Genetic parameters for measures of energetic efficiency of bulls and their relationships with carcass traits of field progeny in Japanese Black cattle[1]

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ABSTRACT: Records on 514 bulls from the sire population born from 1978 to 2004, and on 22,099 of their field progeny born from 1997 to 2003 with available pedigree information (total number = 124,458) were used to estimate genetic parameters for feed intake and energy efficiency traits of bulls and their relationships with carcass traits of field progeny. Feed intake and energetic efficiency traits were daily feed intake, TDN intake, feed conversion ratio (FCR), TDN conversion ratio (TDNCR), residual feed intake (RFI), partial efficiency of growth, relative growth rate, and Kleiber ratio. Progeny carcass traits were carcass weight (CWT), yield estimate, ribeye area, rib thickness, subcutaneous fat thickness (SFT), marbling score (MSR), meat color standard (MCS), fat color standard (FCS), and meat quality grade. All measures of feed intake and energetic efficiency were moderately heritable (ranged from 0.24 to 0.49), except for partial efficiency of growth and relative growth rate, which were high (0.58) and low (0.14), respectively. The phenotypic and genetic correlations between FCR and TDNCR were ≥0.93. Selection for Kleiber ratio will improve all of the energetic efficiency traits with no effect on feed intake measures (daily feed intake and TDN intake). The genetic correlations of FCR, TDNCR, and RFI of bulls with most of the carcass traits of their field progeny were favorable (ranged from −0.24 to −0.72), except with fat color standard (no correlation), MCS, and SFT. Positive (unfavorable) genetic correlations of MCS with FCR, TDNCR, and RFI (0.79, 0.70, and 0.51, respectively) were found. The SFT was negatively genetically correlated with FCR and TDNCR (−0.32 and −0.20, respectively); however, the genetic correlation between RFI and SFT was not significantly different from zero ($r_g = -0.08 \pm 0.12$). Favorable correlated responses in CWT, yield estimate, ribeye area, rib thickness, MSR, and meat quality grade would be predicted for selection against any measure of energetic efficiency. The correlated responses in CWT and MSR of progeny were greater for selection against RFI than for selection against any other energetic efficiency trait. Results of this study indicate that RFI should be preferred over other measures of energetic efficiency to include in selection programs.

Key words: beef cattle, carcass trait, feed efficiency, genetics

INTRODUCTION

The energetic efficiency of an animal is more difficult to quantify than that of growth; consequently, different measures of energetic efficiency of cattle have been developed over the years. These include feed conversion ratio (**FCR**; Brody, 1945), residual feed intake (**RFI**; Koch et al. 1963), partial efficiency of growth (**PEG**; Kellner, 1909), relative growth rate (**RGR**; Fitzhugh and Taylor, 1971), and Kleiber ratio (**KR**; Kleiber, 1947). Although FCR has been used extensively in the past, the use of FCR (ratio trait) for selection presents problems associated with the prediction of the change in the component traits in future generations (Arthur et al., 2001b). This is due to the fact that FCR is genetically correlated with growth, body size, body composition, and appetite. However, RFI describes animal

efficiency without the problems associated with component traits. Recent literature has established the relationship of RFI with FCR and carcass traits (Hoque et al., 2006b). Nkrumah et al. (2007) estimated genetic relationships of measures of energetic efficiency with growth and a few carcass traits in crossbred cattle; however, little is known about how RFI compares with other proposed measures of efficiency (such as PEG, RGR, and KR) in terms of relationships with feed intake and carcass merit in Japanese Black cattle.

In the Japanese beef market, carcass value is determined on the basis of meat quality, especially degree of marbling (intramuscular fat). However, individual bulls have large genetic influence in the Japanese Black population because more than 90% of the progeny are produced by AI. It is, therefore, necessary to evaluate the genetic relationships between energetic efficiency traits of Japanese Black bulls and carcass traits of their progeny. This study was conducted to compare different measures of energetic efficiency of bulls in the sire population and their genetic relationships with carcass traits of their field progeny.

MATERIALS AND METHODS

The animals in this study were managed following the procedures as described by JLIA (2000).

Data Structure

The data used in this study were collected in Japan on 514 station-tested Japanese Black bulls (sire population) and on 22,099 of their field progeny at 10 feedlot farms of Miyagi prefecture, where progeny fattening was being conducted. All of the animals were ear tagged after birth. The number of animals in the sire population was considerably less than that of the field progeny. This is due to the fact that only 20 bull calves from approximately 160 available bulls were selected for performance testing each year. To estimate genetic parameters, a pedigree file was constructed. The pedigrees of the studied animals were traced back 8 generations, and the total number of animals including those without records, but contributing pedigree information, was 124,458.

Bull Performance Data

Records on bulls in the sire population were collected during the period from 1978 to 2004. They were selected from designated farms at the age limits of 6 to 7 mo and BW of 200 to 300 kg. Selection of calves was based on heavier BW. Selected bulls were tested for 112 d at the test station of Miyagi Prefecture Animal Industry Centre. After 3 wk (adjustment period) of being introduced to the feed, the animals were provided ad libitum access to roughage (green forage, silage, or hay); however, feeding of concentrate was restricted to

1 h twice per day. 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% DCP and 73% TDN. In addition to roughage and concentrate, water was supplied ad libitum. Records of roughage and concentrate consumption were maintained on a DM basis. Bulls were fed an average of 5.44 kg of roughage and 2.88 kg of concentrate per day on a DM basis. More detail about feeding and management of animals has been described by Hoque et al. (2006a). A contemporary group was defined as a group of animals of the same age tested under a uniform environment for the same period. A total of 121 contemporary groups were included in the analyses for traits of bulls. Body weight of individual bulls was recorded at the start, end, and at weekly intervals during the test period, and ADG for each animal was calculated from the difference between the start and the end of test BW divided by the number of days on test. Daily feed intake (**DFI**) was measured on a DM basis by the difference between supplied and leftover feed, and FCR was calculated as average DMI divided by ADG. Total digestible nutrient consumption was estimated as total feed intake during the test period multiplied by the TDN content (64%) of feed (JLIA, 2000), and TDN per unit of gain was expressed as TDN conversion ratio (**TDNCR**). Metabolic BW (**MWT**) was calculated as the mean of start and end of test BW of an animal, raised to the power of 0.75 (mean $BW^{0.75}$). Using the general linear model of SAS Inst. Inc. (Cary, NC), a linear regression model of DFI on MWT and ADG, with contemporary group as a class variable, was fitted to data. The model was

$$Y_i = \beta_0 + \beta_1 \times ADG + \beta_2 \times MWT + e_i,$$

where Y_i = DFI of animal i, β_0 = regression intercept, β_1 = partial regression coefficient of DFI on ADG, β_2 = partial regression coefficient of DFI on MWT, and e_i = residual error in feed intake of animal i.

The regression coefficients from this model were used to predict expected feed intake for all animals. Then RFI was calculated as the actual (measured) DFI minus expected feed intake for each bull. Partial efficiency of growth was calculated as ADG ÷ (DFI – Fm). The Fm (feed requirement for maintenance) was calculated as (0.033 × MWT) ÷ 0.70 (Geay and Micol, 1988). Details of the procedure used to calculate the constant terms 0.033 (ME requirement for maintenance/ME concentration of TDN) and 0.70 (TDN concentration of diet) can be obtained from the Japanese beef cattle feeding standards (JLIA, 2000). The RGR (i.e., growth relative to instantaneous size) was expressed as percentage of change in BW per day. It was calculated as 100 × (log finish BW – log start BW) ÷ days on test (Fitzhugh and Taylor, 1971). The KR was computed as the ratio of ADG to MWT.

Table 1. Data structure and basic statistics of slaughter age and carcass traits of field progeny[1]

Sex	No. of animals	No. of contemporary groups	Mean (SD)									
			SLage, d	CWT,* kg	YEM, %	REA,* cm^2	RT,* mm	SFT,* mm	MSR,* score	MCS, score	FCS,* score	MQG, score
Steers	5,921	1,030	936.3 (62.7)	432.67 (46.07)	74.06 (1.31)	54.32 (7.80)	76.64 (8.81)	23.47 (7.89)	6.65 (2.13)	3.82 (0.59)	2.94 (0.30)	3.97 (0.88)
Heifers	16,178	873	924.3 (68.4)	365.44 (40.67)	74.07 (1.28)	52.13 (7.58)	71.93 (8.20)	26.10 (8.05)	6.18 (2.15)	3.89 (0.58)	3.05 (0.31)	3.86 (0.92)
Pooled	22,099	1,191	933.0 (64.5)	414.66 (53.70)	74.07 (1.30)	53.73 (7.80)	75.38 (8.90)	24.17 (8.02)	6.49 (2.14)	3.83 (0.59)	2.98 (0.31)	3.93 (0.89)

*Mean values differ significantly ($P < 0.001$) between steers and heifers.

[1]SLage = slaughter age; CWT = carcass weight; YEM = yield estimate; REA = ribeye area; RT = rib thickness; SFT = subcutaneous fat thickness; MSR = marbling score; MCS = meat color standard; FCS = fat color standard; MQG = meat quality grade.

Progeny Carcass Data

On breeding farms in Japan, calves are raised with their mothers and are weaned between 3 and 5 mo of age. They are sold at calf markets between 8 and 10 mo of age, and purchased by feedlot farmers. Animals on feedlot farms are fed various grains and commercial feeds, as well as a wide range of roughages and fodders, including freshly cut green grass, silage, hay, and rice straw. Data on animals at feedlot farms during the period from 1997 to 2003 were used in this study as field progeny. A contemporary group in field progeny was a group of animals born in same season (spring, summer, autumn, or winter) of the year, managed on the same feedlot farm, and slaughtered on the same day at the same slaughterhouse. The number of contemporary groups for traits of progeny was 1,191. At the end of the fattening period, the animals of this study were slaughtered by the mechanical gunshot method at different slaughterhouses at an average age of about 32 mo. The data structure and the descriptive statistics for carcass traits are presented in Table 1. Traits measured in the field progeny were carcass weight (**CWT**), yield estimate (**YEM**), ribeye area (**REA**), rib thickness (**RT**), subcutaneous fat thickness (**SFT**), marbling score (**MSR**), meat color standard (**MCS**), fat color standard (**FCS**), and meat quality grade (**MQG**). The CWT was obtained 24 h postmortem by weighing the slaughtered animals after the removal of the head, hide, lungs, heart, liver, intestines, and ancillary organs or mesenteries, bladder, reproductive organs, and blood. The REA, SFT, and MSR were measured at the 6th to 7th rib section. Grid approximation was used for REA measurement—placing a transparent sheet with grids (1 cm × 1 cm) on a section and counting the number of intersections in the REA. The RT was measured at the mid-point of the 7th rib. The MSR, a subjective measure of intramuscular or marbling fat on the surface of the longissimus thoracic muscle, was measured in 12 categories, with number 5.0 being the greatest (from 0.0 to 3.0 with intervals of 0.33, and 4.0, 5.0). The YEM, MCS, FCS, and MQG were obtained according to the beef carcass grading standards (JMGA, 1988).

The YEM of individual progeny were calculated using the following formula:

$$YEM\ (\%) = 67.37 + (0.130 \times REA\ cm^2)$$
$$+ (0.667 \times RT\ cm) - (0.025 \times LCWT\ kg)$$
$$- (0.896 \times SFT\ cm).$$

In this formula, the LCWT was left side CWT. The exposed surface of the longissimus thoracic muscle, cut between the 6th and 7th rib, was subjectively evaluated 24-h postmortem for MCS by a certified grader (Japan Meat Grading Association) using a 7-point descriptive (1 = light and 7 = extremely dark). The FCS was evaluated using the same procedure. The MQG was the value equivalent to the least grade among the 4 items MSR, MCS, meat firmness, and FCS.

Statistical Analysis

Variance components, heritabilities, and genetic correlations were estimated by the residual maximum likelihood method using the variance component estimation package developed by Neumaier and Groeneveld (1998). Data were analyzed in a series of 2-trait animal models. The first series of 2-trait analyses included each pair-wise combination of the 8 feed intake and energetic efficiency traits. The models included fixed contemporary group effect, additive genetic and residual effects, and linear covariate for age at finish. The second series of 2-trait analyses included 1 feed intake or energetic efficiency trait and 1 carcass trait. The models included fixed contemporary group effect, additive genetic and residual effects, and linear covariate for age at finish (feed intake and energetic efficiency traits) or age at slaughter (carcass traits). In addition, fixed effect of sex was included in the models for CWT, REA, RT, SFT, MSR, and FCS because sex has a significant effect on these traits (Table 1). To estimate the significance level, ANOVA were made using general linear models of SAS. Significant fixed effects and covariates were contemporary group and age at slaughter.

Table 2. Means with their SD, additive genetic variances, and heritabilities for measures of feed intake and energetic efficiency in bulls[1]

Trait	DFI, kg/d	TDNI, kg	FCR	TDNCR	RFI, kg/d	PEG	RGR, %	KR
Means	8.32	602.99	7.09	4.58	−0.03	0.26	0.16	0.016
SD	0.78	64.15	1.02	0.64	0.69	0.05	0.03	0.002
σ^2_A	0.1841	1,216.63	0.4494	0.20592	0.1078	0.00077	0.00016	0.000001
$h^2 \pm$ SE	0.36 ± 0.09	0.35 ± 0.07	0.38 ± 0.07	0.46 ± 0.08	0.49 ± 0.09	0.58 ± 0.05	0.14 ± 0.11	0.24 ± 0.09

[1]DFI = daily feed intake; TDNI = TDN intake during the test period; FCR = feed conversion ratio; TDNCR = TDN conversion ratio; RFI = residual feed intake; PEG = partial efficiency of growth; RGR = relative growth rate; KR = Kleiber ratio.

The covariance structure for additive genetic effects of animals and residual effects is described below:

$$
E\begin{bmatrix} a_1 \\ a_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, Var\begin{bmatrix} a_1 \\ a_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma^2_{a1} & A\sigma_{a12} & \mathbf{0} & \mathbf{0} \\ & A\sigma^2_{a2} & \mathbf{0} & \mathbf{0} \\ & & I\sigma^2_{e1} & I\sigma_{e12} \\ sym. & & & I\sigma^2_{e2} \end{bmatrix},
$$

where a_1 and a_2 are the vectors of additive genetic effects of animals for trait 1 and trait 2, respectively, and e_1 and e_2 are the residual effects for them. A is the numerator relationship matrix in which diagonal elements consist of 1.0 plus the coefficient of inbreeding and off-diagonal elements consist of the genetic relationships between animals. The symbols σ^2_{a1} and σ^2_{a2} are the additive genetic variances for trait 1 and trait 2, respectively, and σ_{a12} is the additive genetic covariance between them. The symbols σ^2_{e1} and σ^2_{e1} are the residual variances for trait 1 and trait 2, respectively, and σ_{e12} is the residual covariance between them. This model was assumed when the 2 traits were recorded on the same animal. When the 2 traits were recorded on different animals, σ_{e12} was assumed to be zero.

The genetic variances, heritabilities, and SE reported in this paper were the medians of the estimates. The correlated responses were predicted according to Cameron (1997). For predicting correlated responses to downward selection for DFI, TDN intake (**TDNI**), FCR, TDNCR, and RFI, the selection intensity was assumed to be −1.00; to upward selection for PEG, RGR, and KR, the selection intensity was assumed to be +1.00.

RESULTS

The means, additive genetic variances, and heritabilities for measures of feed intake (DFI and TDNI) and energetic efficiency (FCR, TDNCR, RFI, PEG, RGR, and KR) are presented in Table 2. Bulls had DFI of about 8 kg/d and FCR of 7 kg of feed per kg of gain. Each bull consumed an average of about 603 kg of TDN during the test period, and TDNCR was 4.6 kg of TDN per kg of BW gain. The mean value for RFI was close

to zero, as expected by definition, and ranged from −1.98 (most efficient) to 2.05 (least efficient) kg of DM per d. Estimated heritability for all measures of feed intake and energetic efficiency were moderate (ranged from 0.24 to 0.49), except for PEG and RGR, which were high (0.58) and low (0.14), respectively, under the feeding regimen of the Japanese performance testing program.

Genetic and phenotypic correlations among measures of feed intake and energetic efficiency of bulls are presented in Table 3. Phenotypically RGR and KR were lowly correlated with all measures of feed intake and energetic efficiency, except with FCR and TDNCR, which were high (ranged from −0.56 to −0.76). The phenotypic and genetic correlations between FCR and TDNCR were greater than 0.90, implying that they might be regarded as the same trait. The DFI was favorably genetically correlated with most of the energetic efficiency traits (r_g of DFI with FCR, TDNCR, RFI, PEG, and RGR were 0.37, 0.45, 0.70, −0.34, and −0.21, respectively). The TDNI was genetically moderately correlated with TDNCR and RFI (0.34 and 0.42, respectively). The genetic correlations among measures of energetic efficiency were moderate to high (absolute values ranged from 0.27 to 0.97), except between RFI and RGR, which was low (−0.13). Selection for KR would improve most of the energetic efficiency traits with no effect on feed intake traits.

The genetic correlations of measures of feed intake and energetic efficiency of bulls with carcass traits of their progeny are presented in Table 4. The negative genetic correlations between energetic efficiency and carcass traits are considered a favorable indication for the possibility of simultaneous improvement of quality beef production and efficiency of energy utilization. The results show that the genetic correlations of FCR, TDNCR, and RFI of bulls in the sire population with most of the carcass traits of their progeny were favorable (ranged from −0.24 to −0.72), except with FCS (no correlation), MCS, and SFT. The MCS was positively (unfavorably) correlated with the energetic efficiency traits (r_g with FCR, TDNCR, and RFI were 0.79, 0.70, and 0.51, respectively). The SFT was negatively genetically correlated with FCR and TDNCR (−0.32 and −0.20, respectively); however, the genetic correlation between RFI and SFT was close to zero (r_g = −0.08 ± 0.12).

Table 3. Genetic (±SE, above the diagonal) and phenotypic (below the diagonal) correlations among feed intake and energetic efficiency traits in bulls[1]

Trait	DFI	TDNI	FCR	TDNCR	RFI	PEG	RGR	KR
DFI	—	0.44 ± 0.10	0.37 ± 0.09	0.45 ± 0.07	0.70 ± 0.05	-0.34 ± 0.11	-0.21 ± 0.07	0.03 ± 0.19
TDNI	0.92	—	0.13 ± 0.10	0.34 ± 0.10	0.42 ± 0.08	-0.12 ± 0.09	0.05 ± 0.09	0.04 ± 0.12
FCR	0.21	0.10	—	0.93 ± 0.01	0.78 ± 0.06	-0.92 ± 0.09	-0.56 ± 0.12	-0.74 ± 0.07
TDNCR	0.24	0.24	0.96	—	0.87 ± 0.06	-0.94 ± 0.08	-0.47 ± 0.11	-0.68 ± 0.09
RFI	0.83	0.72	0.60	0.62	—	-0.89 ± 0.09	-0.13 ± 0.09	-0.27 ± 0.12
PEG	−0.46	−0.35	−0.32	−0.74	0.76	—	0.38 ± 0.10	0.48 ± 0.08
RGR	0.13	0.18	−0.67	−0.63	−0.03	−0.14	—	0.97 ± 0.01
KR	0.18	0.22	−0.76	−0.56	−0.04	−0.11	0.74	—

[1]DFI = daily feed intake; TDNI = TDN intake during the test period; FCR = feed conversion ratio; TDNCR = TDN conversion ratio; RFI = residual feed intake; PEG = partial efficiency of growth; RGR = relative growth rate; KR = Kleiber ratio.

The correlated responses in carcass traits of progeny to selection against measures of feed intake or energetic efficiency of bulls after 1 generation of selection are shown in Table 5. Selection for improving energetic efficiency traits should be expected to result in favorably positive correlated responses in CWT and MSR. However, greater correlated responses in these traits should be expected from selection against RFI than from selection for or against any other energetic efficiency trait. No responses in FCS and weak correlated responses in YEM and MQG of progeny would be expected from selection for or against any energetic efficiency trait of bulls.

DISCUSSION

The mean values for DFI, TDNI, FCR, and TDN-CR were consistent with other reports (Oikawa et al., 2000, 2006) in the same breed. The estimated moderate heritabilities for most of the energetic efficiency traits are in agreement with published estimates. Available estimates for DFI, FCR, TDNI, and RFI, as used in the review by Koots et al. (1994b) and Archer et al. (1999), ranged from low to moderate heritability, with most of the values falling in the moderate range. Heritability estimates for RFI by Herd and Bishop (2000), Arthur et al. (2001a), Hoque et al. (2006a), and Nkrumah et al. (2007) also fall into the moderate range. The

moderate heritability for TDNCR was greater than the estimates of 0.24 and 0.11 reported by Sasaki et al. (1982) and Oikawa et al. (2000), respectively. However, Oikawa et al. (2000) estimated heritability of 0.36 for TDNI, which was similar to the present estimate. The high heritability for PEG in the present study agrees well with the estimate of 0.56 reported in hybrid bulls by Nkrumah et al. (2007). Estimated low heritability for RGR was close to the average estimate of 0.15 reported in the review by Koots et al. (1994b), but was slightly less than the estimates of 0.33 and 0.24 at 15 and 19 mo of age, respectively, in Charolais bulls reported by Arthur et al. (2001a). Estimated heritability for KR was close to the estimates of 0.31 and 0.21 at 15 and 19 mo of age, respectively, reported by Arthur et al. (2001a), but was less than the estimate of 0.52 reported by Bergh et al. (1992) for Bonsmara bulls. The estimated high to moderate heritabilities for most of the energetic efficiency traits indicate that genetic variation exists in these traits, and they are likely to respond to selection.

There are very few reports in the literature on genetic and phenotypic correlations among measures of feed intake and energetic efficiency, but those available are in general agreement with the findings of the present study. Nkrumah et al. (2007) found strong genetic and phenotypic correlations of RFI with FCR (0.62 and 0.52, respectively), PEG (−0.87 and −0.83, respective-

Table 4. Genetic correlations (±SE) of measures of feed intake and energetic efficiency of bulls with carcass traits of their field progeny[1]

Trait	CWT	YEM	REA	RT	SFT	MSR	MCS	FCS	MQG
DFI	0.78 ± 0.11	-0.18 ± 13	0.37 ± 0.12	0.66 ± 0.13	0.44 ± 0.12	-0.10 ± 0.13	0.11 ± 0.12	0.63 ± 0.14	-0.08 ± 0.13
TDNI	0.09 ± 0.08	-0.15 ± 0.14	-0.21 ± 0.14	-0.11 ± 0.13	-0.14 ± 0.12	-0.49 ± 0.09	0.36 ± 0.13	0.12 ± 0.15	-0.46 ± 0.11
FCR	-0.26 ± 0.11	-0.52 ± 0.10	-0.72 ± 0.07	-0.57 ± 0.07	-0.32 ± 0.11	-0.50 ± 0.08	0.79 ± 0.07	-0.11 ± 0.12	-0.60 ± 0.08
TDNCR	-0.24 ± 0.12	-0.53 ± 0.11	-0.47 ± 0.15	-0.55 ± 0.13	-0.20 ± 0.13	-0.62 ± 0.09	0.70 ± 0.07	-0.08 ± 0.13	-0.52 ± 0.10
RFI	-0.24 ± 0.10	-0.40 ± 0.11	-0.49 ± 0.10	-0.32 ± 0.11	-0.08 ± 0.12	-0.59 ± 0.08	0.51 ± 0.09	-0.04 ± 0.12	-0.56 ± 0.08
PEG	0.18 ± 0.10	0.46 ± 0.09	0.71 ± 0.08	0.43 ± 0.10	0.01 ± 0.11	0.52 ± 0.07	-0.69 ± 0.07	0.07 ± 0.04	0.53 ± 0.08
RGR	0.18 ± 0.08	0.62 ± 0.14	0.56 ± 0.15	0.80 ± 0.09	-0.35 ± 0.12	0.49 ± 0.14	-0.68 ± 0.12	0.28 ± 0.15	0.53 ± 0.14
KR	-0.03 ± 0.10	0.62 ± 0.09	0.87 ± 0.11	0.10 ± 0.08	-0.51 ± 0.09	0.12 ± 0.09	-0.65 ± 0.10	0.80 ± 0.09	-0.62 ± 0.11

[1]CWT = carcass weight; YEM = yield estimate; REA = ribeye area; RT = rib thickness; SFT = subcutaneous fat thickness; MSR = marbling score; MCS = meat color standard; FCS = fat color standard; MQG = meat quality grade; DFI = daily feed intake; TDNI = TDN intake during the test period; FCR = feed conversion ratio; TDNCR = TDN conversion ratio; RFI = residual feed intake; PEG = partial efficiency of growth; RGR = relative growth rate; KR = Kleiber ratio.

Table 5. Correlated responses in carcass traits of field progeny to selection against feed intake or energetic efficiency traits of bulls[1]

Trait	CWT, kg	YEM, %	REA, cm[2]	RT, mm	SFT, mm	MSR, score	MCS, score	FCS, score	MQG, score
DFI,[2] kg/d	−17.02	0.11	−1.05	−2.07	−1.82	0.11	−0.02	−0.04	0.04
TDNI,[2] kg	−1.94	0.09	0.59	0.34	0.57	0.52	−0.06	−0.01	0.20
FCR[2]	5.82	0.32	2.10	1.84	1.36	0.56	−0.13	0.01	0.27
TDNCR[2]	5.92	0.36	1.51	1.95	0.94	0.64	−0.13	0.01	0.26
RFI,[2] kg/d	6.11	0.28	1.62	1.17	0.43	0.74	−0.10	0.00	0.29
PEG[3]	−4.99	0.35	2.56	1.71	0.05	0.72	−0.14	0.01	0.30
RGR,[3] %	−2.45	0.23	0.99	1.57	−0.90	0.33	−0.07	0.01	0.15
KR[3]	0.53	0.30	2.02	0.26	−1.72	0.01	−0.09	0.04	−0.22

[1]CWT = carcass weight; YEM = yield estimate; REA = ribeye area; RT = rib thickness; SFT = subcutaneous fat thickness; MSR = marbling score; MCS = meat color standard; FCS = fat color standard; MQG = meat quality grade; DFI = daily feed intake; TDNI = TDN intake during the test period; FCR = feed conversion ratio; TDNCR = TDN conversion ratio; RFI = residual feed intake; PEG = partial efficiency of growth; RGR = relative growth rate; KR = Kleiber ratio.

[2]Downward selection.

[3]Upward selection.

ly), and DFI (0.73 and 0.64, respectively). Koots et al. (1994a) summarized available estimates between DFI and FCR to be 0.71 and 0.75 for genetic and phenotypic correlations, respectively. The corresponding correlations between RFI and FCR were 0.64 and 0.76, respectively, reported by Hoque et al. (2005). Herd and Bishop (2000) reported phenotypic correlations for RFI to be 0.64 with DFI and 0.70 with FCR for British Hereford cattle. Corresponding genetic correlations reported by Arthur et al. (2001a) were 0.79 and 0.85, respectively, for Charolais bulls. Low phenotypic correlations of RGR and KR with DFI and PEG (ranged from −0.03 to 0.15), and high phenotypic correlations of FCR with RGR and KR (−0.64 and −0.67, respectively) were obtained by Arthur et al. (2001a). They also found a high genetic correlation between RGR and FCR (−0.90), whereas Bergh et al. (1992) obtained the corresponding correlation between the reciprocal of FCR (i.e., G:F) and KR to be 0.88, which supports the present estimates. The estimated high genetic correlations of PEG with FCR, TDNCR, and RFI indicated that animals with low FCR, TDN, or RFI may show significant reductions in the energy requirement for maintenance and increase in growth efficiency above maintenance.

The genetic correlations indicate that selection against DFI (for reduced DFI) will improve all of the energetic efficiency traits (absolute value of coefficients were 0.21 to 0.70), except KR (no correlation), but will have the undesirable effect of reducing CWT ($r_g = 0.78$). These results are in agreement with the report by Arthur et al. (2001a) in beef cattle, who noted that consequences of selection against DFI would include improved energetic efficiency (r_g of DFI with FCR, RFI, PEG, and KR were 0.64, 0.79, −0.82, and −0.15, respectively), and reduced growth performance (r_g of DFI with ADG and BW were 0.39 and 0.83, respectively). The relationships of FCR or TDNCR with each other and with DFI and carcass traits obtained in the present study may indicate that selection against FCR or TDNCR would be similarly beneficial in terms of the correlated

reduction in DFI with increases in most of the carcass traits.

Reports in the literature comparing studies between energetic efficiency traits with respect to effects on carcass merit are few. However, the relationships of CWT with DFI and FCR obtained in the present study agreed well with the estimates (r_g of CWT with DFI and FCR were 0.66 and −0.28, respectively) reported by Nkrumah et al. (2007). In another study, Nkrumah et al. (2004) reported weak and moderate phenotypic correlations of DFI with REA (0.21) and backfat thickness (0.39), respectively. However, their estimated genetic correlations of CWT with RFI (0.05 ± 0.38) and PEG (−0.01 ± 0.29) were not significantly different from zero. Fan et al. (1995) showed that RFI, calculated using feeding standards formulae, was negatively related to yearling BW in Angus (−0.64) and Hereford (−0.05) breeds. Estimated genetic correlation between TDNCR of bulls and SFT of their progeny was less than the estimate of −0.68 ± 0.42 reported by Oikawa et al. (2000) for the same breed. However, the SE of their estimate was large. Herd and Bishop (2000) reported a genetic correlation of −0.47 between RFI and ultrasound rib fat thickness. The corresponding correlations reported between the 2 traits by Arthur et al. (2001b) and Robinson and Oddy (2004) were 0.17 and 0.48, respectively. Schenkel et al. (2004) reported positive phenotypic and genetic correlations between RFI and SFT (0.17 and 0.16, respectively). They also found negative genetic correlations of EMA with FCR and with RFI (−0.28 and −0.17, respectively). A high negative genetic correlation between RFI and EMA (−0.64) was obtained by Nkrumah et al. (2007). Hoque et al. (2006b) found a negative genetic correlation (−0.81) between FCR of bulls and SFT of their progeny, which supports the present result.

The negative genetic correlations between energetic efficiency traits and MSR are favorable, because consumers in Japan prefer marbled beef to lean beef. A favorable genetic correlation coefficient was obtained between MSR and most of the energetic efficiency traits

in present study. However, in the study by Robinson and Oddy (2004), a positive, but smaller, genetic correlation (0.22 ± 0.17) coefficient for RFI and chemically extracted intramuscular fat was reported. The corresponding correlation between RFI and MSR was 0.28 ± 0.38 reported by Nkrumah et al. (2007). Herd and Bishop (2000) estimated moderate and negative genetic correlations between RFI and carcass lean percentage (-0.43 ± 0.23). The reason for the discrepancy between the results from present and published studies is not apparent, but it is worth noting that different breeds were used in the studies, the methods for estimation of RFI and measuring the intramuscular fat were different among the studies, and also that the SE of the reported estimates in the published studies were large. A study by Basarab et al. (2003) indicated that RFI showed weak phenotypic correlations with carcass fat (0.14), carcass lean (-0.21), and MSR (0.22). They also noted that carcass fatness was uncorrelated with RFI, when RFI was adjusted for backfat thickness. Schenkel et al. (2004) noted that there was no correlation between RFI and intramuscular fat. However, Jensen et al. (1992) reported a negative genetic correlation between RFI and carcass fat percentage (-0.24). Recently, Hoque et al. (2006b) reported that RFI of bulls was negatively genetically correlated with CWT and MSR (-0.60 and -0.62, respectively) of their progeny in Japanese Black cattle, which support the present results. The estimated genetic correlation between FCR and carcass lean percentage was -0.32, as reported in a review by Koots et al. (1994a). The large negative genetic correlation between TDNCR of bulls and MSR of their progeny in the present study is in agreement with the estimate of -0.85 reported by Oikawa et al. (2000) in the same breed. The negative associations between measures of energetic efficiency of bulls and CWT, MSR, and MQG of their progeny indicate that downward selection for energetic efficiency traits would lead to heavier carcasses with greater marbling and meat quality to fulfill the demand of the Japanese beef market.

The favorable correlated response in CWT to selection against RFI in our study was in agreement with the reports by Richardson et al. (1998) and Hoque et al. (2006b). Richardson et al. (1998) noted that the steer progeny of decreased RFI (greater feed efficiency) parents grew faster than steers of increased RFI (less feed efficiency) parents. Hoque et al. (2006b) concluded that selection for less RFI would result in progeny with heavier carcasses at slaughter. Thus, decreased RFI progeny would be heavier at a constant age. Estimated correlated responses indicated that downward selection of FCR, TDNCR, or RFI (reducing excessive intake of feed) of bulls would also lead to increases in MSR, REA, and RT of their progeny. Results from divergent selection of postweaning RFI found no change in subcutaneous fat deposition in progeny in a weanling test (Herd et al., 1997). However, a small reduction in subcutaneous fat deposition was observed in response to a single generation of selection against RFI reported by

Richardson et al. (1998). Hoque et al. (2006b) showed that the correlated responses in MSR of progeny tested under field conditions to selection against RFI (kg) or FCR of their sire population to be 0.48 and 0.33 scores, respectively, for the same breed at Okayama prefecture in Japan, which were slightly less than the present results. Relative to selection against FCR, the slightly less correlated response in SFT to selection against RFI is in agreement with the finding by Hoque et al. (2006b). They predicted correlated increase in SFT to selection against RFI (kg) or FCR to be 0.32 and 0.56 mm, respectively. No correlated response in FCS and weak correlated responses in YEM, MCS, and MQG of progeny were found from selection against energetic efficiency traits of bulls, results that are partially in agreement with the findings of Richardson et al. (1998). Richardson et al. concluded that there were no differences ($P > 0.05$) in visual scores for meat and fat color between carcasses from the low RFI and high RFI steers.

Most of the studied energetic efficiency traits (FCR, TDNCR, RGR, and KR) are expressed as ratios of feed intake to product (or the reciprocal), except RFI, which is a linear index. The use of ratio traits has some problems. Gunsett (1984) compared the efficiency of direct selection for a 2-component trait with a linear index trait derived from the same 2 components and concluded that the use of a linear index increases selection responses as compared with direct selection on the ratio trait. Also, selection against feed intake reduces appetite, which may be undesirable (Ollivier et al., 1990). Arthur et al. (2001b) explained that indices of feed efficiency that incorporate linear combinations of measures of growth and metabolic body size seek to capture the variations among animals in energy utilization for growth and maintenance. The choice of which of the energetic efficiency traits to use will depend on the breeding objective and the genetic correlations of the trait with the other traits of interest in the selection criteria, and ease of computation of the trait. For example, computing expected feed intake from linear regression analysis may not be possible to calculate RFI when the number of animals in the test is too small. In such situations, expected feed intake can be computed from standard formulae or derived from known variance components. Because calculation of energy partitioning traits requires prediction of expected feed intake, errors in this prediction have major effects on the reliability of the trait calculated (Arthur et al., 2001a). Accurate estimation of prediction is, therefore, very important.

Results of this study indicate that heritabilities for most measures of feed intake and energetic efficiency (except RGR: low heritability) were high to moderate, highlighting the fact that genetic improvement can potentially be made in these traits. The RFI is quite heritable, and the correlated responses in CWT and beef marbling of progeny were greater due to selection against RFI than to selection against any other energetic efficiency trait. Due to these observations and its favorable nature (linear index), RFI should be preferred

over other measures of efficiency in breeding programs for genetic improvement of energetic efficiency.

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