\dots\dots (1)$$

$$Y_{ijk} = F_i + a_j + c_k + e_{ijk} \dots\dots\dots (2)$$

$$Y_{ijk} = F_i + a_j + m_k + e_{ijk} \dots\dots\dots (3)$$

$$\text{with } \text{Cov}(a_j, m_k) = 0$$

$$Y_{ijk} = F_i + a_j + m_k + e_{ijk} \dots\dots\dots (4)$$

$$\begin{aligned}
 &\text{with Cov}(a_j, m_k) \neq 0 \\
 Y_{ijk} = F_i + a_j + m_k + c_k + e_{ijk} \dots\dots\dots (5) \\
 &\text{with Cov}(a_j, m_k) = 0
 \end{aligned}$$

$$\begin{aligned}
 Y_{ijk} = F_i + a_j + m_k + c_k + e_{ijk} \dots\dots\dots (6) \\
 &\text{with Cov}(a_j, m_k) \neq 0
 \end{aligned}$$

where Y_{ijk} , observation of the trait i of the j th animal with k th dam ; The fixed effects, F_i , were identical for all the models, including effects of linear and quadratic regressions of the age of animal and the age of dam, and cohort ; a_j , the direct additive genetic effect of the j th animal ; c_k , the permanent environmental effect due to the k th dam ; m_k , the maternal additive genetic effect of the k th dam ; e_{ijk} , the random residual error.

Depending on the model, the direct heritability (h^2_a), the maternal heritability (h^2_m), the permanent environmental variance due the dam as a proportion of the phenotypic variance (c^2), the error variance (σ^2_e) and the phenotypic variance (σ^2_p) were estimated. Furthermore, the total heritability (h^2_T) was calculated as (Willham 1972) :

$$h^2_T = (\sigma^2_a + 0.5 \sigma^2_m + 1.5 \sigma_{am}) / \sigma^2_p$$

The numerator of the equation is the covariance of animal's phenotypic record with the sum of its genetic effects, i.e. h^2_T is the regression of an animal's total genotype (direct and maternal) on its phenotype.

Results

Estimates of variance components for feed intake and feed efficiency (FCR and RFI) traits from the six single-trait analyses are presented in Table 1. Direct genetic variances for feed efficiency traits were reduced when maternal effects were included in the model. Measures of feed efficiency accounted phenotypic variance of 0.47-0.88 kg²/day. The covariances of direct and maternal genetic effects were negative for FCR (-0.02) but positive for FI (0.02) and RFI (0.05).

Estimates of variance components for growth traits from the six single-trait analyses are presented in Table 2. Direct genetic variances for growth traits were substantially reduced when maternal effects were included in the model. The covariances between direct and maternal genetic effects were negative for all the growth traits.

Estimates of genetic parameters for feed intake and efficiency traits from different single-trait analyses are presented in Table 3. Direct heritability estimates for feed efficiency traits (FCR and RFI) from the different models ranged from 0.13 to 0.24. For FCR, the correlation between direct and maternal effects was negative for FCR in model 4 and 6, while the corresponding correlations for FI and RFI were positive. Positive environmental covariances would bias

Table 1. Estimates of variance and covariance components for feed intake and efficiency traits

Traits† Estimates‡	Models					
	1	2	3	4	5	6
FI						
σ^2_a	0.44	0.25	0.42	0.42	0.23	0.22
σ^2_m	—	—	0.04	0.04	0.01	0.01
σ_{am}	—	—	—	0.02	—	0.02
σ^2_c	—	0.54	—	—	0.55	0.53
σ^2_e	0.86	0.27	0.85	0.89	0.26	0.28
σ^2_p	1.30	1.06	1.31	1.35	1.05	1.06
FCR						
σ^2_a	0.12	0.11	0.07	0.09	0.11	0.11
σ^2_m	—	—	0.01	0.01	0.01	0.01
σ_{am}	—	—	—	-0.02	—	-0.01
σ^2_c	—	0.22	—	—	0.22	0.20
σ^2_e	0.76	0.49	0.48	0.44	0.48	0.39
σ^2_p	0.88	0.82	0.56	0.52	0.82	0.70
RFI						
σ^2_a	0.17	0.13	0.11	0.12	0.10	0.10
σ^2_m	—	—	0.02	0.03	0.02	0.02
σ_{am}	—	—	—	0.05	—	0.01
σ^2_c	—	0.32	—	—	0.32	0.33
σ^2_e	0.54	0.18	0.34	0.25	0.18	0.19
σ^2_p	0.71	0.63	0.47	0.49	0.62	0.65

† FI, feed intake; FCR, feed conversion ratio; RFI, residual feed intake.

‡ σ^2_a , σ^2_m , σ^2_c , σ^2_e , σ^2_p , and σ_{am} : genetic direct, genetic maternal, maternal permanent environmental, residual and phenotypic variances, and direct and maternal genetic covariance, respectively.

heritability estimates downwards for RFI, and negative environmental covariances would bias estimates of heritability upwards for FCR. The estimates of direct heritabilities for RFI were reduced up to 37% when covariances between direct and maternal effects were considered in the model. The c^2 for feed efficiency traits explained from 13 to 23% of the phenotypic variance. The common environmental effects were significant source of variation for FI and feed efficiency traits, and the common environmental variation as proportion to phenotypic variation (c^2) accounted for 0.27 to 0.52 for these traits.

Genetic parameters for growth traits estimated from different models are presented in Table 4. The estimates of direct heritabilities for growth traits were reduced up to 34% when maternal heritability was considered in the model. The

Table 2. Estimates of variance and covariance components for growth traits

Traits [†] Estimates [‡]	Models					
	1	2	3	4	5	6
ADG						
σ^2_a	0.014	0.005	0.004	0.003	0.005	0.009
σ^2_m	—	—	0.001	0.001	0.001	0.001
σ_{am}	—	—	—	-0.001	—	-0.001
σ^2_c	—	0.004	—	—	0	0.008
σ^2_e	0.057	0.017	0.017	0.015	0.027	0.033
σ^2_p	0.071	0.026	0.022	0.018	0.033	0.050
MWT						
σ^2_a	11.59	13.21	7.17	7.22	6.76	8.99
σ^2_m	—	—	1.16	1.20	0.45	0.76
σ_{am}	—	—	—	-0.34	—	-1.28
σ^2_c	—	0	—	—	4.47	0
σ^2_e	12.06	16.90	14.20	14.12	12.31	13.95
σ^2_p	23.65	30.11	22.53	22.20	22.54	22.42
BWT						
σ^2_a	570.43	514.62	342.82	347.50	369.66	361.26
σ^2_m	—	—	80.25	90.97	71.88	80.28
σ_{am}	—	—	—	-55.93	—	-25.53
σ^2_c	—	0	—	—	222.95	218.85
σ^2_e	617.97	576.79	622.64	609.93	362.35	368.65
σ^2_p	1188.40	1091.41	1045.71	992.47	1026.84	1003.51

[†] ADG, average daily gain; MWT, metabolic body weight; BWT, body weight at finish.

[‡] σ^2_a , σ^2_m , σ^2_c , σ^2_e , σ^2_p , and σ_{am} : genetic direct, genetic maternal, maternal permanent environmental, residual and phenotypic variances, and direct and maternal genetic covariance, respectively.

maternal heritability estimates for growth traits were low (ranged from 0.03 to 0.09). The direction of the bias on the heritability estimates depend partly on the size of the additive maternal estimates, and the size of correlation between direct additive and maternal genetic effects. The correlations between direct and maternal effects in Model 4 and 6 were negative for growth traits. The common environmental effects for these traits explained up to 22% of the phenotypic variances.

Discussion

For feed intake and efficiency traits, including covariance of maternal genetic and direct genetic effect reduced estimates of direct heritabilities so that the

Table 3. Estimates of genetic parameters for feed intake and efficiency traits

Traits†	Models						
	Estimates‡	1	2	3	4	5	6
FI							
h^2_a		0.34±0.11	0.24±0.05	0.32±0.14	0.31±0.15	0.22±0.05	0.21±0.03
h^2_m		—	—	0.03±0.05	0.03±0.06	0.01±0.01	0.01±0.03
r_{am}		—	—	—	0.26±0.14	—	0.38±0.01
c^2		—	0.51±0.02	—	—	0.52±0.02	0.50±0.04
h^2_T		0.34±0.11	0.24±0.05	0.34±0.08	0.33±0.09	0.23±0.04	0.24±0.03
FCR							
h^2_a		0.14±0.04	0.13±0.06	0.13±0.07	0.17±0.07	0.13±0.06	0.16±0.05
h^2_m		—	—	0.02±0.01	0.02±0.01	0.01±0.01	0.02±0.02
r_{am}		—	—	—	-0.50±0.01	—	-0.49±0.01
c^2		—	0.27±0.03	—	—	0.27±0.02	0.28±0.03
h^2_T		0.14±0.04	0.13±0.06	0.14±0.04	0.12±0.06	0.14±0.05	0.14±0.04
RFI							
h^2_a		0.24±0.11	0.21±0.05	0.23±0.04	0.15±0.06	0.16±0.05	0.15±0.05
h^2_m		—	—	0.04±0.02	0.06±0.02	0.03±0.01	0.03±0.01
r_{am}		—	—	—	0.49±0.12	—	0.31±0.21
c^2		—	0.50±0.02	—	—	0.52±0.02	0.50±0.02
h^2_T		0.24±0.11	0.17±0.05	0.25±0.03	0.37±0.07	0.18±0.09	0.19±0.04

† FI, feed intake; FCR, feed conversion ratio; RFI, residual feed intake.

‡ h^2_a , direct heritability; h^2_m , maternal heritability; r_{am} , direct and maternal genetic correlation; c^2 , maternal and environmental variance as proportion of phenotypic variance; $h^2_T = (\sigma^2_a + 0.5\sigma^2_m + 1.5\sigma_{am}) / \sigma^2_p$, (Willham, 1972).

resulting values for total heritabilities differed slightly between corresponding models. The results also indicate that maternal effects play an important role in feed intake or efficiency traits. We are not aware of any published studies using different models for partitioning variance components for feed efficiency traits to compare with the present result. However, a few heritability estimates are available in the literature for the direct genetic effect of feed efficiency traits in beef cattle, with most of the estimates being for FI and FCR, and more recently RFI. Estimates for this traits, included in the reviews by Koots *et al.* (1994a) and Archer *et al.* (1999), range from low to moderate heritability, with most of the values falling in the moderate range. Heritability estimates for these traits by Herd & Bishop (2000), Arthur *et al.* (2001), Robinson & Oddy (2004) and Hoque *et al.* (2006), also fall into the moderate range, although component traits were not partitioned into direct and maternal effects in their studies.

Due to the antagonism observed between direct and maternal effects on growth traits and FCR, it is necessary to combine in a selection index both direct

Table 4. Estimates of genetic parameters for growth traits

Traits [†] Estimates [‡]	Models					
	1	2	3	4	5	6
ADG						
h^2_a	0.20±0.10	0.19±0.10	0.16±0.08	0.17±0.09	0.15±0.01	0.18±0.09
h^2_m	—	—	0.04±0.01	0.06±0.01	0.03±0.01	0.03±0.02
r_{am}	—	—	—	-0.69±0.01	—	-0.55±0.04
c^2	—	0.15±0.21	—	—	0	0.16±0.24
h^2_T	0.20±0.10	0.19±0.10	0.18±0.08	0.12±0.05	0.17±0.01	0.16±0.08
MWT						
h^2_a	0.49±0.09	0.44±0.07	0.32±0.08	0.33±0.07	0.31±0.06	0.40±0.03
h^2_m	—	—	0.05±0.06	0.05±0.05	0.03±0.01	0.03±0.01
r_{am}	—	—	—	-0.11±0.18	—	-0.28±0.16
c^2	—	0	—	—	0.19±0.83	0
h^2_T	0.49±0.09	0.44±0.07	0.35±0.06	0.33±0.07	0.32±0.05	0.39±0.03
BWT						
h^2_a	0.48±0.08	0.47±0.15	0.33±0.08	0.35±0.06	0.36±0.08	0.36±0.02
h^2_m	—	—	0.08±0.06	0.09±0.06	0.07±0.01	0.08±0.04
r_{am}	—	—	—	-0.31±0.21	—	-0.65±0.07
c^2	—	0	—	—	0.22±0.07	0.22±0.10
h^2_T	0.48±0.08	0.47±0.15	0.37±0.06	0.31±0.06	0.40±0.07	0.36±0.03

[†] ADG, average daily gain; MWT, metabolic body weight; BWT, body weight at finish.

[‡] h^2_a , direct heritability; h^2_m , maternal heritability; r_{am} , direct and maternal genetic correlation; c^2 , maternal and environmental variance as proportion of phenotypic variance; $h^2_T = (\sigma^2_a + 0.5\sigma^2_m + 1.5\sigma_{am}) / \sigma^2_p$, (Willham, 1972).

and maternal estimated breeding values of these traits in order to increase the economical efficiency of beef cattle. Baschnagel *et al.* (1999) concluded that estimates of direct-maternal correlations may be negative not only because of genetic antagonism, but also because of the influence of sire×erd interaction effects. In their study, when sire×herd was not included in the estimation model, estimates of direct and maternal (co)variance components were larger than when sire×herd effects were included in the model. Their estimated correlation between direct and maternal genetic effects with sire×herd effects ignored was negative and significantly stronger (-0.50) than with a model including both the direct-maternal correlation and sire×herd effects (-0.16).

The phenotypic variances estimated for BWT using different models were higher than the estimates reported for yearling weight of Angus (yearling weight 324.0 kg), Hereford (yearling weight 267.4 kg) and Zebu cross (yearling weight 189.9 kg) by Meyer (1992). However, much of this difference could be attributed

to breed and age differences. The long term selection (over 33 years) for heavier body weight might be other cause for the larger phenotypic variances in present study. The maternal genetic and maternal environmental variances for BWT were within the range of estimates reported in the literature (e.g., Meyer 1992; Koots *et al.* 1994a; Haile-Mariam & Kassa-Mersha 1995). The estimates of direct heritabilities for BWT (0.33–0.48) were similar to the corresponding estimates for Angus (0.32–0.50), and higher than Hereford (0.12–0.21) and Zebu cross (0.18–0.27) reported by Meyer (1992), who used the same models for estimating variance components in her study.

Meyer (1997) concluded that inflated estimates of the direct-maternal correlation might have been partly caused by unaccounted sources of variation, such as management groups, inflating the covariance between paternal sibs in a contemporary group. The negative genetic correlations between direct and maternal effects on growth traits were in agreement with the results by Koots *et al.* (1994b, a review), who derived a mean (–0.30) of the direct-maternal correlation for weaning weight across 23 studies. Estimated negative genetic correlations between direct and maternal effects for growth traits were also supported by other researchers (Meyer 1992; Meyer 1994; Demeke *et al.* 2003). A possible link between negative estimates for maternal genetic correlation was given by Meyer (1997). Because of inappropriate identification of management groups (herd, paddock, etc.), records of related calves from the same group might be more similar to each other than expected from their degree of relationship.

Numerous studies of pre-weaning growth rate of beef cattle have found an antagonistic correlation between direct and maternal genetic effects (r_{am}). A weak negative genetic relationship between direct and maternal effects has been considered plausible (Cundiff 1972), strong negative estimates have been met with justified scepticism (Meyer 1997). For Angus cattle, Meyer (1997) obtained estimates of approximately –0.50 for the direct-maternal genetic correlation, indicating that the direct-maternal genetic covariance is much more important than its environmental counterpart. Estimated maternal heritability for the studied growth traits were 0.02 to 0.09. The estimates of direct heritabilities were reduced up to 37% for feed efficiency traits and 34% for growth traits when maternal and associate effects were considered in the model.

Conclusion

The estimated low genetic variances and low heritability estimates obtained for ADG and FCR indicate the need for improved and uniform animal management to increase the precision of parameter estimates as well as animal performance. The results showed that an antagonistic relationship might exist between direct and maternal genetic effect for growth and feed conversion ratio, which

indicates the necessity of combination both direct and maternal estimated breeding values of these traits in a selection index to increase the economic efficiency. Further research on this area should be focused.

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