

## ORIGINAL ARTICLE

# Genetic relationship of feed efficiency traits of bulls with growth and carcass traits of their progeny for Japanese Black (Wagyu) cattle

Md Azharul HOQUE,<sup>1</sup> Keiji HIRAMOTO<sup>2</sup> and Takuro OIKAWA<sup>3</sup>

<sup>1</sup>Graduate School of Natural Science and Technology, Okayama University, Okayama-shi, <sup>2</sup>Okayama Prefecture Animal Industry Center, Asahi-cho, Okayama-ken and <sup>3</sup>Field Science Center, Faculty of Agriculture, Okayama University, Okayama-shi, Japan

### ABSTRACT

Genetic parameters for feed efficiency traits of 740 Wagyu bulls and growth and carcass traits of 591 of their progeny, and the genetic relationship between the traits of bulls and their progeny were estimated with the residual maximum likelihood procedure. The estimations were made for the test periods of 140 days (77 bulls), 112 days (663 bulls) and 364 days (591 steer progeny). Feed efficiency traits of bulls included feed conversion ratio (FCR), phenotypic residual feed intake ( $RFI_{\text{phe}}$ ) and genetic residual feed intake ( $RFI_{\text{gen}}$ ). Progeny traits were bodyweight at the start of the test (BWS), bodyweight at finish (BWF), average daily gain (ADG), rib eye area (REA), marbling score (MSR), dressing percentage (DRS) and subcutaneous fat thickness (SFT). The estimated heritability for MSR (0.52) was high and for BWS (0.35), BWF (0.40) and ADG (0.30) were moderate, whereas REA, DRS and SFT were low. Positive genetic correlations among BWS, BWF, ADG and SFT and negative genetic correlations between MSR and DRS and between REA and SFT were found. The genetic correlations between residual feed intake ( $RFI_{\text{phe}}$  and  $RFI_{\text{gen}}$ ) of bulls and bodyweights (BWS and BWF) of their progeny ranged from  $-0.27$  to  $-0.61$ . Residual feed intake was positively correlated with REA and DRS and negatively correlated with MSR and SFT. No responses in ADG and weakly correlated responses in REA and DRS of progeny were found to select against feed efficiency traits of bulls. The present experiment provides evidence that selection against lower RFI (higher feed efficiency) would be better than selection against lower FCR for getting better correlated responses in bodyweights.

**KEYWORDS:** correlated response, feed efficiency, genetic parameter, progeny traits, Wagyu cattle.

### INTRODUCTION

Selection programs that improve the efficiency of feed utilization are expected to be beneficial to the beef industry. However, the efficiency of feed utilization is more difficult to be quantified than that of growth; consequently, different measures of feed efficiency (e.g. feed conversion ratio (FCR), residual feed intake (RFI), etc.) have been developed over the years (Arthur *et al.* 2001b). The scope to reduce costs through genetic means seems to be present as the scientific published reports indicates that feed intake and efficiency traits are heritable (Archer *et al.* 1998; Hoque & Oikawa 2004). The opportunity to improve

whole-herd production efficiency through exploitation of genetic variation in feed efficiency traits is dependent not only on the existence of genetic variation in young cattle, but also on its genetic relationship with their progeny traits. However to date, no expected responses in growth and carcass traits of progeny to select against residual feed intake of sire population have been published for Wagyu cattle, which are needed to maximize selection efficiency.

Correspondence: Takuro Oikawa, Field Science Center, Faculty of Agriculture, Okayama University, Okayama-shi, 700-0081, Japan. (Email: toikawa@cc.okayama-u.ac.jp)  
Received 27 May 2004; accepted for publication 24 September 2004.

Residual feed intake might be an alternative measure to include in selection programs for the improvement of efficiency of feed utilization (Hoque & Oikawa 2004). Feed conversion ratio is expressed as a ratio, whereas RFI is a linear index. The use of ratio traits for genetic selection presents problems associated to the prediction of the change in the component traits in future generations (Arthur *et al.* 2001a). This is due to disproportionate fashion by which selection pressure is exerted on the component traits. Residual feed intake has gained interest from researchers as a trait that may describe animal efficiency without the problems associated with ratio traits. However, there are no research endeavors in Japan that are looking at the relationship between feed efficiency traits of bulls and growth and carcass traits of their progeny. The objectives of the present study were to estimate the genetic parameters for feed efficiency traits of bulls along with their genetic relationships with growth and carcass traits of their progeny and to estimate the effect of selection against feed efficiency traits of bulls on growth and carcass traits of their progeny in Wagyu population.

## MATERIALS AND METHODS

### Data structure

A total of 740 bulls and 591 steer progeny (produced from 62 sires among 740 bulls) of Wagyu cattle were tested at the Okayama Prefecture Animal Industry Center, Japan during the period from 1971 to 2002. Pedigrees of the recorded bulls were traced back to three generations and, including the tested animals, totaled 4897. The data structure is presented in Table 1.

### Performance test for bulls

The bull calves were collected from designated farms within the age limits of 6–7 months and bodyweight 200–300 kg. Each year, 20–30 bull calves were selected for performance tests from approximately 200 bulls. Seventy-seven bulls were tested for 140 days and the remaining 663 bulls for 112 days. The cohort

was defined as a group of animals of the same age tested under a uniform environment for the same period. After 3 weeks of being introduced to the feed, the animals were provided ad libitum access to roughage; however, feeding of concentrate was restricted to 1 h twice a day. 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. Feeding and management to animals throughout the test were performed as described by Hoque and Oikawa (2004). The weekly bodyweight of the individual bull during the test period was recorded and daily feed intake (FI) was measured by the difference between supplied and left-over feed. The average daily gain (ADG) for each animal was calculated from the difference of the start and the end of test weights divided by the number of days. The mean weight at mid-test (MBW) for each animal was computed as the average of the start and the end of test weights. Metabolic bodyweight at mid-test (MWT) was calculated as MBW, raised to the power of 0.75 ( $MBW^{0.75}$ ). The FI was then combined with ADG and MWT to compute different measures of feed efficiency: FCR and RFI. The FCR was calculated as FI divided by ADG. The RFI was estimated as phenotypic RFI ( $RFI_{phe}$ ) and genetic RFI ( $RFI_{gen}$ ) by the residual of multiple regression ( $RFI_{phe}$ ) and genetic regression ( $RFI_{gen}$ ) from the multivariate analysis for FI, MWT and ADG according to Hoque and Oikawa (2004).

### Progeny test for steers

Each year, three to four animals were selected for progeny test from 20 to 30 tested bulls by their own performance. The selection was based on the growth and feed conversion of the bulls. Steer calves (eight to 10 animals) sired by the same bulls at cooperative farms were transferred to the test station at 6–7 months of age, and housed together in a feedlot (45–50 m<sup>2</sup>) with an adjacent paddock (36–40 m<sup>2</sup>) for exercise. Thus a cohort in progeny test was a group of half-sibs in the same feedlot. The testing period was 364 days and the animals were given ad libitum intake

**Table 1** Description of the data structure

Data sets	No. traits	No. animals	MBW $\pm$ SD	AGS $\pm$ SD	No. sires	No. dams	No. cohort
Feed efficiency traits of bulls	3	740	338.33 $\pm$ 35.75	230.29 $\pm$ 17.35	61	555	171 (1971–2002)
Growth and carcass of progeny	7	591	405.88 $\pm$ 44.11	259.00 $\pm$ 18.41	62	572	62 (1981–1998)

AGS, age of the animals in days at the start of the test; MBW, mean bodyweight in kg at the mid-test.

to a concentrate mixed with 10% chopped rice straw by weight. Traits studied were bodyweight at the start of the test (BWS), bodyweight at finish (BWF), ADG, rib eye area (REA), marbling score (MSR), dressing percentage (DRS) and subcutaneous fat thickness (SFT). The REA, MSR and SFT were measured at the sixth to seventh rib section on the left side of the carcass. The REA was measured by grid approximation as described by Oikawa *et al.* (2000) and the MSR was measured according to the Beef Marbling Standard (JMGA 1988) of 12 categories, with number 5.0 being the highest (from 0.0–3.0 with intervals of 0.33, and 4.0, 5.0). The carcass weight was obtained by weighing the weight of slaughtered steers after the removal of the lungs, heart, liver, intestines and ancillary organs or mesenteries, bladder, reproductive organs and blood. The DRS was calculated as carcass weight divided by live weight of steers at slaughter multiplied by 100.

### Statistical analysis

The (co)variance components and heritabilities were estimated by the residual maximum likelihood (REML) method with the variance component estimation (Neumaier & Groeneveld 1998) computer program. We planned to consider ADG as common trait for both the test to increase the validity of the data sets, but the preliminary results showed that the genetic variances were different between ADG of bulls and their progeny and also their genetic correlation was moderate. According to the preliminary result, heritabilities for ADG in bulls and their progeny were  $0.18 \pm 0.09$  and  $0.45 \pm 0.22$ , respectively, with a genetic correlation of  $0.48 \pm 0.39$ . The corresponding values were  $0.40 \pm 0.11$  and  $0.35 \pm 0.13$  with  $0.80 \pm 0.28$  for bodyweight at the start of the test and  $0.49 \pm 0.11$  and  $0.47 \pm 0.18$ , with  $0.56 \pm 0.33$  for bodyweight at the finish of the test. Estimates of additive genetic variances (268.42 and 235.63, respectively) as well as residual variances (402.62 and 437.61, respectively) were also close between bodyweight at the start of the test of bulls and their progeny; the bodyweight at the start of the test of both tests was included as a common trait to increase connectedness of the data set and to reduce the effect of selection. The statistical model used in the analysis was as follows:

$$Y_{ij} = F_{ij} + a_{ij} + e_{ij}$$

with  $F_{ij} = CH_i + b_1(AGF_{ij} - \overline{AGF})$  for  $RFI_{phe}$ ,  $RFI_{gen}$ ,  
 FCR, BWF, ADG, MSR, REA, DRS, SFT, or  
 $F_{ij} = CH_i + b_1(AGS_{ij} - \overline{AGS})$  for BWS,

where  $Y_{ij}$  = the phenotypic value for an animal;  $a_{ij}$  = the additive genetic effect for an animal;  $e_{ij}$  = the random residual;  $CH_i$  = the fixed effect of  $i$ th cohort of the test;  $b_1$  = the linear regression coefficient of the observation on age;  $AGX_{ij}$  = the age of  $j$ th animals in  $i$ th cohort at either the start (S as X) or the finish (F as X);  $\overline{AGX}$  = the mean age of the animals. The (co)variances for growth and carcass traits of progeny were estimated by two-trait analysis, while those for between the traits (feed efficiency) of bulls and traits (growth and carcass) of progeny were estimated by three-trait (pooled-BWS and others) analysis except for correlations including BWS itself. The covariance structure for additive genetic effects of animals and residual effects is described below:

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

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 consisting of the genetic relationships between animals.  $\sigma_{a1}^2$  and  $\sigma_{a2}^2$  are the additive genetic variances for trait 1 and trait 2, respectively, and  $\sigma_{a12}$  is the additive genetic covariance for them.  $\sigma_{e1}^2$  and  $\sigma_{e2}^2$  are the residual variances for trait 1 and trait 2, respectively, and  $\sigma_{e12}$  is the residual covariance for them. This model was assumed while the two traits were recorded on the same animal. When the two traits were recorded on different animals the  $\sigma_{e12}$  was assumed to be zero. This two-trait model for variance structure can be extended for the three-trait model straightforwardly, including  $a_3$  and  $e_3$  for the third trait.

The estimated genetic variances and heritabilities were averaged for the results, while their standard errors (SE) were the median of the estimates. The correlated responses were estimated according to Cameron (1997).

## RESULTS AND DISCUSSION

The means, heritabilities and correlations (genetic and phenotypic) among different measures of feed efficiency are shown in Table 2. Estimated genetic and phenotypic correlations between RFI ( $RFI_{phe}$  and  $RFI_{gen}$ ) and FCR were high which are in agreement with the findings of Herd and Bishop (2000) and

**Table 2** Means, heritabilities ( $h^2$ ) and genetic (above the diagonal) and phenotypic (below the diagonal) correlations among feed efficiency traits of bulls

Traits	Means	$h^2$	Correlations		
			RFI <sub>phe</sub>	RFI <sub>gen</sub>	FCR
RFI <sub>phe</sub> (kg/d)	-0.05 <sup>†</sup>	0.24 ± 0.11 <sup>†</sup>	—	0.97 ± 0.02 <sup>†</sup>	0.64 ± 0.10
RFI <sub>gen</sub> (kg/d)	-2.21 <sup>†</sup>	0.25 ± 0.10 <sup>†</sup>	0.98 <sup>†</sup>	—	0.62 ± 0.11
FCR	7.60	0.15 ± 0.04	0.76	0.76	—

<sup>†</sup>Estimated by Hoque and Oikawa (2004) for the same population. FCR, feed conversion ratio; RFI<sub>gen</sub>, genetic residual feed intake; RFI<sub>phe</sub>, phenotypic residual feed intake; —, not applicable.

**Table 3** Means, additive genetic variances ( $V_A$ ), phenotypic variances ( $V_p$ ) and heritabilities ( $h^2$ ) for growth and carcass traits of progeny

Traits	BWS (kg)	BWF (kg)	ADG (kg/d)	MSR	REA (cm <sup>2</sup> )	DRS (%)	SFT (mm)
Means	253.81	558.01	0.85	2.44	46.88	62.73	16.33
$V_A$	235.63	971.38	0.003	0.41	0.58	0.28	2.82
$V_p$	673.24	2428.45	0.01	0.79	19.33	2.00	17.63
$h^2$	0.35 ± 0.15	0.40 ± 0.17	0.30 ± 0.18	0.52 ± 0.27	0.03 ± 0.04	0.14 ± 0.10	0.16 ± 0.21

ADG, average daily gain; BWF, bodyweight at finish; BWS, bodyweight at the start of the test; DRS, dressing percentage; MSR, marbling score; REA, rib eye area; SFT, subcutaneous fat thickness.

Arthur *et al.* (2001a). Herd and Bishop (2000) estimated genetic and phenotypic correlations between RFI<sub>phe</sub> and FCR to be 0.70 and 0.61, respectively, for the Hereford breed. The corresponding values were 0.66 and 0.53, respectively, for the Angus breed estimated by Arthur *et al.* (2001a). However, Fan *et al.* (1995) reported a genetic correlation between RFI (calculated from feeding standards formulae as described by NRC 1984) and FCR of 0.90 and 1.00 for Angus and Hereford breeds, respectively, and phenotypic correlations of 0.91 and 0.97, 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.

Estimated variance components and heritabilities, and mean values for growth and carcass traits of progeny are presented in Table 3. The mean values for all the traits were consistent with other reports (Fukuhara *et al.* 1989; Oikawa *et al.* 2000; Uchida *et al.* 2001) in the same breed. The genetic and phenotypic variations in bodyweights were large in the current study which can be used for the improvement of these traits.

Estimated heritability for MSR was high and for BWS, BWF and ADG were moderate, whereas REA, DRS and SFT were low. Considerable numbers of heritability estimates have been published for growth and carcass 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 bodyweight, 0.22 for growth rate, 0.38 for MSR, 0.42 for REA, 0.39 for DRS, and 0.44 for SFT. The moderate heritabilities for bodyweights and low heritability for DRS in the present study were close to those reported in the same breed by Oikawa *et al.* (2000), who estimated heritabilities for BWS, BWF and DRS to be 0.31, 0.36 and 0.15, respectively. Estimated heritability for ADG was higher than the estimates of 0.18 from Japanese Black steers by Sasaki (1991) and 0.22 from Japanese Brown steers by Hirooka *et al.* (1996), but considerably lower than the estimate of 0.56 from Japanese Black steers by Uchida *et al.* (2001). The differences in methods of estimation may explain the discrepancy, because Uchida *et al.* (2001) used an animal model within a test program with Gibbs sampling. The low heritability for REA in the present study was close to the estimate of 0.02 by Oikawa *et al.* (2000), but lower than those reported by Oikawa *et al.* (1994) and Uchida *et al.* (2001) in the same breed (0.29 and 0.27, respectively). A possible reason for the low heritability is considered to be irregular pre-, post-slaughter treatment and sectioning or measuring of REA in the testing program. Estimated heritability for MSR corresponds with the estimates of 0.46 by Mukai (1994) and 0.49 by Oikawa *et al.* (2000) for the same breed and 0.40 by Hirooka

**Table 4** Genetic and phenotypic correlations<sup>†</sup> among growth and carcass traits of progeny

Traits	BWS	BWF	ADG	MSR	REA	DRS	SFT
BWS	—	0.86 ± 0.16	0.71 ± 0.15	0.36 ± 0.34	-0.98 ± 0.03	-0.38 ± 0.42	0.92 ± 0.25
BWF	0.73	—	0.98 ± 0.05	0.25 ± 0.11	-0.31 ± 0.07	-0.26 ± 0.46	0.56 ± 0.28
ADG	0.19	0.75	—	0.23 ± 0.15	-0.28 ± 0.08	-0.15 ± 0.69	0.54 ± 0.12
MSR	-0.08	0.09	-0.01	—	0.72 ± 0.32	-0.99 ± 0.01	-0.09 ± 0.79
REA	0.22	0.35	0.32	0.15	—	0.98 ± 0.12	-0.99 ± 0.19
DRS	0.08	-0.01	-0.11	-0.14	-0.05	—	0.03 ± 0.08
SFT	0.30	0.33	0.25	-0.14	0.06	-0.05	—

<sup>†</sup>Genetic (± SE) and phenotypic correlations are above and below the diagonal, respectively. ADG, average daily gain; BWF, bodyweight at finish; BWS, bodyweight at the start of the test; DRS, dressing percentage; MSR, marbling score; REA, rib eye area; SFT, subcutaneous fat thickness; —, not applicable.

**Table 5** Genetic correlations (± SE) between feed efficiency traits of bulls and growth and carcass traits of progeny

Traits	BWS	BWF	ADG	MSR	REA	DRS	SFT
RFI <sub>phe</sub>	-0.27 ± 0.42	-0.43 ± 0.26	-0.07 ± 0.14	-0.31 ± 0.47	0.99 ± 0.14	0.94 ± 0.16	-0.66 ± 0.47
RFI <sub>gen</sub>	-0.33 ± 0.43	-0.61 ± 0.23	0.03 ± 0.21	-0.41 ± 0.23	0.83 ± 0.31	0.84 ± 0.28	-0.74 ± 0.41
FCR	-0.14 ± 0.45	-0.31 ± 0.23	-0.17 ± 0.33	-0.95 ± 0.30	0.99 ± 0.07	0.98 ± 0.01	-0.81 ± 0.46

ADG, average daily gain; BWF, bodyweight at finish; BWS, bodyweight at the start of the test; DRS, dressing percentage; FCR, feed conversion ratio; MSR, marbling score; REA, rib eye area; RFI<sub>gen</sub>, genetic residual feed intake; RFI<sub>phe</sub>, phenotypic residual feed intake; SFT, subcutaneous fat thickness.

*et al.* (1996) for Japanese Brown steers. Estimated heritability for SFT was also similar to the estimate of 0.13 reported by Fukuhara *et al.* (1989) for the same breed.

The genetic and phenotypic correlations among growth and carcass traits of progeny are presented in Table 4. Moderate to high genetic correlations among BWS, BWF, ADG and SFT are in agreement with the correlations reported by Uchida *et al.* (2001) who also estimated moderate to high genetic correlations (ranging from 0.50 to 0.97) among these traits for the same breed in the Miyagi prefecture. The genetic correlation between MSR and ADG was positive and low in the present study, being consistent with the reviewed averages (0.21) by Koots *et al.* (1994b), but higher than that for Japanese Brown steers (0.09) reported by Hirooka *et al.* (1996) and lower than that for Hereford cattle (0.46) reported by Lamb *et al.* (1990). Estimated genetic correlations of REA with MSR and DRS were positive and high and of REA with BWS and SFT were negative and high, while the phenotypic correlations between them were low. The reasons for the estimates of high genetic correlations of REA with BWS, DRS and SFT and between MSR and DRS (absolute value >0.95) need to be further investigated with a large number of dataset. However, almost the same correlations were estimated by Oikawa *et al.* (2000) who estimated the genetic correlations of REA with MSR, DRS, BWS and SFT to be 0.81, 0.92, -0.83 and -1.00, respectively. They also made a hypothesis that the

high genetic correlation between MSR and DRS might be caused by a positive relationship of high roughage utilization with high marbling.

The low and negative genetic correlation between MSR and SFT is in agreement with the correlations reported by many authors. For example, Yang *et al.* (1985) and Fukuhara *et al.* (1989) reported genetic correlations of -0.10 and -0.04, respectively, in Japanese Black steers. Hirooka *et al.* (1996) and Wilson *et al.* (1993) also reported negative genetic correlations for Japanese Brown cattle (-0.13) and Angus field data (-0.12), respectively. However, Koots *et al.* (1994b) reported a weighted mean genetic correlation of 0.36 between MSR and SFT in their review paper. The negative genetic correlation between MSR and SFT in the present study is considered a favorable indication for further improvement of MSR, which can be achieved without increasing subcutaneous fat. The phenotypic correlations of BWF with BWS and ADG were high, while the phenotypic correlations among all the other traits were low to moderate. These genetic and phenotypic correlations among progeny carcass traits indicate that selection for improvement of live weight was accompanied by faster daily gain and subcutaneous fat.

The genetic correlations between feed efficiency traits of bulls and growth and carcass traits of progeny are presented in Table 5. The genetic correlations between RFI (RFI<sub>phe</sub> and RFI<sub>gen</sub>) of bulls and



bodyweights (BWS and BWF) of their progeny ranged from  $-0.27$  to  $-0.61$  indicating that selection to lower RFI (higher feed efficiency) of bulls would increase bodyweights of their progeny. Estimated genetic correlation between FCR and BWF was negative and moderate, whereas between FCR and BWS was negative and low. Feed conversion ratio and  $RFI_{phe}$  were reported to be moderately and favorably related to bodyweight at 200 days ( $-0.21$  and  $-0.45$ , respectively) and 400 days ( $-0.09$  and  $-0.26$ , respectively) by Arthur *et al.* (2001a) in the Angus breed. Fan *et al.* (1995) showed that RFI negatively related with yearling bodyweight in Angus ( $-0.64$ ) and Hereford ( $-0.05$ ) breeds. However,  $RFI_{phe}$  and  $RFI_{gen}$  of bulls were genetically independent of ADG of progeny in the current study. Almost the same correlation ( $-0.06$ ) between  $RFI_{phe}$  and ADG was estimated by Arthur *et al.* (2001a). A favorable negative genetic correlation between FCR and ADG in the present study is in agreement with the reports by Bishop (1992), Nieuwhof *et al.* (1992) and Fan *et al.* (1995) for British breeds.

Estimated genetic correlations of RFI with REA and DRS were positive and high, while RFI with SFT were negative and high. No information is available on the genetic relationships that exist for RFI of bulls with growth and carcass traits of their progeny for Wagyu cattle. However, Arthur *et al.* (2001a) reported a genetic correlation of 0.17 between  $RFI_{phe}$  and ultrasound rib fat thickness in Angus bulls and heifers. Their report is further substantiated by the genetic correlation of  $-0.43$  between  $RFI_{phe}$  and carcass lean content in Hereford bulls reported by Herd and Bishop (2000). The genetic correlations of FCR with MSR and SFT were negative and high, whereas FCR with REA and DRS were positive and high in the present study. Oikawa *et al.* (2000) estimated a negative genetic correlations of total digestible nutrient conversion of bulls with MSR ( $-0.85$ ) and SFT ( $-0.68$ ) of their progeny carcass in the same breed, which supports the present

results. Because of the negative genetic correlations of feed efficiency traits of bulls with MSR and SFT of progeny, the selection against feed efficiency traits of bulls may have contributed to the increase in marbling and subcutaneous fat of progeny carcass.

The correlated responses in growth and carcass traits of progeny to selection against feed efficiency traits of bulls after one generation of selection are shown in Table 6. Selection for RFI ( $RFI_{phe}$  and  $RFI_{gen}$ ) have resulted in favorably positive correlated responses in bodyweights (BWS and BWF), particularly in BWF indicating that selection to lower RFI (higher feed efficiency) would result in heavier progeny at harvest (614 days of age). This result is in agreement with the reports by Richardson *et al.* (1998) who concluded that the steer progeny of low RFI (higher feed efficiency) parents grew faster than steers of high RFI (lower feed efficiency) parents.

Estimated correlated responses indicating that downward selection of RFI (lowering excessive intake of feed) of bulls would lead to an increase in MSR and SFT of their progeny carcass. No responses in ADG and weakly correlated responses in REA and DRS of progeny were found for selection against feed efficiency traits of bulls. We are not aware of any published studies for correlated responses in progeny traits to select against feed efficiency traits of bulls in the Wagyu population. However, Archer *et al.* (1998) showed that the correlated responses in ADG to select against  $RFI_{phe}$  or  $RFI_{gen}$  to be  $-0.001$  and  $0.00$ , respectively, for Angus cattle, supporting our results. The correlated responses in growth and carcass traits of progeny were similar to selection against  $RFI_{phe}$  or  $RFI_{gen}$  in the present study. These results are supported by Hoque and Oikawa (2004) who showed that  $RFI_{phe}$  and  $RFI_{gen}$  are regarded as the same traits and selection for  $RFI_{gen}$  would give results similar to selection for  $RFI_{phe}$ . The results of the current study indicate that the selection objectives in Wagyu breeding should include feed efficiency traits to

**Table 6** Correlated responses in growth and carcass traits of progeny to selection against feed efficiency traits of bulls

Traits	BWS	BWF	ADG	MSR	REA	DRS	SFT
$RFI_{phe}$	2.030	6.565	0.0018	0.099	$-0.369$	$-0.243$	0.543
$RFI_{gen}$	2.533	9.506	$-0.0008$	0.131	$-0.316$	$-0.222$	0.621
FCR	0.832	3.742	0.0036	0.236	$-0.292$	$-0.201$	0.527

Correlated responses after one generation of selection with selection intensity equal to  $-1.00$ . ADG, average daily gain; BWS, bodyweight at the start of the test; BWE, bodyweight at finish; DRS, dressing percentage; FCR, feed conversion ratio; MSR, marbling score; REA, rib eye area;  $RFI_{gen}$ , genetic residual feed intake;  $RFI_{phe}$ , phenotypic residual feed intake; SFT, subcutaneous fat thickness.

reduce the feed cost and simultaneous improvement in heavier bodyweight with little compromise in carcass traits of progeny.

## Conclusion

It can be concluded that the genetic correlations among bodyweights, ADG and SFT were moderate to high. Large genetic and phenotypic variations with moderate heritabilities for bodyweights of progeny indicate that further improvement is possible for these traits. Because of negative genetic correlations of feed efficiency traits in bulls with MSR and SFT in their progeny, the selection against feed efficiency traits in bulls may have contributed to the increase in marbling and subcutaneous fat in their progeny carcass. The correlated responses in bodyweights of progeny were higher to select against RFI than that one to select against FCR and the heritabilities for RFI of bulls were higher than that of FCR – indicating that RFI might be better than FCR to include in the selection program for the improvement of heavier bodyweight and better utilization of feed.

## ACKNOWLEDGMENTS

The authors thank Mr Makoto Baba and Mr Osamu Inoue, Okayama Prefecture Animal Industry Center, Japan for providing the data of this experiment.

## REFERENCES

- Archer JA, Arthur PF, Herd RM, Richardson EC. 1998. Genetic variation in feed efficiency and its component traits. *Proceedings of the 6th World Congress on Genetics Applied to Livestock Production*. 11–16 January, Vol. 25, pp. 81–84, Armidale, Australia.
- Arthur PF, Archer JA, Johnston DJ, Herd RM, Richardson EC, Parnell PF. 2001a. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other post weaning traits in Angus cattle. *Journal of Animal Science* **79**, 2805–2811.
- Arthur PF, Renand G, Krauss D. 2001b. Genetic and phenotypic relationships among different measures of growth and feed efficiency in young Charolais bulls. *Livestock Production Science* **68**, 131–139.
- Bishop SC. 1992. Phenotypic and genetic variation in body weight, food intake and energy utilization in Hereford cattle. I. Performance test results. *Livestock Production Science* **30**, 1–8.
- Cameron ND. 1997. *Selection Indices and Prediction of Genetic Merit in Animal Breeding*, pp. 62–64. Cab International, Wallingford, Oxon.
- Fan LQ, Bailey DRC, Shannon NH. 1995. Genetic parameter estimation of postweaning gain, feed intake, and efficiency for Hereford and Angus bulls fed two different diets. *Journal of Animal Science* **73**, 365–372.
- Fukuhara R, Moriya K, Harada H. 1989. Estimation of genetic parameters and sire evaluation for carcass characteristics with special reference to yield grade of the new beef carcass grading standards. *Japanese Journal of Zootechnical Science* **60**, 1128–1133.
- Herd RM, Bishop SC. 2000. Genetic variation in residual feed intake and its association with other production traits in British Hereford cattle. *Livestock Production Science* **63**, 111–119.
- Hirooka H, Groen AF, Matsumoto M. 1996. Genetic parameters for growth and carcass traits in Japanese Brown cattle estimated from field records. *Journal of Animal Science* **74**, 2112–2116.
- Hoque MA, Oikawa T. 2004. Comparison and relation among different estimates of residual feed intake for Japanese Black (Wagyu) bulls. *Animal Science Journal* **75**, 201–205.
- Japan Meat Grading Association (JMGA). 1988. *New Beef Carcass Grading Standards*. Japan Meat Grading Association, Tokyo.
- Koots KR, Gibson JP, Smith C, Wilton JW. 1994a. Analysis of published genetic parameters for beef production traits. 1. Heritability. *Animal Breeding Abstracts* **62**, 309–338.
- Koots KR, Gibson JP, Wilton JW. 1994b. Analysis of published genetic parameters for beef production traits. 1. Phenotypic and genetic correlations. *Animal Breeding Abstracts* **62**, 826–853.
- Lamb MA, Robison OW, Tess MW. 1990. Genetic parameters for carcass traits in Hereford bulls. *Journal of Animal Science* **68**, 64–69.
- Mukai F. 1994. Genetic evaluation and selection methods for carcass traits in Japanese Black cattle. *Animal Science and Technology* **65**, 890–894.
- National Research Council (NRC). 1984. *Nutrient Requirement of Beef Cattle*, 6th edn. National Academy Press, Washington, DC.
- Neumaier A, Groeneveld EG. 1998. Restricted maximum likelihood estimation of covariances in sparse linear models. *Genetics Selection Evolution* **30**, 3–26.
- Nieuwhof GJ, Arendonk JAMV, Vos H, Korver S. 1992. Genetic relationships between feed intake, efficiency and production traits in growing bulls, growing heifers, and lactating heifers. *Livestock Production Science* **32**, 189–194.
- Oikawa T, Sanehira T, Sato K, Mizoguchi Y, Yamamoto H, Baba M. 2000. Genetic parameters for growth and carcass traits of Japanese Black (Wagyu) cattle. *Animal Science* **71**, 59–64.
- Oikawa T, Sato K, Kawamoto Y, Mizoguchi Y, Nakahara H, Hiramoto K. 1994. The effect of pedigree information on variance components estimation with field carcass records of beef cattle. *Animal Science and Technology* **65**, 75–77.
- Richardson EC, Herd RM, Archer JA, Woodgate RT, Arthur PF. 1998. Steers bred for improved net feed efficiency eat less for the same feedlot performance. *Animal Production in Australia* **22**, 213–216.
- Sasaki Y. 1991. Sire evaluation systems for beef cattle. *Kyoto School on Breeding and Improvement for Beef Cattle*, p. 117. Kyoto University, Kyoto.

- Uchida H, Oikawa T, Suzuki K, Yamagishi T. 2001. Estimation of genetic parameters using an animal model for traits in performance and progeny testing for meat production of Japanese Black cattle herd in Miyagi prefecture. *Animal Science Journal* **72**, 89–96.
- Wilson DE, Willium RL, Northcut SL, Rouse GH. 1993. Genetic parameters for carcass traits estimated from Angus field records. *Journal of Animal Science* **71**, 2365–2370.
- Yang M, Mukai F, Sasaki Y. 1985. Estimation of heritabilities for growth and carcass traits and their genetic and phenotypic correlations in Japanese Black cattle. *Japanese Journal of Zootechnical Science* **56**, 193–198.