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Genetic parameters for fatty acid composition and feed efficiency traits in Japanese Black cattle

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*We estimated the genetic parameters related to feed intake (FI), feed efficiency traits (including feed conversion ratio (FCR) and residual feed intake (RFI) of digestible crude protein (DCP) and total digestible nutrients (TDN)), beef marbling score (BMS), melting point of fat (MP) and fatty acid composition. Fat and meat (*Musculus trapezius*) samples were taken from the carcasses of 863 Japanese Black steers derived from 65 sires, for determination of the MP and fatty acid composition of the total lipid in intramuscular adipose tissue. Genetic parameters were estimated using uni- and bivariate animal models. In addition, pedigree information for 4841 animals was used. Heritability estimates for BMS, MP, individual fatty acids, monounsaturated fatty acids (MUFA), the ratio of saturated fatty acids to MUFA (MUS) and the ratio of elongation (ELONG) were generally high. The FI values of TDN and DCP were also high, but FCRs and RFIs of those were low (0.09 to 0.22). Genetic correlation of BMS with MP was −0.34 (favorable) and with C18:1, MUFA, MUS and ELONG values were 0.40, 0.28, 0.29 and 0.37, respectively (favorable). Genetic correlations of MP with C18:1, MUFA, MUS and ELONG were negative (also favorable) and high (−0.85, −0.98, −1.00 (−0.996) and −0.66, respectively). The correlation estimates for feed efficiency traits of DCP were quite similar to those of TDN. Genetic correlations of BMS with FCRs and RFIs of TDN and DCP were all positive (unfavorable; 0.21 to 0.51), and in particular, the correlations with RFIs of those were high. The correlations of C18:1, MUFA, MUS and ELONG with RFIs of TDN and DCP were positive (unfavorable) but low (0.06 to 0.17), whereas the corresponding correlations with FCRs of those were all negative (favorable; −0.38 to −0.10). These results suggest that the quantity and quality of beef fat can be simultaneously improved and that the quality of beef fat (fatty acid composition) can be improved directly or indirectly with MP. Furthermore, selecting MP or fatty acid traits does not significantly affect feed efficiency.*

Keywords: genetic parameter, beef cattle, fatty acid composition, feed efficiency

Implications

Fat quantity and fat quality traits have high heritability estimates and show favorable genetic relationships with each other. Some genetic relationships between fat quality traits and feed efficiency traits are unfavorable, but all of these are weak relationships. These results indicate that it may be convenient to improve fat quality traits genetically and to simultaneously improve the quantity and quality of beef fat. Furthermore, selecting fat quality traits does not significantly affect feed efficiency. We can expect to improve the quality of beef fat without reducing feed utilization efficiency.

Introduction

In the Japanese market, the beef marbling score (BMS), an index of the quantity of fat in beef, is the most important factor determining the market price of a carcass. Therefore, we have been breeding Japanese Black beef cattle with a focus on increasing BMS. Beef content includes lipids and various biomolecules, such as fatty acids. Fatty acid composition is related to the taste and flavor of beef (Westerling and Hedrick, 1979; Melton *et al.*, 1982; Mandell *et al.*, 1998). Therefore, the quality of fat as measured by fatty acid composition and fat melting point (MP), which has a high correlation with fatty acid composition, is one of the most important factors affecting beef quality.

Fatty acid composition is influenced by sex (Yoshimura and Namikawa, 1985; Zembayashi *et al.*, 1995), diet (Melton *et al.*, 1982; Mandell *et al.*, 1998) and age (Huerta-Leidenz *et al.*, 1996). Genetic influences, such as breed (Yoshimura and Namikawa, 1985; May *et al.*, 1993) and sire (Xie *et al.*, 1996), have also been reported, including sire-based differentiation in Japanese Black cattle (Oka *et al.*, 2002). However, to genetically improve MP and fatty acid composition,

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it is necessary to confirm the relationship between these traits and BMS by estimating genetic parameters. Few studies have estimated genetic parameters in Japanese Black cattle. We previously found that it is possible to obtain simultaneous genetic improvements in BMS (quantity) and fatty acid composition (quality; Inoue *et al*., 2008).

In addition, it is important to improve not only the quantity or quality of beef fat but also the feed efficiency, which affects farmers' running costs. Among various feed efficiency traits, feed conversion ratio (FCR) and residual feed intake (RFI) are typical. FCR is the ratio of feed intake (FI) to body weight gain (WTG). RFI is the difference between actual FI and the expected feed requirement for maintenance and production (Koch *et al*., 1963). Several studies have examined the relationships of RFI with WTG and carcass traits in Japanese Black cattle (Hoque *et al*., 2006; Okanishi *et al*., 2008; Hoque *et al*., 2009), but none have evaluated the genetic relationships between RFI and fatty acid composition.

Therefore, the objective of this study was to estimate the genetic parameters of MP, fatty acid composition and feed efficiency traits and to evaluate the relationships among these parameters in Japanese Black steers that were fattened for the same period, under the same conditions, and slaughtered at similar ages.

Table 1 *Numbers of arranged progeny*

		Test station/herd			
		Hokkaido		Hiroshima	
Year	Step (beginning day)	Herd 1	Herd 2	Herd 1	Herd 2
Year 1					
	1 (April 07)	14	14	14	14
	2 (April 14)	15	12		
	3 (April 21)	14	13	15	14
	4 (May 12)	13	13	10	10
	5 (May 19)	14	14	15	12
	6 (May 26)	13	12	14	15
	7 (June 02)	15	13	14	14
	8 (June 16)			12	13
	9 (June 23)	12	13	8	8
	10 (July 14)	12	12	15	
Year 2					
	1 (April 13)	14	11	12	10
	2 (April 20)	13	14	13	12
	3 (May 11)	14	14	12	12
	4 (May 18)	11	13	12	13
	5 (May 25)	11	12	14	14
	6 (June 01)	13	14	14	15
	7 (June 15)	15	15	13	13
	8 (June 29)	14	13	7	11

Material and methods

Animals and samples

All animals were cared for and slaughtered according to Japanese rules and regulations for animal care. A total of 863 Japanese Black steers derived from 65 sires were progeny tested at stations of the Livestock Improvement Association of Japan Inc. in Hokkaido and Hiroshima prefectures (Table 1). These steers were fattened beginning at an average age of 9.1 months (8.0 to 9.6 months) for 364 days. Body weight (BW) was measured at the beginning and at the end of the test. These steers were born over a 2-year period. Therefore, the progeny tests were carried out in two groups, one per year. In order to arrange the beginning ages, progeny tests were begun with 10 steps in the first year and in eight steps in the second year (Table 1). All steers were fitted with an automatic radio frequency identification transponder (Nedap Cattlecode, Groenlo, The Netherlands) to obtain access to the individual concentrate diet (73.3% total digestible nutrients (TDN), 10.3% digestible crude protein (DCP)) provided by the automatic feeder (Nedap Cattlecode). The amounts of the individual concentrate intake were measured and recorded automatically each day during the test period (364 days). However, roughage (hay; 54.0% TDN, 5.0% DCP) was supplied and recorded by technicians per herd unit.

All steers were slaughtered after fattening. BMS, which is scored from 1 (poor) to 12 (abundant), was evaluated between the 6th and 7th rib in accordance with the Japan Meat Grading Association (JMGA, 1988).

After carcass grading, about 2-mm sliced samples including muscle and adipose tissue were shaved off *Musculus trapezius* at the 6th and 7th rib of the carcasses of these fattened cattle. Although evaluation of BMS is typically performed at the surface of *M. longissimus*, we obtained samples from *M. trapezius*, because *M. longissimus* is one of the most valuable muscle parts of beef in the Japanese market and we wished to preserve the *M. longissimus* section. We obtained samples from *M. trapezius* close to *M. longissimus* that showed marbling and MPs similar to those of *M. longissimus*. The total lipids of intramuscular adipose tissue were extracted from these samples according to the method of Folch *et al*. (1957).

MP determination

MP was determined using method 2 according to The Japanese Pharmacopoeia published by the Ministry of Health, Labour and Welfare (MHLW, 2001). The samples were drawn into capillary tubes to a depth of about 10 mm. The charged tubes were allowed to stand for 24 h at a temperature below 10°C and were then placed in a beaker filled with water. The water temperature was raised by 1°C/min from 10°C. The temperature at which the sample is observed to rise in the capillary tube is identified as the MP.

Fatty acid analysis

The lipids were methylated by the method of O'Keefe *et al*. (1968). Methyl esters were analyzed by gas liquid chromatography (Hitachi G-3000, Tokyo, Japan) using a 3 mm × 1.5 m glass column packed with Unisole-3000 (GL Science, Tokyo, Japan). The gas pressures were 1.0 kg/cm^2 for the carrier gas (nitrogen), 1.0 kg/cm^2 for hydrogen and 1.1 kg/cm^2 for air. Each peak was identified by retention times compared with those of authentic samples. The percentage of major

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Table 2 *Partial regression coefficients and intercepts of multiple regressions used in calculating residual feed intakes*

	MWT	WTG	Intercept
Residual feed intake of TDN (RFI_{TDN}; kg)	10.08	1.99	622.02
Residual feed intake of DCP (RFI_{DCP}; kg)	1.35	0.28	73.43

MWT = metabolic weight; WTG = weight gain; TDN = total digestible nutrients; RFI = residual feed intake; DCP = digestible crude protein.

fatty acids was calculated from corresponding peak areas. Total monounsaturated fatty acids (MUFA) were calculated by summing appropriate components. In addition, the ratio of saturated fatty acids to MUFA (MUS) as an index of desaturation, and the ratio of elongation (ELONG) were calculated as follows:

$$\begin{aligned} \text{MUFA} &= \text{C14:1} + \text{C16:1} + \text{C18:1} \\ \text{MUS} &= (\text{C14:1} + \text{C16:1} + \text{C18:1})/ \\ &\quad (\text{C14:0} + \text{C16:0} + \text{C18:0}) \\ \text{ELONG} &= (\text{C18:0} + \text{C18:1})/(\text{C16:0} + \text{C16:1}) \end{aligned}$$

Calculation of FI and feed efficiency traits

Feed intake of TDN (FI_{TDN}) and DCP (FI_{DCP}) were estimated as total intakes of concentrate diet and roughage multiplied by their TDN and DCP content, respectively. Roughage intake per steer was calculated as the total intake of roughage per herd unit divided by the number of steers in the unit. Feed conversion ratios of TDN (FCR_{TDN}) and DCP (FCR_{DCP}) are expressed as the values of FI_{TDN} and FI_{DCP} per unit of WTG during the testing period, respectively. RFI of TDN (RFI_{TDN}) and DCP (RFI_{DCP}) were derived as follows:

$$\text{RFI} = \text{FI} - (b_1 \times \text{MWT} + b_2 \times \text{WTG} + \text{intercept})$$

where, MWT is the metabolic weight that is calculated as the mean BW during the test, raised to the 0.75 power (mean $BW^{0.75}$), b_1 and b_2 are partial regression coefficients of MWT and WTG, respectively. Coefficients and intercepts of TDN and DCP obtained by multiple regression analysis are presented in Table 2.

Statistical analysis

Genetic parameters were estimated using the following univariate animal model containing fixed effects of tested year–step–station–herd, prefecture of birth and regressions for beginning age. In addition, the pedigree information for 4841 animals was used.

$$Y_{ijk} = \text{CKGP}_i + L_j + \text{a1}t_{ijk} + u_{ijk} + e_{ijk}$$

where, Y_{ijk} is the observation of traits, CKGP_i is the fixed effect of *i*-th tested year–step–station–herd, L_j is the fixed effect of the *j*-th prefecture of birth of tested steers, a1 is the linear regression coefficient for the beginning age, t_{ijk} is the age of the animal at the beginning of the test, u_{ijk} is the random additive genetic effect of the *ijk*-th animal and e_{ijk} is the random residual. The program AIREMLF90 (Misztal *et al.*, 2002) was used for this analysis. Bivariate animal models with the same effects were used for estimations of phenotypic and genetic correlations.

Results and discussion

Phenotypic measurements

The results of the phenotypic measurements are shown in Table 3. The average values for BMS, MP, MUFA, FCR_{TDN} and FCR_{DCP} were found to be 7.8, 26.0, 58.3, 6.79 and 0.90, respectively.

The BMS value determined in this study was found to be higher than the value (4.0) reported by Oka *et al.* (2002), using Japanese Black steers fattened in a similar fattening test. However, the present value is similar to the value of 7.1, which was reported by Inoue *et al.* (2008), using steers and heifers. In addition, the average values for fatty acid composition and MUFA were found to be similar to those of intramuscular adipose tissue of *M. longissimus* reported by Oka *et al.* (2002), although the percentages of saturated fatty acids in their report were slightly higher and those of unsaturated fatty acids and MUFA were slightly lower than the percentages determined in this study.

The MP was found to be slightly higher than the value of 22.8 reported by Inoue *et al.* (2008) but much lower than the value of 39.1 reported by Pitchford *et al.* (2002). MP has a high correlation with fatty acid composition and there are reports that fatty acid composition is influenced by sex and age. These studies have confirmed that the fat of heifers tends to be more unsaturated than the fat of steers (Yoshimura and Namikawa, 1985; Zembayashi *et al.*, 1995) and aging increases MUFA (Huerta-Leidenz *et al.*, 1996). Furthermore, effects of breed differences are also reported; purebred Wagyu cattle or the other breeds derived from Wagyu generally tend to have higher proportions of unsaturated fatty acids than other breeds (Yoshimura and Namikawa, 1985; May *et al.*, 1993). Inoue *et al.* (2008) used field data from heifers and steers with an average slaughter age of 31.6 months. However, Pitchford *et al.* (2002) analyzed data from heifers and steers of Hereford cows mated to sires from seven different breeds, including Jersey, Wagyu, Angus, Hereford, South Devon, Limousin and Belgian Blue. Thus, differences among MP values would be expected.

The FCR_{TDN} and FCR_{DCP} values were found to be 6.79 and 0.90, respectively and these values are almost the same as the national averages based on the progeny tests of Japanese Black in 2007 (Statistics in Japan).

Heritability

Heritability estimates of BMS and MP were found to be high (0.64 and 0.63, respectively), and those of each fatty acid, MUFA, MUS and ELONG were also high (0.65 to 0.86, 0.66, 0.75 and 0.67, respectively) except for C18:2 (0.34) as presented in Table 4. However, the values of FI and feed efficiency traits were low to high (0.09 to 0.70).

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Table 3 *Descriptive statistics of fatness traits and feed efficiency traits*

Trait	Abbreviation	Mean	s.d.	Minimum	Maximum
Beef marbling score (*n*)	BMS	7.8	1.9	3	12
Melting point (°C)	MP	26.0	3.4	16.0	35.4
Myristic acid (%)	C14:0	2.9	0.5	1.7	5.0
Myristoleic acid (%)	C14:1	1.5	0.4	0.9	3.1
Palmitic acid (%)	C16:0	24.2	1.7	19.4	30.0
Palmitoleic acid (%)	C16:1	6.6	1.0	3.6	9.7
Stearic acid (%)	C18:0	8.5	1.2	5.3	16.8
Oleic acid (%)	C18:1	50.2	2.5	42.3	57.0
Linoleic acid (%)	C18:2	2.5	0.6	1.0	6.5
Total monounsaturated fatty acids (%)	MUFA	58.3	2.4	48.6	65.2
Ratio of saturated fatty acids to MUFA	MUS[a]	1.7	0.2	1.1	2.3
Ratio of elongation	ELONG[b]	19.2	2.0	12.9	25.2
Feed intake of TDN (kg)	FI_{TDN}	2213.3	197.7	1652.1	2817.1
Feed intake of DCP (kg)	FI_{DCP}	292.6	27.1	215.4	374.9
Feed conversion ratio of TDN (kg)	FCR_{TDN}	6.79	0.64	5.01	9.76
Feed conversion ratio of DCP (kg)	FCR_{DCP}	0.90	0.08	0.66	1.30
Residual feed intake of TDN (kg)	RFI_{TDN}	0.0	151.6	−494.6	578.1
Residual feed intake of DCP (kg)	RFI_{DCP}	0.0	20.6	−69.2	78.9

TDN = total digestible nutrients; DCP = digestible crude protein.
[a]MUS = total MUFA (sum of C14:1, C16:1 and C18:1) per total saturated fatty acids (sum of C14:0, C16:0 and C18:0).
[b]ELONG = sum of C18:0 and C18:1 per sum of C16:0 and C16:1.

Table 4 *Estimated heritability, genetic variances and residual variances*

Trait[a]	Heritability	s.e.	Genetic variance	Residual variance
BMS	0.64	0.10	2.31	1.32
MP	0.63	0.09	6.64	3.84
C14:0	0.82	0.10	0.18	0.04
C14:1	0.86	0.10	0.13	0.02
C16:0	0.65	0.09	1.78	0.96
C16:1	0.66	0.10	0.59	0.30
C18:0	0.71	0.10	1.02	0.42
C18:1	0.73	0.09	4.02	1.50
C18:2	0.34	0.08	0.13	0.25
MUFA	0.66	0.09	3.47	1.76
MUS	0.75	0.10	2.37×10^{-2}	0.77×10^{-2}
ELONG	0.67	0.10	2.55×10^{-2}	1.25×10^{-2}
FI_{TDN}	0.70	0.11	21 557	9221
FI_{DCP}	0.70	0.11	423.4	182.3
FCR_{TDN}	0.11	0.05	0.03	0.28
FCR_{DCP}	0.09	0.05	0.05×10^{-2}	0.51×10^{-2}
RFI_{TDN}	0.22	0.07	0.35	1.21
RFI_{DCP}	0.22	0.07	0.69×10^{-2}	2.38×10^{-2}

TDN = total digestible nutrients; DCP = digestible crude protein.
[a]See Table 3 for abbreviations; MUS = total MUFA (sum of C14:1, C16:1 and C18:1) per total saturated fatty acids (sum of C14:0, C16:0 and C18:0); ELONG = (sum of C18:0 and C18:1) per (sum of C16:0 and C16:1).

The high estimates of fatness traits showed that characteristics of station progeny tests, or heritabilities estimated using the data obtained from station tests are generally higher than the field data. Failure to synthesize only C18:2 *in vivo* may cause lower heritability of C18:2 than the heritability of the other fatty acids. In addition, these estimated results may provide evidence of the propriety of the sampling data, the analysis method and the model. Heritabilities of MP and fatty acids in this study were found to be high compared not only with the other breeds (MP and fatty acids were 0.28 and 0.14 to 0.21) estimated by Pitchford *et al*. (2002) but also within the same breeds (MP and fatty acids were 0.41 and 0.38 to 0.73) estimated by Inoue *et al*. (2008). The difference in the same breed might be caused by variations in characteristics between data from station progeny tests and from field progeny. However, the estimates of Japanese Black were higher than those of the other breeds. Therefore, it is likely that the difference between the breeds may be caused by differences in enzyme activities related to desaturation. Abe *et al*. (2009) detected a difference in the allele frequency of fatty acid synthase (FASN), which affects the proportions of fatty acid composition among different breeds. The estimated high heritabilities for MP, each fatty acid, MUFA, MUS and ELONG suggested that there are advantages in genetically improving the ratio of unsaturated fatty acids.

Heritability estimates of FI and feed efficiency traits ranged from low to high. The estimates of FIs were found to be high (0.70) and similar to fatness traits but those of FCRs and RFIs were low (0.09 to 0.22) in this study. Hoque *et al*. (2006) reported that heritability estimates of FCR and phenotypic RFI in the study of individual performance tests (Wagyu Registry Association (WRA), 2000) on Japanese Black bulls were 0.15 and 0.24, respectively. These estimates are similar to the FCR and RFI values determined in this study. However, Hoque *et al*. (2009) also reported slightly higher estimates of the two traits (FCR and RFI were 0.38 and 0.49) and of FI_{TDN} (0.35) and FCR_{TDN} (0.46) in another Japanese Black population. Okanishi *et al*. (2008) reported heritability estimates for FIs of TDN and DCP were 0.27 and 0.25, FCRs of those were 0.14 and 0.03, and RFIs of those were 0.10 and 0.12,

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respectively, in performance tests on Japanese Black bulls. Our results were similar or slightly higher than their results except for FIs.

Relationships between fatness traits

The phenotypic correlations between BMS, which is an index of the amount of fat within beef, and each fatty acid were found to be low and the range of these was about ±0.15 between C14:0 and C18:1 (Table 5). Although the genetic correlations of these values were higher overall than the phenotypic values, these values were −0.42 (C14:1) to 0.40 (C18:1). Standard error estimates of the genetic correlations were relatively small and most of the genetic correlations were statistically different from zero. The negative genetic correlation between BMS and MP (−0.34), and the positive correlation of BMS with C18:1 (0.40), MUFA (0.28), MUS (0.29) and ELONG (0.37) were different from zero and suggest that these relationships are favorable for enhancing desaturation and elongation, and that it is possible to improve both the quantity and quality of fat in beef. However, we previously estimated that BMS shows low genetic correlations with MP (0.08), C16:0 (0.15) and C18:1 (−0.09). This study employed 5314 Japanese Black steers and heifers from field data of different populations. The main cause of these differences between this and the earlier studies might be the differences of age between the two data populations. It is known that the degree of fat deposition on the intramuscular sections differs according to age in lines of Japanese Black cattle. In any case, these relationships are not unfavorable for improving both quantity and quality of beef fat. Additional research will be required to confirm the relationships between BMS and fatty acid composition.

The positive phenotypic and genetic correlations between MP and each saturated fatty acid were found to be between 0.53 to 0.69 for phenotypic parameters and 0.72 to 0.91 for genetic parameters. The negative correlations between MP and each unsaturated fatty acid were −0.05 to −0.66 for phenotypic parameters and −0.11 to −0.85 for genetic parameters except for C14:1 (0.05 for the genetic correlation), although the genetic estimates of MP with C14:1 and C16:1 were not surely different from zero or identical with zero. Furthermore, the genetic correlations of MP with MUFA, MUS and ELONG were also highly negative (−0.98, −1.00 (−0.996) and −0.66, respectively). These results follow a trend similar to our previous results (Inoue *et al.*, 2008) and show that a higher percentage of saturated fatty acid raises the MP and a higher percentage of unsaturated fatty acids lowers the MP.

It is known that C16:0 is converted to C16:1 via stearoyl-CoA-desaturase (SCD) and C18:0 via fatty acid elongase. The latter is also converted to C18:1 by SCD *in vivo*. Thus, it is considered that the equilibrium between C16:0 and C16:1, and between C18:0 and C18:1 is maintained. Therefore, the phenotypic and genetic correlations between these fatty acids might be low. The phenotypic and genetic correlations between C16:1 and C18:0 were moderately negative (−0.63 and −0.51, respectively). This relationship between these

Table 5 *Estimated genetic (above diagonal) and phenotypic (below diagonal) correlations (±s.e.) between fatness traits*

Trait[a]	BMS	MP	C14:0	C14:1	C16:0	C16:1	C18:0	C18:1	C18:2	MUFA	MUS	ELONG
BMS		−0.34*** ± 0.12	−0.35*** ± 0.11	−0.42*** ± 0.05	−0.31*** ± 0.12	−0.22 ± 0.12	−0.04 ± 0.13	0.40*** ± 0.11	0.05 ± 0.16	0.28* ± 0.12	0.29* ± 0.12	0.37*** ± 0.11
MP	−0.12***		0.74*** ± 0.06	0.05 ± 0.12	0.91*** ± 0.04	−0.11 ± 0.12	0.72*** ± 0.07	−0.85*** ± 0.04	−0.53*** ± 0.12	−0.98*** ± 0.02	−1.00***[b] ± 0.00[c]	−0.66*** ± 0.08
C14:0	−0.14***	0.53***		0.51*** ± 0.08	0.70*** ± 0.06	0.37*** ± 0.10	0.16 ± 0.12	−0.91*** ± 0.02	−0.09 ± 0.14	−0.74*** ± 0.06	−0.72*** ± 0.06	−0.81*** ± 0.04
C14:1	−0.09***	−0.05	0.48***		0.22* ± 0.11	0.64*** ± 0.07	−0.38*** ± 0.10	−0.43*** ± 0.09	0.07 ± 0.14	−0.01 ± 0.12	−0.03 ± 0.11	−0.54*** ± 0.08
C16:0	−0.11***	0.69***	0.68***	0.20***		0.10 ± 0.12	0.28* ± 0.12	−0.88*** ± 0.03	−0.26 ± 0.14	−0.89*** ± 0.03	−0.90*** ± 0.03	−0.86*** ± 0.03
C16:1	−0.04	−0.20***	0.40***	0.69***	0.11***		−0.51*** ± 0.09	−0.34** ± 0.11	0.23 ± 0.15	0.17 ± 0.12	0.13 ± 0.12	−0.56*** ± 0.08
C18:0	−0.06*	0.57***	0.02	−0.49***	0.19***	−0.63***		−0.29* ± 0.11	−0.64*** ± 0.11	−0.60*** ± 0.08	−0.64*** ± 0.07	0.08 ± 0.12
C18:1	0.17***	−0.66***	−0.84***	−0.36***	−0.85***	−0.27***	−0.22***		0.15 ± 0.14	0.86*** ± 0.03	0.87*** ± 0.03	0.92*** ± 0.02
C18:2	−0.07*	−0.29***	−0.14***	−0.05	−0.24***	0.00	−0.27***	0.04		0.26 ± 0.15	0.36** ± 0.13	−0.02 ± 0.15
MUFA	0.15***	−0.77***	−0.62***	0.08*	−0.80***	0.25***	−0.57***	0.86***	0.03		0.99***[d] ± 0.00[d]	0.67*** ± 0.07
MUS	0.14***	−0.81***	−0.64***	0.04	−0.87***	0.20***	−0.60***	0.85***	0.22***	0.96***		0.67*** ± 0.07
ELONG	0.12***	−0.45***	−0.79***	−0.53***	−0.85***	−0.57***	0.20***	0.87***	0.08**	0.57***	0.61***	

[a]See Table 3 for abbreviations; MUS = total MUFA (sum of C14:1, C16:1 and C18:1) per total saturated fatty acids (sum of C14:0, C16:0 and C18:0); ELONG = (sum of C18:0 and C18:1) per (sum of C16:0 and C16:1).
[b]The precise estimate was −0.996.
[c,d]The precise s.e. of MUS with MP and MUFA were 0.09×10^{-2} and 0.3×10^{-2}, respectively.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

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fatty acids seems to be contrary because both are synthesized from C16:0. There are several reports, including our previous report, which indicate that the relationship between the percentages of C16:1 and C18:0 might produce a negative correlation where, as the percentage of C16:1 increases, that of C18:0 decreases, and vice versa. Our present results are in agreement with these reports. There is a high negative genetic correlation between C16:0 and C18:1. Although C18:1 is synthesized from C16:0 via C18:0 *in vivo*, the relationship might be an inverse relationship because C16:0 and C18:1 represent the largest proportions of unsaturated fatty acids and saturated fatty acids, respectively, and C18:1 is the last species of unsaturated fatty acid synthesized from C16:0. The correlation between C14:0 and C18:1 was also highly negative. It has been reported that mutations of the FASN gene have opposite effects on the percentages of C14:0 and C18:1 (Morris *et al*., 2007; Abe *et al*., 2009). The results of this study are in agreement with these reports.

A strong negative genetic correlation was identified between C16:0, a major saturated fatty acid and C18:1, a major unsaturated fatty acid. Moreover, the MP, which contributes to the softness and flavor of fat, was found to have strong negative (favorable) genetic correlations with C18:1, MUFA and MUS, and a strong positive (favorable) genetic correlation with C16:0. These results followed a similar trend as the results of our previous report. These results suggest that it is possible to improve each trait indirectly by improving the ratio of unsaturated fatty acids or improving the MP. In particular, the genetic correlations between MP and MUS and between MP and MUFA were very strong (-1.00 (-0.996) and -0.98, respectively). Thus, MP and MUS as well as MP and MUFA appear to be almost same traits for selection. Determination of these traits requires much time and effort and analysis of fatty acid composition requires an analytical laboratory with gas/liquid chromatography. Furthermore, the meat becomes damaged when the samples are taken. Recent reports have described new ways to measure the MP or MUS of beef quickly and without damage to the meat. Irie *et al*. (2003) have developed a hand-held, portable device capable of measuring MUFA content and saturated fatty acid content using spectroscopy with a fiber-optic probe and near-infrared light. This report identified correlations of the reflectance of the intermuscular fat of beef with MUFA content and saturated fatty acid of -0.69 and 0.72, respectively. This fiber optic probe allows results to be obtained within seconds. Maehara *et al*. (2008) are engaged in development of methods for measuring the degree of unsaturation of fatty acids in beef using imaging analysis. This work involves research into the relationships of the traits measured by the image analysis device including the overall coarseness of the marbling and average luminance of marbling with fatty acid composition and MUFA. This image analysis technique is expected to enable rapid estimation of MUFA. We are hopeful that these new techniques will improve rapidly and allow us to improve the quality of beef.

Relationships between fatness traits and feed efficiency traits

Genetic correlations and standard error estimates between fatness traits and feed efficiency traits are shown in Table 6. The range of correlations of fatness traits according to FCR_{TDN} and FCR_{DCP} were found between -0.38 (ELONG and FCR_{DCP}) and 0.43 (C14:1 and FCR_{DCP}). Their standard error estimates were rather large (0.19 to 0.31) and the genetic correlations seemed to be not statistically different from zero. Likewise, the range of correlations of fatness traits according to RFI_{TDN} and RFI_{DCP} were -0.22 (C16:0) to 0.51 (BMS), respectively, although the genetic correlations were not surely considered different from zero or identical with zero except for those between RFIs and BMS. The correlation estimates for feed efficiency traits of DCP were quite similar to those of TDN. Genetic correlations of BMS with FCRs and RFIs were all positive (unfavorable; 0.21 to 0.51), in particular, the correlations with RFIs were high. These results suggest that animals with high values of BMS would be expected to have a low feed efficiency.

Robinson and Oddy (2004) reported positive genetic correlations of intramuscular fat with FCR and RFI, and there was a higher correlation with RFI (0.22 ± 0.17) than with FCR (0.08 ± 0.28) in their study. These estimates represent trends similar to those identified in our study results between BMS and FCRs or RFIs, although degrees of estimation were different. Nkrumah *et al*. (2007) also reported a similar positive genetic correlation between the carcass marbling score, which was evaluated according to the Canadian beef carcass grading system and RFI (0.28 ± 0.38). Both groups estimated genetic parameters using European breeds and/or tropically adapted breeds such as Brahman and Belmont Red. Robinson and Oddy (2004) studied tropical breeds, such as Angus and Hereford, whereas Nkrumah *et al*. (2007) investigated crossbreds of Angus and Charolais, among others. The different degrees of correlations between our results and the previous reports may be due to differences in genetic backgrounds of the cattle and environmental effects. In the European breed, however, Bouquet *et al*. (2010) estimated genetic correlations of carcass fatness score (CF) with FCR of -0.41 ± 0.17 and -0.03 ± 0.18, and with RFI of 0.00 ± 0.20 and 0.07 ± 0.14 in Blonde d'Aquitaine and Limousin breeds, respectively. Likewise, in the same Japanese Black breed, Hoque *et al*. (2009) reported genetic correlations of BMS with FCR_{TDN} and RFI of -0.62 ± 0.09 and -0.59 ± 0.08, respectively. These results are in opposition to the results of this study. In the results of Robinson and Oddy (2004) and our study, however, standard errors of genetic correlations between fatness and FCR were large and the reliability of the estimates seems to be low. Therefore, the genetic relationship of those appears to be not statistically different from zero or even negative as reported by Hoque *et al*. (2009) and Bouquet *et al*. (2010). However, the relationship between fatness and RFI was surely positive in the results of Robinson and Oddy (2004) and our study using fatness and RFI of progeny or feedlot animals, whereas the surely negative relationship was identified by Hoque *et al*. (2009) and no relationship was

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Table 6 *Estimated genetic correlations (±s.e.) between fatness traits and feed efficiency traits*

Trait[a]	BMS	MP	C14:0	C14:1	C16:0	C16:1	C18:0	C18:1	C18:2	MUFA	MUS	ELONG
FCR_{TDN}	0.21 ± 0.22	0.13 ± 0.21	0.19 ± 0.19	0.40 ± 0.21	0.28 ± 0.21	0.23 ± 0.21	−0.29 ± 0.21	−0.23 ± 0.19	−0.30 ± 0.29	−0.11 ± 0.21	−0.11 ± 0.20	−0.37 ± 0.20
FCR_{DCP}	0.26 ± 0.24	0.11 ± 0.23	0.19 ± 0.21	0.43 ± 0.23	0.28 ± 0.22	0.25 ± 0.23	−0.32 ± 0.23	−0.23 ± 0.21	−0.27 ± 0.31	−0.11 ± 0.22	−0.10 ± 0.22	−0.38 ± 0.21
RFI_{TDN}	0.51** ± 0.16	−0.20 ± 0.16	−0.02 ± 0.16	0.05 ± 0.16	−0.22 ± 0.16	0.00 ± 0.17	−0.13 ± 0.17	0.06 ± 0.16	0.23 ± 0.19	0.08 ± 0.17	0.16 ± 0.16	0.10 ± 0.17
RFI_{DCP}	0.51** ± 0.16	−0.20 ± 0.16	−0.02 ± 0.16	0.05 ± 0.16	−0.22 ± 0.16	0.01 ± 0.17	−0.13 ± 0.17	0.06 ± 0.16	0.24 ± 0.19	0.08 ± 0.17	0.16 ± 0.16	0.10 ± 0.17

TDN = total digestible nutrients; DCP = digestible crude protein.
[a]See Table 3 for abbreviations; MUS = total MUFA (sum of C14:1, C16:1 and C18:1) per total saturated fatty acids (sum of C14:0, C16:0 and C18:0); ELONG = (sum of C18:0 and C18:1) per (sum of C16:0 and C16:1).
**$p < 0.01$.

showed by Bouquet *et al.* (2010) using RFI of young bulls and fatness of their progeny. These results suggest that the difference of animals, whose RFI is measured, may affect the genetic relationship between fatness and RFI. In Japanese Black breed, to be concrete, the estimates by Hoque *et al.* (2009) were derived from a study on the relationships between feed efficiency traits, which were the results of individual performance tests (WRA, 2000) on candidate young bulls before their selection, and the BMS of the field progeny of the selected bulls. However, we studied the relationships between feed efficiency traits and BMS of the progeny of the selected bulls in the progeny test. Therefore, the populations of bulls and the effects of selection may be the cause of the differences between the results. The age of animals may also be the cause of the differences of correlations. Arthur *et al.* (2001b) reported that the genetic correlation between post-weaning and yearling measures of RFI was 0.75 in bulls. The RFI from animals in the study of Hoque *et al.* (2009) were obtained from young bulls with ages of about 7 to 11 months, whereas the RFI from animals in our study were obtained from progeny with ages between 9.1 months and 21.1 months.

Stronger genetic correlations were generally estimated between fatty acids and FCRs rather than between fatty acids and RFIs, although standard error estimates were large, in contrast with the relationships of FCRs and RFIs with BMS (Table 6). This may be related to the fact that BMS represents the fat amount, whereas the fatty acid composition represents the ratio of fatty acids within a given portion of fat, and RFI represents the residual energy intake over the energy required for maintenance and production of the animal. In short, RFI rather than FCR has less of an effect on the fatty acid composition. Genetic correlations of C18:1, MUFA, MUS and ELONG with RFIs were positive (unfavorable) but all low (0.06 to 0.17), whereas those with FCRs were all negative (favorable; −0.38 to −0.10). These estimates were not surely different from zero or identical with zero. Similarly, genetic correlations of MP with RFIs were found to be unfavorable, although the sign has changed. These were low values (−0.20), whereas the correlations of MP with FCRs were all favorable (0.11 and 0.13), although not statistically different from zero. According to this result, FCR appears to be more appropriate for the selection traits than RFI. However, it is known that ratio traits such as FCR may be problematic for selection. In a study comparing the selection responses of direct selection on a ratio trait consisting of two components to a linear index trait derived from the same components, Gunsett (1984) concluded that the use of a linear index increases selection responses compared to direct selection. Archer *et al.* (1999) and Arthur *et al.* (2001a) pointed out that selection to improve FCR does not always lead to improvement of feed efficiency in future generations since selection against FCR can also produce larger animals, which need more energy for maintenance even if they have superior WTG. RFI can represent feed efficiency without these problems. Besides, Okanishi *et al.* (2008) reported that selection based on RFI values, particularly RFI of TDN, can produce favorable correlated responses in WTG and all feed

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intakes without changing body size. Therefore, we should use RFI rather than FCR as a selection index for feed efficiency.

Although fatty acid composition is also a ratio trait, in the case of fatty acid composition, we can avoid these kinds of selection problems by choosing the amount of fat content (BMS or intramuscular fat content) as a selection trait. In addition, we can use MP, (which is expressed as a linear trait), for selection instead of fatty acid composition since the relationships between MP and MUFA and between MP and MUS are similar and appear to represent the same traits (Table 5).

Recently, there have been several studies and breeding schemes in Japan that focused on MUFA, which enhance the taste and flavor of beef. However, when we conduct selection according to new traits such as MUFA or MP, it is important that the relationships between these new traits and the other conventional traits be well defined. In order to prevent decreasing the performance of the other conventional traits and reducing the efficiency of selection, we need to research the relationships before using the new traits for selection. The present results suggest that selecting MP or fatty acid traits does not significantly affect feed efficiency, although the standard error estimates in this study were rather high. Furthermore, the relationships between MP or fatty acid traits and feed efficiency were found to be relatively lower than the effect of increasing BMS on feed efficiency. The high standard errors generally reflect the relatively small data set. Although we still need to examine the unfavorable relationships, we can expect that fat quality should improve without loss of feed efficiency.

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