Evaluation of feed efficiency traits for genetic improvement in Japanese Black cattle

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ABSTRACT: We evaluated the genetic relationships (1) among feed efficiency traits with different fattening periods, (2) between feed efficiency traits and growth traits, and (3) between feed efficiency traits and carcass traits, to determine the influence of genetic factors on feed efficiency traits. In total, 4,578 Japanese Black cattle from a progeny testing program were used. Residual feed intake (RFI), residual BW gain (RG), and residual intake and BW gain (RIG) were defined as feed efficiency traits, and were measured for the first half (approximately 9 to 15 months of age), latter half (approximately 15 to 21 months of age), and total period of fattening (approximately 9 to 21 months of age). A single-trait animal model for estimating heritability and a two-trait animal model for estimating genetic and phenotypic correlations were used. The heritability estimates for RFI, RG, and RIG were different in each fattening period, ranging from 0.36 to 0.46, 0.19 to 0.28, and 0.28 to 0.34, respectively, and the heritability estimates for the

total fattening period were greater than those for the first and latter halves separately. RIG showed the greatest preferred genetic correlation, with a greater feed conversion ratio than the other feed efficiency traits (ranging from –0.84 to –0.96). RG in the first and latter halves of the fattening period had different genetic correlations with the growth starting point (0.82 and –0.06, respectively) and maturity rate (0.49 and –0.51, respectively) of the Gompertz growth curve parameters, and is strongly dependent on the different fattening periods. Feed efficiency traits in different fattening periods had low genetic correlations with the carcass traits (from –0.05 to 0.19 for RFI; from 0.02 to 0.31 for RG; and from –0.11 to 0.20 for RIG). This study indicated the possibility for genetic improvement through the selection of high-RIG animals to decrease feed intake and increase BW gain without any unfavorable correlated responses affecting mature (asymptotic) weight and carcass grade.

Key words: feed efficiency traits, genetic parameters, growth curve, Japanese Black cattle, residual intake and BW gain

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INTRODUCTION

Global interest in feed efficiency has increased recently, and residual feed intake (RFI), also

known as net feed efficiency, has been a popular measurement in feed efficiency traits (Koch et al., 1963; Exton et al., 2000). However, Berry and Crowley (2012) indicated that slow-growing animals may show high RFI rankings, and proposed an alternative feed efficiency index: residual intake and BW gain (RIG), which combines the desired

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characteristics of both RFI and residual BW gain (RG; Koch et al., 1963).

Feed efficiency traits are controlled by the age of cattle (Arthur et al., 2001; Berry and Pryce, 2014), and thus could be affected by different periods of fattening. However, most studies have focused on the estimation of feed efficiency traits in growing or early fattening cattle (Berry and Crowley, 2013). In addition, genetic understanding of the biological characteristics affecting the growth curve of feedlot cattle may be useful for determining the relationship of feed efficiency with the growth phase and the asymptotic (mature) weight. However, few studies have reported the genetic effects of different fattening periods and growth curves on feed efficiency traits. The profitability of beef production is dependent on both inputs and outputs, which are mainly derived from feed costs, and carcass yield and meat quality grades, respectively. Consequently, the genetic relationship between feed efficiency and other economically important traits must be evaluated.

This study aimed to understand the influence of genetic factors on feed efficiency traits from growth phase, growth traits and economic traits of Japanese Black cattle breeding. Hence, we evaluated the genetic relationships between (1) feed efficiency traits and different fattening periods, (2) feed efficiency traits and growth traits, and (3) feed efficiency traits and carcass traits.

MATERIALS AND METHODS

All animals were cared for and slaughtered according to Japanese rules and regulations for animal care.

Animals

In total, 4,578 Japanese Black steers were performance tested at the Livestock Improvement Association of Japan Inc. (LIAJ) in Hokkaido and Hiroshima prefectures, from 1998 to 2008. Among these, 863 steers were performance tested from 2001 to 2002 to evaluate the genetic relationship between feed efficiency and fatness traits (Inoue et al., 2011). All steers were fattened for 52 wk (364 d) beginning at an average of 9.1 (ranging from 7.9 to 9.5) months of age. Body weight was routinely measured every 8 wk, from the first week of fattening to the 48th wk, and also in the final 52nd wk. An automatic radio frequency identification transponder (Nedap Cattlecode, Groenlo, the Netherlands) was attached to each steer to

obtain access to the individuals' concentrated diets (73.3% total digestible nutrients, 10.3% digestible crude protein) provided by an automatic feeder (Nedap Cattlecode). Concentrated feed intake by the steers was recorded automatically each day during the test period.

Feed Efficiency Traits

RFI, RG, and RIG were defined as feed efficiency traits in this study. Estimation of RFI and RG was based on the method described by Koch et al. (1963) as follows:

$$\text{RFI} = \text{FI} - (\beta_1 \times \text{MBW} + \beta_2 \times \text{DG})$$

$$\text{RG} = \text{DG} - (\beta_3 \times \text{MBW} + \beta_4 \times \text{FI})$$

where FI is average daily concentrated feed intake, MBW is the metabolic body weight ($\text{BW}^{0.75}$), β_1 and β_2 are partial regression coefficients on MBW and daily gain (DG) respectively, and β_3 and β_4 are partial regression coefficients on MBW and FI, respectively. A positive RG value and a negative RFI value are favorable. RIG was calculated based on the method of Berry and Crowley (2012) as below:

$$\text{RIG} = (-1) \times \frac{\text{RFI}}{\sigma_{\text{RFI}}} + \frac{\text{RG}}{\sigma_{\text{RG}}}$$

where σ_{RFI} and σ_{RG} are the SDs of RFI and RG of tested steers, respectively. A positive RIG value and a negative RFI value are favorable.

These feed efficiency traits were calculated in three separate periods: the first half of the fattening period (week 0 to 24), latter half of the fattening period (week 24 to 52), and total fattening period (week 0 to 52). The RFIs for the first half, latter half, and total period were named as RFI_F , RFI_L , and RFI_T (similarly hereinafter in RG and RIG), respectively.

A desirable trait in Japanese Black cattle is a high level of fat marbling. We evaluated the difference in genetic correlations between the RFI originally estimated and RFI_{bms} , which included the beef marbling score (BMS) measured at the time of slaughter as an independent variable in the regression model in the preliminary analysis. The genetic correlations between RFI and RFI_{bms} were close to 1 in the different fattening periods (Supplementary Table S1). Hence, we used the original method to estimate RFI.

Growth Traits

In this study, FI, DG, feed conversion ratio (FCR), and parameters of the growth curve were defined as growth traits. Feed intake and DG were calculated in the total fattening period, with FCR calculated as FI divided by DG. To determine the growth curve parameters of each animal, we used the Gompertz growth curve (Winsor, 1932) with the BW dataset recorded at eight points, as described above, using R software (<http://www.r-project.org>). The Gompertz growth curve depends on three parameters having a biological implication and is represented as the following equation:

$$BW = a \times \exp\{-b \times \exp(-ct)\},$$

where, t is the age (weeks) of the animal, and a , b , and c are the asymptotic weight, growth starting point, and maturity rate of the growth curve, respectively.

Carcass Traits

After weighing on the 52nd week, all the steers were slaughtered at an average of 21 (range 19.9 to 21.5) months of age. Carcass weight (CW) was obtained from the sum of the left and right sides of the chilled carcasses of the animals. The rib-eye area (REA) was measured at the sixth and seventh rib sections and subcutaneous fat thickness (SFT) was also measured. Rib thickness (RT) was measured at the mid-point of the seventh rib section. Fat marbling (BMS), which was measured at the surface of the longissimus thoracis muscle between the sixth and seventh rib in accordance with the Japan Meat Grading Association (JMGA, 1988), was classified using the Beef Marbling Standard, with scores of 1 (poor) to 12 (abundant).

Statistical Analysis

Animals that were found to be outside the interval of ± 3 SDs from the mean were eliminated. For the three parameters of Gompertz growth curve, when any of the parameters is eliminated, the other two parameters were also eliminated. Genetic parameters of all traits were estimated by the following animal model (Inoue et al., 2011):

$$Y_{ik} = CKGP_{ij} + \alpha_i t_{ik} + u_{ik} + e_{ik}$$

where Y_{ik} is the observation of the k^{th} animal for the i^{th} trait, $CKGP_{ij}$ is the fixed effect of the j^{th}

tested year–step–station–herd (classes based on 11 years, 10 steps, 2 stations, and 3 herds) for the i^{th} trait, α_i is the linear regression coefficient for the beginning age for the i^{th} trait, t_{ik} is the age of the k^{th} animal at the beginning of the test for the i^{th} trait, and u_{ik} and e_{ik} are the random additive genetic and residual effects of the k^{th} animal for the i^{th} trait. A single-trait animal model for estimating heritability and a two-trait animal model for estimating genetic and phenotypic correlations were applied. The significance of the correlation coefficient was analysed by Student's t test. We used a total of 30,012 animals as pedigree information. Genetic parameters with SEs were estimated using ASReml 3.0 software (Gilmour et al., 2009).

RESULTS

Genetic Relationships Among Feed Efficiency Traits

Table 1 presents the descriptive statistics and heritability estimates for the feed efficiency traits of the three different fattening periods. Heritability estimates for RFI, RG, and RIG ranged from 0.36 to 0.46, 0.19 to 0.28, and 0.28 to 0.34, respectively. Heritability estimate for RG_F was greater than that for RG_L , whereas heritability estimates for RFI_F and RIG_F were lower than those for RFI_L and RIG_L , respectively. In all the traits, heritability estimates of the total fattening period were greater than those of the first and latter halves of the fattening period.

Table 2 shows the estimated genetic and phenotypic correlations among feed efficiency traits for the different fattening periods. The genetic correlations among all traits for the total fattening period were relatively high (0.73 to 0.94), but the genetic correlations among the traits for the first and latter halves of the fattening period were lower (0.43 to 0.72). This trend was more pronounced in the phenotypic correlation than in the genetic correlation. For example, the genetic correlation between RG_F and RG_L was moderate (0.43), whereas that of phenotypic correlation was low (0.14). Regarding the relationship among the feed efficiency traits, the genetic and phenotypic correlations of RIG with RFI and RG were high, but the genetic and phenotypic correlations between RFI and RG were low. For example, the genetic correlations between RIG and the two other traits (RFI and RG) in the total fattening period were -0.83 and 0.75 , respectively, whereas the genetic correlation between RFI and RG in the total fattening period was -0.27 . For

Table 1. Descriptive statistics for feed efficiency traits, growth traits, and carcass traits

Traits	Abbreviation	N	Mean	SD	Min	Max
Feed efficiency traits ^a						
Residual feed intake, kg/d	RFI _F	4,555	-0.01	0.62	-1.90	1.91
	RFI _L	4,560	0.00	0.58	-1.70	1.75
	RFI _T	4,556	0.00	0.53	-1.60	1.62
Residual BW gain, kg/d	RG _F	4,559	0.00	0.10	-0.30	0.31
	RG _L	4,555	0.00	0.09	-0.26	0.26
	RG _T	4,559	0.00	0.07	-0.21	0.21
Residual intake and BW gain	RIG _F	4,540	0.01	1.64	-5.40	5.33
	RIG _L	4,537	0.01	1.70	-5.30	5.42
	RIG _T	4,539	0.00	1.66	-5.28	5.37
Growth trait						
Average daily concentrated feed intake, kg/d	FI	4,568	6.93	0.73	4.80	9.10
Average daily gain, kg/d	DG	4,564	0.91	0.10	0.59	1.22
Feed conversion ratio	FCR	4,550	7.67	0.70	5.51	9.85
Parameters of Gompertz growth curve						
<i>a</i> , kg		4,459	768	116	471	1224
<i>b</i>		4,459	3.40	0.61	2.00	5.48
<i>c</i>		4,459	0.03	0.01	0.01	0.05
Carcass trait						
Carcass weight, kg	CW	4,566	349	36	244	457
Rib-eye area, cm ²	REA	4,562	47.8	5.7	31	65
Rib thickness, cm	RT	4,559	6.36	0.72	4.20	8.50
Subcutaneous fat, cm	SFT	4,546	2.00	0.52	0.50	3.60
Beef marbling standard	BMS	4,578	8.3	2.0	3	12

^aThe abbreviations of traits with subscription are the traits measured in the first half (F), latter half (L), and total (T) fattening periods.

Table 2. Heritability estimates (SEs), genetic correlations, and phenotypic correlations (SEs) among feed efficiency traits^a

Traits ^b	RFI _F	RFI _L	RFI _T	RG _F	RG _L	RG _T	RIG _F	RIG _L	RIG _T
RFI _F	0.36 (0.05)**	0.72 (0.05)**	0.91 (0.02)**	-0.24 (0.11)*	-0.53 (0.10)**	-0.36 (0.10)**	-0.78 (0.04)**	-0.74 (0.06)**	-0.82 (0.04)**
RFI _L	0.59 (0.01)**	0.46 (0.05)**	0.94 (0.01)**	-0.02 (0.11)	-0.47 (0.09)**	-0.17 (0.10)	-0.46 (0.08)**	-0.92 (0.02)**	-0.73 (0.05)**
RFI _T	0.86 (0.00)**	0.90 (0.00)**	0.46 (0.05)**	-0.12 (0.11)	-0.56 (0.09)**	-0.27 (0.10)**	-0.65 (0.06)**	-0.92 (0.02)**	-0.83 (0.03)**
RG _F	-0.37 (0.02)**	-0.07 (0.02)**	-0.24 (0.02)**	0.26 (0.04)**	0.43 (0.12)**	0.93 (0.02)**	0.79 (0.04)**	0.21 (0.11)	0.62 (0.07)**
RG _L	-0.26 (0.02)**	-0.40 (0.01)**	-0.42 (0.01)**	0.14 (0.02)**	0.19 (0.04)**	0.73 (0.07)**	0.59 (0.11)**	0.78 (0.05)**	0.81 (0.05)**
RG _T	-0.37 (0.02)**	-0.22 (0.02)**	-0.36 (0.02)**	0.84 (0.00)**	0.63 (0.01)**	0.28 (0.04)**	0.82 (0.04)**	0.45 (0.09)**	0.75 (0.05)**
RIG _F	-0.80 (0.01)**	-0.37 (0.02)**	-0.64 (0.01)**	0.86 (0.00)**	0.24 (0.02)**	0.75 (0.01)**	0.28 (0.04)**	0.58 (0.08)**	0.90 (0.03)**
RIG _L	-0.51 (0.01)**	-0.84 (0.01)**	-0.79 (0.01)**	0.12 (0.02)**	0.84 (0.01)**	0.51 (0.01)**	0.36 (0.01)**	0.33 (0.05)**	0.87 (0.03)**
RIG _T	-0.73 (0.01)**	-0.66 (0.01)**	-0.81 (0.01)**	0.67 (0.01)**	0.64 (0.01)**	0.84 (0.01)**	0.84 (0.00)**	0.78 (0.01)**	0.34 (0.05)**

^aDiagonal is heritability, upper diagonal is genetic correlation, and lower diagonal is phenotypic correlation.

^bAbbreviations of feed efficiency traits are shown in Table 1.

* $P < 0.05$; ** $P < 0.01$.

the first and latter halves of the fattening period, the genetic relationships of RIG with RFI and RG were slightly different; the genetic correlations between RIG_F and the two other traits (RFI_F and RG_F) were -0.78 and 0.79, respectively, whereas the genetic correlations between RIG_L and the two other traits (RFI_L and RG_L) were -0.92 and 0.78, respectively.

Genetic Relationships Between Feed Efficiency Traits and Growth Traits

Table 1 presents the descriptive statistics for growth traits and Table 3 presents the heritability estimates. Heritability estimates for FI, DG, and FCR were moderate, and ranged from 0.34 to 0.58. The heritability estimate for parameter *a* of the

Table 3. Heritability estimates (SEs) for growth traits and estimated genetic correlations (SEs) between feed efficiency traits and growth traits

Item	FI _T	DG _T	FCR _T	<i>a</i>	<i>b</i>	<i>c</i>
Heritability	0.58 (0.05)	0.54 (0.05)	0.34 (0.05)	0.61 (0.14)	0.08 (0.10)	0.17 (0.11)
Genetic correlations ^a						
RFI _F	0.53 (0.06)**	0.00 (0.09)	0.76 (0.05)**	−0.04 (0.11)	0.18 (0.12)	0.08 (0.14)
RFI _L	0.57 (0.06)**	0.08 (0.09)	0.70 (0.05)**	0.04 (0.10)	0.33 (0.11)**	0.08 (0.13)
RFI _T	0.63 (0.05)**	0.08 (0.09)	0.77 (0.04)**	0.03 (0.10)	0.28 (0.11)*	0.11 (0.13)
RG _F	0.27 (0.10)**	0.61 (0.07)**	−0.63 (0.07)**	0.22 (0.12)	0.82 (0.05)**	0.49 (0.11)**
RG _L	−0.14 (0.11)	0.33 (0.10)**	−0.80 (0.06)**	0.42 (0.10)**	−0.06 (0.15)	−0.51 (0.12)**
RG _T	0.16 (0.10)	0.59 (0.06)**	−0.76 (0.04)**	0.36 (0.11)**	0.64 (0.09)**	0.17 (0.15)
RIG _F	−0.16 (0.09)	0.39 (0.08)**	−0.88 (0.03)**	0.14 (0.11)	0.44 (0.10)**	0.28 (0.14)*
RIG _L	−0.47 (0.07)**	0.10 (0.09)	−0.84 (0.03)**	0.17 (0.10)	−0.26 (0.12)*	−0.29 (0.13)*
RIG _T	−0.34 (0.08)**	0.28 (0.08)**	−0.96 (0.01)**	0.17 (0.11)	0.20 (0.12)	0.02 (0.14)

^aAbbreviations of feed efficiency traits and growth traits are shown in Table 1.

* $P < 0.05$; ** $P < 0.01$.

Table 4. Heritability estimates (SEs) for carcass traits and estimated genetic correlations (SEs) between feed efficiency traits and carcass traits

Item	CW	REA	RT	SFT	BMS
Heritability	0.66 (0.05)	0.59 (0.05)	0.51 (0.05)	0.57 (0.05)	0.77 (0.06)
Genetic correlations ^a					
RFI _F	0.00 (0.09)	−0.05 (0.09)	0.03 (0.09)	0.12 (0.09)	0.19 (0.08)*
RFI _L	0.03 (0.08)	0.03 (0.08)	0.14 (0.09)	0.07 (0.08)	0.14 (0.08)
RFI _T	0.06 (0.08)	0.02 (0.08)	0.12 (0.09)	0.09 (0.08)	0.17 (0.08)*
RG _F	0.31 (0.09)**	0.29 (0.10)**	0.16 (0.10)	0.01 (0.10)	0.14 (0.09)
RG _L	0.14 (0.10)	0.04 (0.11)	0.02 (0.11)	0.07 (0.11)	0.10 (0.11)
RG _T	0.27 (0.09)**	0.24 (0.09)*	0.10 (0.10)	0.05 (0.10)	0.15 (0.09)
RIG _F	0.19 (0.09)*	0.20 (0.09)*	0.06 (0.10)	−0.06 (0.10)	−0.03 (0.09)
RIG _L	0.03 (0.09)	0.00 (0.09)	−0.11 (0.10)	−0.01 (0.09)	−0.07 (0.09)
RIG _T	0.10 (0.09)	0.11 (0.09)	−0.05 (0.10)	−0.03 (0.09)	−0.04 (0.09)

^aAbbreviations of feed efficiency traits and carcass traits are shown in Table 1.

* $P < 0.05$; ** $P < 0.01$.

Gompertz growth curve was moderate (0.61), while heritability estimates for parameter *b* and *c* were low (0.08 and 0.17, respectively).

Table 3 shows the estimated genetic correlations between feed efficiency traits and growth traits. The RFIs showed moderate genetic correlations with the FI (0.53 to 0.63) and low genetic correlations with the DG (0.00 to 0.08). The RGs showed moderate genetic correlations with the DG (0.33 to 0.61) and low correlations with the FI (−0.14 to 0.27). These three feed efficiency traits showed the greatest correlation with FCR (the absolute values ranged from 0.63 to 0.96), with RIGs showing the greatest correlations (ranged from −0.84 to −0.96), compared to the other feed efficiency traits. Regarding the three parameters (*a*, *b*, and *c*) of the Gompertz growth curve, the estimated genetic correlation of parameter *a* with RG_F (0.22) was lower than that of *a* with RG_L (0.42). RG_F had

a high genetic correlation (0.82) with parameter *b*, whereas RG_L had a low genetic correlation (−0.06) with parameter *b*. The estimated genetic correlation between RGs and parameter *c* was positive in the first half of the fattening period (0.49) and negative in the latter half of the fattening period (−0.51). RFI and RIG showed weak genetic correlations with all parameters (ranged from −0.04 to 0.33 in RFI and from −0.29 to 0.28 in RIG), with the exception of the moderate genetic correlation between RIG_F and parameter *b* (−0.44).

Genetic Relationships Between Feed Efficiency Traits and Carcass Traits

Table 1 presents the descriptive statistics for carcass traits and Table 4 presents the heritability estimates. The heritability estimate for BMS was the greatest (0.77), whereas those for CW, REA,

RT, and SFT were moderate (0.66, 0.59, 0.51, and 0.57, respectively).

Table 4 shows the estimated genetic correlations between the feed efficiency traits and carcass traits. These three feed efficiency traits, in the different fattening periods, showed low correlations with all of the carcass traits (-0.05 to 0.19 in RFI, 0.02 to 0.31 in RG, and -0.11 to 0.20 in RIG). The genetic correlations of RG and RIG with CW and REA were significantly positive in the first half of the fattening period but was not significantly positive in the latter half.

DISCUSSION

Genetic Relationships Among Feed Efficiency Traits

Several studies have demonstrated the genetic effects of feed efficiency traits in cattle breeds. For example, Ceacero et al. (2016) found that the heritability estimates for RFI, RG, and RIG in Nellore cattle, aged 287 ± 38 days at the start of the experiment, were 0.24, 0.19, and 0.15, respectively. For Japanese Black cattle, the genetic effects of RFI were reported by Hoque et al. (2009) and Inoue et al. (2011). Hoque et al. (2009) used performance tested bulls with an initial age of 6 to 7 mo, and a test period of 112 d, and obtained a heritability estimate for RFI as 0.49. On the other hand, Inoue et al. (2011) showed that the heritability estimate for RFI after the whole fattening period was 0.22. The heritability estimate for RFI obtained in the present study was similar to that reported by Hoque et al. (2009) but differed from that reported by Inoue et al. (2011). These discrepancies could be due to the difference in the magnitude of the study populations, or a difference in the definition of RFI. Unlike the present study, Inoue et al. (2011) obtained data from residual total digestible nutrients, or digestible crude protein intake, which was measured during the test period.

The feed efficiency during whole fattening period should be evaluated in the shorter period of time, because it is difficult to measure feed intake and BW gain for the whole fattening period. It would be useful if we could evaluate long-term feed efficiency by estimating shorter periods. However, genetic relationships among feed efficiency traits for different fattening periods were not reported. In addition, there are very few studies that have estimated genetic parameters of feed efficiency traits in feedlot cattle, indicating that there may be not enough available phenotypes in the period. Hence, we evaluated the genetic effects of dividing the

fattening period into two shorter periods on these three feed efficiency traits. In this study, the heritability estimates in the first and latter halves of the fattening period were different for the three feed efficiency traits, and the heritability estimates in the total fattening period were greater (0.46, 0.28, and 0.34 for RFI, RG, and RIG, respectively) than in the two halves of the fattening period separately. The genetic correlations among the traits for the first and latter halves of the fattening period separately were lower than those for the total fattening period as a whole. Heritability estimates for RIG_T and RIG_L (0.34 and 0.33, respectively) were lower than that for RIG_F , and the results of RFI also indicated a similar tendency. RIG for the total fattening period had a greater genetic correlation with RFI_T (-0.83) than with RG_T (0.75). The genetic correlations between RIG and RG were equivalent for the first and latter halves of the fattening period. However, the genetic correlation between the RIG and RFI traits in the latter half of the fattening period was greater than those in the first half. The high genetic correlation in the latter period was due to RIG being more genetically related to RFI than RG. The genetic correlations of feed efficiency traits with MBW, FI, and DG during different fattening periods were shown in Supplementary Table S2. Each independent variable had low genetic correlation with dependent variables (Ex., the genetic correlations of RFI with MBW and DG were low). No large difference of genetic correlation in different fattening periods was shown between RFI and FI (ranged from 0.41 to 0.66), but the large difference was shown between RG and DG (ranged from 0.13 to 0.65), and thus the genetic correlation of DG_F with RIG_F and RIG_L were also different (0.40 and 0.00, respectively). Therefore, the differences between the first and latter halves periods could be due to differences in DG and not in FI or MBW. These results indicate that it is possible to obtain the greatest heritability estimate by measuring feed intake over the whole fattening period, when implementing genetic improvement with RIG as an indicator. However, it may be possible to evaluate the genetic capacity by measuring feed intake only during the latter half of the fattening period if it is not possible to measure for the whole fattening period.

Genetic Relationships Between Feed Efficiency Traits and Growth Traits

Feed intake, DG, and FCR are indicators of growth traits with low-to-moderate heritability. For example, Arthur et al. (2001) reported that

the heritability estimates for FI, DG, and FCR in Angus cattle were 0.39, 0.28, and 0.29, respectively. Additionally, [Hoque et al. \(2009\)](#) reported that the heritability estimates for FI and FCR in Japanese Black cattle were 0.36 and 0.38, respectively. FCR, which is the amount of consumed feed divided by weight gain, is an important trait; it is an indicator of overall performance in feed utilization. However, selecting FCR as a trait could lead to animals with heavier mature weights and thus greater maintenance requirements ([Smith et al., 2010](#)), and has the potential to cause bias in breeding value prediction ([Gunsett, 1984](#)). Therefore, feed efficiency traits, such as RFI, are becoming popular as a measurement of feed efficiency in cattle ([Exton et al., 2000](#)), and RIG has the potential to be an index of FCR indirectly ([Berry and Crowley, 2012](#)). [Berry and Crowley \(2012\)](#), [Retallick \(2013\)](#), and [Nascimento et al. \(2016\)](#) observed a lower FI and greater DG in high-RIG animals. In this study, the heritability estimates for FI, DG, and FCR were moderate, and RFI and RG had moderate genetic correlations with FI and DG, respectively. The RIG, RFI, and RG traits had high genetic correlations with FCR, especially RIG, which had the greatest correlation. This is in agreement with the results from [Retallick \(2013\)](#), who found that FCR had high genetic correlations with RG (-0.97) and RIG (-0.95). Hence, our results suggest that the selection of high-RIG cattle could lead to both decrease in feed intake and increase in BW gain.

A growth curve based on the BW of an individual animal is a typical example of longitudinal data ([Fitzhugh, 1976](#)), and the curve in this study represents individual's growth process during whole fattening period. The shape of a growth curve provides biological interpretable parameters directly; the Gompertz growth curve comprises three parameters, a , b , and c ([Winsor, 1932](#)). Parameter a indicates the asymptotic limit of the weight when age approaches infinity. Parameter b is the ratio of asymptotic weight to birthweight. When parameter b is larger, the growth start time is earlier. Parameter c is maturity rate. When parameter c is larger, maturity rate is also large. These parameters can be used as indicators to represent the step-wise influence of growth. In our study, a two-step approach, where individual growth curve parameters are firstly estimated prior to the subsequent estimation of genetic parameters, was performed, because of comparing our results with previous reports and obtaining the genetic relationship between growth curve parameters and feed efficiency traits. There are some reports that have estimated

the genetic parameters of the growth curve for cattle by a two-step approach as in this study. [Meyer \(1995\)](#) reported that the heritability estimates in Hereford cattle for mature weight and rate of maturity were 0.47 and 0.32, respectively. [Kaps et al. \(1999\)](#) estimated a heritability of 0.44 for mature weight in Angus cattle. [Crispim et al. \(2015\)](#) showed that the estimated heritability for mature weight and maturity rate were 0.23 and 0.32, respectively, in Brahman cattle. In our study, the heritability estimates for growth curve parameters were low to moderate (0.08 to 0.61), and thus our study agreed with these previous results. Recently, [Forni et al. \(2009\)](#) estimated the growth curve parameters and genetic parameters simultaneously by one-step approach in beef cattle. In addition, [Coyne et al. \(2017\)](#) reported the different results of genetic parameters between one-step and two-step approaches in pig population. The detailed studies on the genetic relationship between growth curve parameters and other economical traits by estimating in one-step approach have not been reported, and further study is necessary to characterize the methods in detail. For the genetic relationship between growth curve parameters and feed efficiency traits, no study has been reported to our knowledge. In our study, the growth curve parameters had a high genetic correlation with RG and a low correlation with RFI. In addition to the genetic correlations between the three feed efficiency traits and growth curve parameters, we preliminarily investigated the relationship between DG and growth curve parameters (Supplementary Table S3). Regardless of the difference in the fattening period, DGs had high genetic correlations (ranged from 0.70 to 0.95) with the parameter a . The genetic correlation of the parameter b with DG_F was moderate (0.47), but b showed low (0.14) correlation with DG_L . The genetic correlations of parameter c with DG_F and DG_L were moderate to low (0.39 and -0.19 , respectively). It is interesting to note that RGs had a greater genetic correlation with parameters b and c than with DGs, and had a lower genetic correlation with parameter a than with DGs. DG is a result of various overlapping factors, which are biological growth characteristics affected by genetic and environmental factors (for example, feed intake). The present study indicated that DG is affected by the genetic effect of mature weight (i.e., parameter a). However, RG, from the regression of DG on MBW and FI, is affected by the genetic effect of the growth starting point (b) and maturity rate (c). It is presumed that RG strongly reflects the individual's genetic growth ability compared to DG, and thus RG could be an

alternative indicator for DG to improve the performance of beef cattle.

Genetic Relationships Between Feed Efficiency Traits and Carcass Traits

The genetic relationships between feed efficiency and other economically important traits, such as carcass traits, must be evaluated to increase the overall profitability of beef cattle breeding. In this study, we investigated the genetic relationship between five carcass traits and three feed efficiency traits with different fattening periods, and then showed low genetic correlations among all of the traits. A few studies have reported relationships between RIG and carcass traits in beef cattle. For example, [Santana et al. \(2014\)](#) reported that the genetic correlations of RIG with REA and SFT were low (0.02 and -0.03 , respectively) in Nellore cattle. In addition, [Retallick \(2013\)](#) reported that the genetic correlations of RIG with CW, loin eye area, backfat, and marbling score were low (ranged from -0.09 to 0.20). [Ceacero et al. \(2016\)](#) reported that low-to-moderate favorable genetic correlations were shown between RIG and carcass traits (0.16 for loin eye and -0.38 for SFT). Thus, the present study and previous studies indicate selecting high-RIG individuals can improve overall cattle performance, and show no unfavorable correlated response to carcass traits.

The genetic relationships between RFI and carcass traits in Japanese Black cattle were similar to those in previous studies, except for the relationship with BMS. [Hoque et al. \(2009\)](#) reported a correlation between RFI and BMS of -0.59 , whereas [Inoue et al. \(2011\)](#) reported a correlation of 0.51 . This discrepancy may be due to a difference in magnitude of the populations, or a difference in their definitions of RFI. [Hoque et al. \(2009\)](#) used 514 bulls from 22,029 progenies, and [Inoue et al. \(2011\)](#) used 863 bulls from the 4,578 animals in the present study population. Because [Hoque et al. \(2009\)](#) observed the genetic correlation between the RFI of performance tested bulls, fed mainly roughage, and the carcass traits of their progenies, the composition of feed in this study was different. Unlike the present study, the genetic correlation results in [Inoue et al. \(2011\)](#) were obtained from the residual total digestible nutrients or digestible crude protein intake measured during the test period. In the present study, we measured RFI focusing on the concentrated feed, which is particularly important in the fattening period. It is likely that the definition of RFI has an effect on BMS, and further studies are needed to clarify this genetic relationship.

The present study evaluated genetic relationships among feed efficiency traits with different fattening periods, between feed efficiency traits and growth traits, and between feed efficiency traits and carcass traits in Japanese Black cattle. With regard to RIG, it could be possible to perform a genetic evaluation in the latter half of the fattening period if it is not possible to collect feed intake data for the whole fattening period. RFI had no unfavorable genetic correlations with carcass traits and close to zero with DG. On the other hand, RIG had high and favorable genetic correlations with FI, DG, and FCR, and had low genetic correlations with carcass traits. In conclusion, selection of animals with a high RIG is recommended to increase the feed efficiency and BW gain, as well as avoid any unfavorable correlated responses that could affect the carcass grade, while selection of animal with a low RFI could lead only feed efficiency improvement. Additionally, further studies on RG as an indicator of growth would improve our understanding of cattle growth and maturity, as well as feed efficiency.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Animal Science* online.

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