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Genetic relationship between different measures of feed efficiency and its component traits in Japanese Black (Wagyu) bulls

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Abstract

Genetic parameters of average daily gain (ADG), metabolic body weight (MWT), body weight at finish (BWF), daily feed intake (DFI), feed conversion ratio (FCR), and residual feed intake (RFI) were estimated in 740 Japanese Black bulls. RFI was calculated as the difference between actual and expected feed intake predicted by the residual of multiple regression (RFI_{phe}) and genetic regression (RFI_{gen}) from the multivariate analysis for DFI, MWT, and ADG. The estimations were made for the test periods of 140 days (77 bulls) and 112 days (663 bulls). The mean for RFI_{phe} was close to zero and RFI_{gen} was negative. Most of the traits studied were moderately heritable (ranging from 0.24 to 0.49), except for ADG and FCR (0.20 and 0.15, respectively). The genetic correlations among growth traits (ADG, MWT and BWF) and between DFI and growth traits were high, while the phenotypic correlations between them were moderate to high. The genetic and phenotypic correlations between RFI_{phe} and RFI_{gen} were >0.95 implying that they are regarded as the same trait and the genetic correlations of RFI (RFI_{phe} and RFI_{gen}) with FCR and DFI were favorably high. RFI_{phe} was phenotypically independent of its component traits, MWT ($r_p = -0.01$) and ADG ($r_p = 0.01$). RFI_{gen} was genetically independent of MWT ($r_g = -0.07$), while there was a weak genetic relationship ($r_g = 0.18$) between RFI_{gen} and ADG. These results provide evidence that RFI_{gen} should be included for genetic improvement of feed efficiency in Japanese Black breeding program.

Keywords: Beef cattle; Feed efficiency; Growth; Genetic parameters

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1. Introduction

Production of domestic Japanese beef is competitive only because of its outstanding meat quality. Japanese Black is the major beef breed in Japan and is famous for its good meat quality, but has lower mature size and

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growth rate relative to other domestic breeds (Hirooka et al. 1996). The potential for improving growth performance of this breed by selection needs to be evaluated. Estimates of genetic parameters are requisite for implementing sound breeding programs and for accelerating the progress of on going programs. Selection for growth rate has received considerable attention in most beef improvement projects. For growth traits of European and some prominent tropical beef breeds, numerous heritability and correlation estimates are available (Koots et al., 1994a,b). However, there is a paucity of reports on estimates of genetic parameters and the relationships among feed efficiency and other performance traits for Japanese Black cattle.

The feed resource for animals is a major cost determinant for profitability in livestock production enterprises, and thus any effort at improving the efficiency of feed use will help to reduce feed cost. It is, therefore, of interest to determine whether the inclusion of feed intake in the selection criteria would improve efficiency of beef production. The efficiency of feed utilization is more difficult to quantify than that of growth; consequently, different measures of feed efficiency have been developed over the years (Arthur et al., 2001b). Research has shown that there is considerable individual animal variation in feed intake above and below that expected or predicted on the basis of size and growth rate (Archer et al., 1999). This difference in intake is generally calculated as residual feed intake. Estimates of genetic parameters for such measures in beef cattle are limited. Hoque and Oikawa (2004), however, have compared residual feed intake by three different methods and have suggested that phenotypic and genetic residual feed intake contribute more than that of regression residual feed intake, calculated from the linear regression with adjusted daily gain, in selection programs for the improvement of growth performance.

Opportunities for improving production efficiency by exploiting genetic variation in feed efficiency depend not only on the existence of genetic variation within a target population but also on genetic correlations with other key production traits, such as growth and feed intake. A few studies (Fan et al., 1995; Renand and Krauss, 2002) have examined the interrelationship among some of the measures of growth and feed efficiency; however, a comprehensive assessment and comparison involving most of these measurements has not been carried out on Japanese Black population. Therefore, the objective of this study was to estimate genetic parameters for and genetic relationships between different measures of feed efficiency and its component traits, and to examine the benefits of selecting of feed efficiency traits in respect of biological point of view.

2. Materials and methods

2.1. 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 to 2002. 77 bulls were tested for 140 days and the remaining 663 bulls for 112 days. The bull calves, collected from designated farms, were within the age limit of 7–8 months and body weight of 200–300 kg. Each year, 20–30 bulls were selected based on heavier body weight for performance test from approximately 200 bulls. The selected bulls were introduced to the test station and housed in individual box stalls (2.7×3.6 m^2) with an adjacent 10 m^2 paddock for voluntary exercise. Cohort was defined as a group of bulls of same birth date and introduced to the test station on the same day and managed together. A total of 171 cohorts were used in the analyses. In order to estimate genetic parameters for the traits measured, a pedigree file was constructed. The tested bulls were produced from 61 sires and 555 dams and the pedigrees of the tested bulls were traced back to three generations and, including the tested bulls, totaled 4897. After three weeks of being introduced 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 h, 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. In addition to roughage and concentrate, water was supplied ad libitum. Sufficient feed was given to each animal according to its prior 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

Table 1
Descriptive statistics of the raw data of bulls

Traits[a]	AGS (day)	AGF (day)	MBW (kg)
Mean	230.29	345.20	338.33
Minimum	194	306	235.21
Maximum	296	408	440.14
S.D.	17.35	18.59	35.75

[a] AGS, age of the bulls at the start of the test; AGF, age of the bulls at finish; MBW, mean body weight at the mid-test.

leftover feed. Descriptive statistics of the data are presented in Table 1.

2.2. 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, body weight at finish (BWF), daily feed intake (DFI), feed conversion ratio (FCR) and residual feed intake (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 ($\mathrm{MBW}^{0.75}$). DFI was then combined with ADG and MWT to compute different measures of feed efficiency: FCR and RFI. FCR was calculated as DFI divided by ADG. Kennedy et al. (1993) showed that genetic regression may provide additional insight into the true relationship in cases where phenotypic measurements such as weight gain are subjected to considerable measurement errors. They suggested that although RFI is phenotypically independent of production, it may be genetically correlated to production. The RFI was therefore calculated as phenotypic RFI ($\mathrm{RFI}_{\mathrm{phe}}$) and genetic RFI ($\mathrm{RFI}_{\mathrm{gen}}$) by the residual of multiple regression ($\mathrm{RFI}_{\mathrm{phe}}$) and genetic regression ($\mathrm{RFI}_{\mathrm{gen}}$) from the multivariate analysis of DFI on MWT and ADG.

$\mathrm{RFI}_{\mathrm{phe}}$was calculated as :

$$\mathrm{RFI}_{\mathrm{phe}} = \mathrm{DFI} - \beta_{\mathrm{w}} \times \mathrm{MWT} - \beta_{\mathrm{g}} \times \mathrm{ADG}$$

where phenotypic regression coefficient, $\begin{bmatrix} \beta_{\mathrm{w}} \\ \beta_{\mathrm{g}} \end{bmatrix} = \mathbf{P}^{-1}\boldsymbol{c}$; $\mathbf{P}$=phenotypic covariance matrix of two production traits (MWT and ADG); and $\boldsymbol{c}$=vector of the phenotypic covariance of feed intake with production traits.

$\mathrm{RFI}_{\mathrm{gen}}$was calculated as :

$$\mathrm{RFI}_{\mathrm{gen}} = \mathrm{DFI} - \beta_{\mathrm{w}} \times \mathrm{MWT} - \beta_{\mathrm{g}} \times \mathrm{ADG}$$

where genetic regression coefficient, $\begin{bmatrix} \beta_{\mathrm{w}} \\ \beta_{\mathrm{g}} \end{bmatrix} = \mathbf{G}^{-1}\boldsymbol{c}$; $\mathbf{G}$=genetic covariance matrix of two production traits (MWT and ADG); and $\boldsymbol{c}$=vector of the genetic covariance of feed intake with production traits estimated using the residual maximum likelihood (REML) method.

2.3. Statistical analysis

The covariance components for all traits were estimated by the REML method with the VCE program (Neumaier and Groeneveld, 1998). The optimization in VCE was done with quasi-Newton procedure and includes setting up the mixed model equation, numerical factorization, solving the triangular system, computing the sparse inverse and assembling the gradients. The conversion is defined to be reached when a change is less than 0.005 over the last 9 iterates and followed by the current estimates of the ratios. The analyzed traits are described by the following model:

$$Y_{ij} = F_i + b\left(A_j - A\right) + a_j + e_{ij}$$

where Y_{ij}=phenotype of jth animal in ith cohort; F_i=fixed effect of ith cohort; b=linear regression coefficient of observation on age; A_j=age of the animals at the start of the test; A=average age of the animals at the start of the test; a_j=random additive genetic effect; e_{ij}=random residual.

The genetic parameters were estimated from bivariate analyses and the estimated genetic variances and heritabilities were averaged for the results, while their standard errors (S.E.) were the median of the estimates.

3. Results

The means, variance components and heritabilities for feed efficiency and its component traits are

Table 2
Means (± S.E.), phenotypic variances (V_p), additive genetic variances (V_A) and heritabilities (h^2) (± S.E.) for different traits

Traits[a]	ADG (kg/day)	MWT (kg$^{0.75}$)	BWF (kg)	DFI (kg/day)	FCR	RFI_{phe} (kg/day)	RFI_{gen} (kg/day)
Means	1.23 ± 0.01	78.88 ± 0.23	408.88 ± 1.47	9.26 ± 0.04	7.60 ± 0.03	−0.05 ± 0.03	−2.21 ± 0.03
V_p	0.071	14.69	796.13	1.30	0.89	1.04	0.92
V_A	0.014	7.20	374.18	0.44	0.13	0.25	0.23
h^2	0.20 ± 0.10	0.49 ± 0.09	0.47 ± 0.10	0.34 ± 0.11	0.15 ± 0.04	0.24 ± 0.11	0.25 ± 0.10

[a] ADG, average daily gain; MWT, metabolic body weight at mid-test; BWF, body weight at finish; DFI, daily feed intake; FCR, feed conversion ratio; RFI_{phe}, phenotypic residual feed intake; RFI_{gen}, genetic residual feed intake.

presented in Table 2. The mean values for ADG, BWF and DFI were consistent with other reports (Oikawa et al., 2000; Uchida et al., 2001) in the same breed. It should be noted that the lower values of RFI or FCR indicate better efficiency of an animal. In our study, the mean for RFI_{phe} was close to zero and RFI_{gen} was negative. Estimated heritability for ADG was low, whereas the heritabilities for MWT and BWF were moderate. Heritability of DFI was moderate and higher than those for feed efficiency traits. Both the RFI were moderately heritable ($h^2=0.24$ and 0.25 for RFI_{phe} and RFI_{gen}, respectively), whereas heritability of FCR was low indicating that variation in RFI of Japanese Black cattle contains genetic components which should respond to selection.

The correlations among DFI and growth traits (ADG, MWT and BWF) are shown in Table 3. Estimated genetic correlations between DFI and growth traits were high, ranging from 0.74 to 0.88, whereas the phenotypic correlations between them were moderate ranging from 0.55 to 0.56. The results show that the genetic correlations among ADG, MWT and BWF were practically unity (>0.95), while the phenotypic correlations between them were moderate to high.

The genetic and phenotypic correlations among different measures of feed efficiency are shown in Table 4. The genetic and phenotypic correlations between RFI_{phe} and RFI_{gen} were higher than 0.95, implying that they may be regarded as the same traits. Corresponding correlations between FCR and RFI_{phe} (0.64 and 0.76, respectively) and between FCR and RFI_{gen} (0.62 and 0.76, respectively) were high but less than one, indicating that they should be regarded as distinct traits. The positive correlations between RFI and FCR indicate that lower RFI (higher efficiency) was associated with improved FCR.

The correlation coefficients between different measures of feed efficiency and its component traits are presented in Table 5. DFI was positively correlated with all the measures of feed efficiency traits but was more strongly correlated with RFI (RFI_{phe} and RFI_{gen}) than with FCR. By definition, RFI_{phe} should not be phenotypically correlated with its component traits, and the results confirmed this (i.e. r_p with MWT and ADG were zero). In addition, the result show that RFI_{gen} was genetically independent of MWT ($r_g=-0.07$), whereas low genetic correlation was found between RFI_{gen} and ADG ($r_g=0.18$). Favorable (negative) genetic and

Table 3
Genetic (above the diagonal) and phenotypic (below the diagonal) correlations among feed intake and growth traits

Traits[a]	DFI	ADG	MWT	BWF
DFI		0.87 ± 0.08	0.74 ± 0.15	0.88 ± 0.11
ADG	0.56		0.96 ± 0.09	0.95 ± 0.10
MWT	0.55	0.36		0.97 ± 0.08
BWF	0.55	0.49	0.89	

[a] DFI, daily feed intake; ADG, average daily gain; MWT, metabolic body weight at mid-test; BWF, body weight at finish.

Table 4
Genetic (above the diagonal) and phenotypic (below the diagonal) correlations among different measures of feed efficiency

Traits[a]	RFI_{phe}	RFI_{gen}	FCR
RFI_{phe}		0.97 ± 0.02	0.64 ± 0.10
RFI_{gen}	0.98		0.62 ± 0.11
FCR	0.76	0.76	

[a] RFI_{phe}, phenotypic residual feed intake; RFI_{gen}, genetic residual feed intake; FCR, feed conversion ratio.

Table 5
Phenotypic and genetic correlations between different measures of feed efficiency and its component traits

Traits[a]	Correlations[b]	DFI	ADG	MWT	BWF
FCR	r_p	0.40	−0.52	0.14	0.11
	r_g	0.34 ± 0.15	−0.58 ± 0.24	−0.57 ± 0.25	−0.52 ± 0.25
RFI_{phe}	r_p	0.72	0.01	−0.01	−0.01
	r_g	0.78 ± 0.06	0.25 ± 0.16	0.16 ± 0.13	0.19 ± 0.15
RFI_{gen}	r_p	0.59	−0.13	−0.18	−0.18
	r_g	0.61 ± 0.10	0.18 ± 0.20	−0.07 ± 0.14	−0.04 ± 0.15

[a] DFI, daily feed intake; ADG, average daily gain; MWT, metabolic body weight at mid-test; BWF, body weight at finish; FCR, feed conversion ratio; RFI_{phe}, phenotypic residual feed intake; RFI_{gen}, genetic residual feed intake.

[b] r_p and r_g denote phenotypic and genetic correlations, respectively.

phenotypic correlations were observed between FCR and its component trait, ADG.

4. Discussion

Considerable numbers of heritability estimates have been published for growth traits in beef cattle. A comprehensive review (Koots et al., 1994a) of these estimates indicates that the traits are all moderately heritable, with heritability weighted averages of 0.33 for yearling weight and 0.22 for weight gain. The heritability for ADG in our study was close to the estimates of 0.18 by Sasaki (1991) and 0.20 by Oikawa et al. (2000) for Japanese Black steers and 0.22 by Hirooka et al. (1996) for Japanese Brown steers. However, Uchida et al. (2001) estimated heritabilities for performance traits in Japanese Black steers using an animal model with Gibbs sampling and found that heritability for ADG to be 0.57, which are considerably higher than the present result. The differences in source of data and sampling error may explain the discrepancy. Estimated heritability for DFI was close to the estimate of 0.36 by Oikawa et al. (2000) and of 0.37 by Uchida et al. (2001) for the same breed and 0.37 by Arthur et al. (2001a) for Angus breed. Our study has shown that considerable genetic variation exists in RFI, DFI and BWF in Japanese Black cattle, and that this variation should be exploited in the selection program for the improvement of feed utilization and growth performance.

Relatively small numbers of heritability estimates are available in the literature for feed efficiency traits in beef cattle, with most of the estimates being for European beef breeds and a few for Japanese Black cattle. Estimated heritability for FCR was close to the heritability reported in the same breed (0.11) by Oikawa et al. (2000) and (0.14) by Uchida et al. (2001) but lower than those reported in Angus breed (0.32) by Arthur et al. (2001a). The genetic variation found in RFI agrees well with the reports by Arthur et al. (1998) and Archer et al. (1999). Our estimates of the heritabilities for RFI_{phe} and RFI_{gen} were moderate and within the range (0.14–0.41) of five estimates reported in a review by Arthur et al. (1998), but higher than the estimate of 0.16 for RFI_{phe} reported in Hereford breeds by Herd and Bishop (2000), and lower than the estimate of 0.38 for RFI_{phe} reported in Angus breeds by Arthur et al. (2001a). The heritabilities available for feed efficiency traits, as used in the reviews by Koots et al. (1994a) and Archer et al. (1999), range from low to moderate, with most of the values falling within the moderate range supporting our results.

The genetic and phenotypic correlations among growth traits (ADG, MWT and BWF) were higher than the estimates by Arthur et al. (2001b), who reported that the genetic and phenotypic correlations between live-weight and ADG to be 0.69 and 0.60, respectively, for young Charolais bulls. However, our estimated genetic correlation between ADG and BWF was close to the estimate of 0.97 by Oikawa et al. (2000) for the same breed. Estimated high genetic correlations and moderate to high phenotypic correlations between DFI and growth traits in our study were partially supported by Arthur et al. (2001b), who estimated genetic and phenotypic correlations between DFI and live-weight to be 0.83 and 0.54, respectively, and between DFI and ADG to be 0.39 and 0.47, respectively. Moderate to high correlations between DFI and ADG and between DFI and body weight for growing bulls were reported by Bishop (1992) and Nieuwhof et al. (1992).

There are few reports of genetic and phenotypic correlations among different estimates of feed efficiency in the literature, but those available are in general agreement with the findings of this study. Estimated genetic and phenotypic correlations between RFI_{phe} and RFI_{gen} were higher than 0.95 implying that they can be practically regarded as the same trait. Archer et al. (1998) have also reported a very high genetic correlation (0.99) between RFI_{phe} and RFI_{gen}, concluding that selection for RFI_{gen} would give results similar to selection for RFI_{phe}. The genetic correlation between RFI (RFI_{phe} and RFI_{gen}) and FCR in the present study was high which is in agreement with the findings of Herd and Bishop (2000) and Arthur et al. (2001a). Herd and Bishop (2000) estimated genetic correlation between RFI_{phe} and FCR to be 0.70 for Hereford breed. Corresponding correlation was 0.66 for Angus breed, estimated by Arthur et al. (2001a), and 0.85 for Charolais breed, estimated by Arthur et al. (2001b). However, Fan et al. (1995) reported a genetic correlation between RFI and FCR of 0.90 and 1.00 for Angus and Hereford breeds, respectively. The difference in correlation coefficients might be reflected due to the differences in calculating the RFI, because Fan et al. (1995) used NRC (1984) feeding standards formulae instead of regression approach.

Estimated correlations (genetic and phenotypic) between FCR and DFI were lower than those from other studies. Koots et al. (1994b) summarized published estimates between DFI and FCR to be 0.71 and 0.75 for the genetic and phenotypic correlations, respectively. Our high genetic and phenotypic correlations between RFI and DFI were in agreement with the reports by Herd and Bishop (2000) and Arthur et al. (2001a,b). Herd and Bishop (2000) estimated genetic and phenotypic correlations between RFI_{phe} and DFI to be 0.64 and 0.70, respectively, for Hereford breed. Corresponding correlations were 0.69 and 0.72, respectively, for Angus breed reported by Arthur et al. (2001a) and 0.79 and 0.60, respectively, for Charolais breed estimated by Arthur et al. (2001b). However, the genetic and phenotypic correlations between RFI_{phe} and DFI were 0.38 and 0.56, respectively, reported by Archer et al. (1998), which were lower than our estimates.

Estimates of genetic correlations between RFI and its component traits reported here appears to be the first published estimates of these correlations for Japanese Black cattle. The calculation of RFI requires the estimation of expected feed intake, which can be obtained through regression, as was the case in this study, or can be obtained through the use of feeding standards formula. Kennedy et al. (1993) showed that when expected feed intake is obtained by phenotypic regression, the RFI_{phe} is expected to be phenotypically independent of the component traits and in the other case, when expected feed intake is obtained by genetic regression, the RFI_{gen} is expected to be genetically independent of its component traits. They also mentioned that even with RFI calculated by regression (as RFI_{gen} in this study), there is no guarantee that its genetic correlations with these component traits will be close to zero. In our study, both MWT and ADG were phenotypically independent of RFI_{phe}, and MWT was genetically independent of RFI_{gen}, while there was a weak genetic correlation between RFI_{gen} and ADG. This weak genetic correlation between RFI_{gen} and ADG was not conclusive because of large standard error, which might be due to the small size of the dataset as well as the low heritabilities of the component traits. However, when RFI is estimated with expected feed intake calculated from feeding standards formulae, it is not automatically independent of production and is usually correlated with these traits, as observed in the studies by Fan et al. (1995) and Arthur et al. (2001b).

The favorable (negative) genetic correlations between FCR and growth traits observed in our study were in agreement with the estimates by Brown (1988), Fan et al. (1995) and Arthur et al. (2001a). The high negative genetic relationship between ADG and FCR (−0.84 and −0.74 for Angus and Hereford breed, respectively) has been reported by Brown (1988) and (−0.62 and −0.57 for Angus and Hereford breed, respectively) by Fan et al. (1995). Arthur et al. (2001a) found the high negative genetic correlation (−0.62) between these traits for Angus breed. Weighted mean values for genetic and phenotypic correlations reported in a review by Koots et al. (1994b) were −0.67 and −0.64 for FCR with ADG, respectively, and corresponding correlations were −0.60 and −0.46 for FCR with yearling weight, respectively. These estimates suggesting that as ADG increased, the FCR decreased. Therefore, selection for weight gain at the end of test (1 year of age) could result in an increase in the efficiency of feed utilization.

Considering the origin of secondary traits, FCR is expressed as a ratio, whereas RFI is a linear index. The use of ratio traits for genetic selection may cause problems associating to prediction of the change in the component traits in future generations (Arthur et al. 2001a). This is due to disproportionate fashion in which selection pressure is exerted on the component traits. A linear index, however, places a predetermined amount of selection pressure on the traits and thus in principle results in a more predictable genetic change in each trait. Gunsett (1984) compared the efficiency of direct selection for a two-component trait with a linear index trait derived from the same two components and concluded that the use of linear index increases selection responses as compared with direct selection on the ratio trait. RFI is the trait derived from the combination of feed consumption and production traits and our study has shown that RFI was more favorably and more strongly correlated with DFI than FCR was with DFI. For RFI, the weights of the component traits in the index are determined by only biological (co)variances. However, profitability will be maximized when index weights on feed intake (or RFI), growth, and other traits are determined by both biological and economic parameters, which need to be investigated.

5. Conclusion

Generally, the estimates of heritability reported here indicate that sufficient additive genetic variance exists in RFI, DFI and body weight, which should lead to further response from selection on these traits. $\mathrm{RFI}_{\mathrm{gen}}$ was genetically independent of body weight, while there was a weak genetic relationship between $\mathrm{RFI}_{\mathrm{phe}}$ and body weight. RFI was more heritable than FCR, and a stronger genetic correlation was observed between RFI and DFI than between FCR and DFI. Due to these observations, and the favorable nature of RFI (linear index), we conclude that $\mathrm{RFI}_{\mathrm{gen}}$ should be included in beef breeding program for genetic improvement of feed efficiency.

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