

JOURNAL OF ANIMAL SCIENCE

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J Anim Sci 2008.86:40-46.

doi: 10.2527/jas.2007-0359 originally published online Oct 2, 2007;

The online version of this article, along with updated information and services, is located on the World Wide Web at:

<http://jas.fass.org/cgi/content/full/86/1/40>



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Genetic parameters for image analysis traits on *M. longissimus thoracis* and *M. trapezius* of carcass cross section in Japanese Black steers¹

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ABSTRACT: In Japan, the degree of marbling in ribeye (*M. longissimus thoracis*) is evaluated in the beef meat grading process. However, other muscles (e.g., *M. trapezius*) are also important in determining the meat quality and carcass market prices. The purpose of this study was to estimate genetic parameters for *M. longissimus thoracis* (M-LONG) and *M. trapezius* (M-TRAP) of carcass cross section of Japanese Black steers by computer image analysis. The number of records of Japanese Black steers and the number of pedigree records were 2,925 and 10,889, respectively. Digital images of the carcass cross section were taken between the sixth and seventh ribs by photographing equipment. Muscle area (MA), fat area ratio (FAR), overall coarseness of marbling particles (OCM), and coarseness of maximum marbling particle (MMC) in M-LONG and M-TRAP were calculated by image analysis. Genetic parameters

for these traits were estimated using the AIREMLF90 program with an animal model. Fixed effects that were included in the model were dates of arrival at the carcass market and slaughter age (mo), and random effects of fattening farms, additive genetic effects and residuals were included in the model. For M-LONG, heritability estimates (\pm SE) were 0.46 ± 0.06 , 0.59 ± 0.06 , 0.47 ± 0.06 , and 0.20 ± 0.05 for MA, FAR, OCM, and MMC, respectively. Heritability estimates (\pm SE) in M-TRAP were 0.47 ± 0.06 , 0.57 ± 0.07 , 0.49 ± 0.07 , and 0.13 ± 0.04 for the same traits. Genetic correlations between subcutaneous fat thickness and FAR for M-LONG and M-TRAP were negative (-0.21 and -0.19 , respectively). Those correlations between M-LONG and M-TRAP were moderate to high for MA, FAR, OCM, and MMC (0.38 , 0.52 , 0.39 , and 0.60 , respectively). These results indicate that other muscles including M-LONG should be evaluated for more efficient genetic improvement.

Key words: Japanese Black steer, image analysis, genetic parameter

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J. Anim. Sci. 2008. 86:40–46
doi:10.2527/jas.2007-0359

INTRODUCTION

In Japan, beef carcass is ribbed on the left side between the sixth and seventh ribs. The yield and meat quality scores are evaluated by certified graders of the Japan Meat Grading Association. In general, marbling in ribeye (*M. longissimus thoracis*; **M-LONG**) is an important factor in determining the meat quality and carcass value. Marbling score is currently visually evaluated on only ribeye. However, buyers consider other

muscles in making a purchase. Thus, degrees of marbling in other muscles are also important in determining the meat quality and carcass value.

Image analysis is appropriate for the objective evaluation of muscle of carcass cross section. Gerrard et al. (1996) and Kuchida et al. (2000) reported that beef marbling and color scores can be measured and that crude fat content can be predicted by image analysis, respectively. Vote et al. (2003) reported that a computer vision system is effective in predicting beef tenderness. However, those reports analyzed only ribeye; detailed image analysis for muscles other than ribeye is scarcely reported.

Osawa et al. (2004b) analyzed coarseness of marbling particles and ribeye shape for Japanese Black cattle by image analysis and estimated genetic parameters for those traits. Also using image analysis, Osawa et al. (2004a) investigated genetic relationships among muscle area and intramuscular fat ratio in multiple muscles for the carcass cross section, as well as traditional car-

¹Acknowledgments: The authors give thanks to Hokkaido Meat Packer Incorporation, Japan Meat Grading Association and Hokkaido Dairy and Livestock Association for providing data. This study was in part supported by Grant-in-Aid for the 21st Century Center of Excellence Program at Iwate University from the Ministry of Education, Culture, Sports, Science and Technology, Japan.

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Received June 15, 2007.

Accepted September 3, 2007.

cass traits for 404 Japanese Black steers in progeny testing at test stations. However, because the animals reported were younger than those shipped to carcass markets in Japan and the number of records was small, the results may be different when field data are used. Thus, it is necessary to get more reliable results by analyzing larger field data. The objective of this study was to estimate genetic parameters for image analysis traits of M-LONG and M. trapezius (**M-TRAP**) of Japanese Black steers in the general carcass market.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because data were collected from beef cattle shipped to a meat processing plant in Hokkaido, Japan.

Carcass Traits

The carcass data were collected from Japanese Black steers shipped between April 2000 and March 2004 to a meat processing plant in Hokkaido, Japan. Animals with any inflammations in M-LONG and M-TRAP were excluded from the data set. This data set was edited so that at least 5 animals were included for each of the following: subclass of date at carcass market, subclass of slaughter age in months, fattening farm, and sire. The final number of animals was 2,925. There were 87 subclasses for dates at carcass market, 12 subclasses for slaughter age (25 to 35 and 36 to 37 mo), 107 fattening farms, and 38 sires.

The carcass traits considered in this study were carcass weight (**CW**), ribeye area (**REA**), rib thickness (**RT**), subcutaneous fat thickness (**SFT**), yield estimate (**YE**), and beef marbling score (**MS**). All carcass traits were evaluated by certified graders of the Japan Meat Grading Association according to the carcass grading standards (JMGA, 1988). The REA, RT, SFT, and MS were evaluated at the cross section between the sixth and seventh ribs on the left side, and YE was calculated using CW, REA, RT, and SFT as the estimated percentage of salable meat ($YE, \% = 69.419 + 0.130 \times REA + 0.667 \times RT - 0.025 \times CW - 0.896 \times SFT$; JMGA, 1988). The REA was measured using the grid method. The RT was the distance between the pleural membranes and the lateral side of *M. latissimus dorsi* in the center of the rib. The SFT was the distance between the lateral side of *M. latissimus dorsi* and the surface of the carcass at a right angle from the line between the *M. iliocostalis* side and the surface of the carcass. The MS was ranked 1 to 12 according to the beef marbling standard (1 = poor; 12 = very abundant).

Image Analysis Traits

Digital images of the carcass cross section were taken between the sixth and seventh ribs by photographing equipment developed by Kuchida et al. (2001). This

equipment is composed of 2 parts: a dome with 1,000 white light-emitting diodes and a digital camera (2 megapixels, FinePix2900Z, Fujifilm, Tokyo, Japan). The distance between the camera and the surface of the carcass was fixed, and the lens was always parallel to the carcass cross section. As a result, area and length could be measured with high accuracy using the equipment.

To evaluate the characteristics of M-LONG and M-TRAP, muscle area (**MA**), fat area ratio (**FAR**), overall coarseness of marbling particles (**OCM**), and coarseness of maximum marbling particle (**MMC**) were calculated by image analysis. The OCM and MMC correspond to “Coarseness index 2 (5)” and “Coarseness index 4 (5)” reported by Kuchida et al. (2002), and can quantify the degree of coarseness of marbling particles. The MS is comprehensive, and there are some differences in coarseness of marbling within the same grade. In general, rough marbling particles are not preferred by buyers. A flowchart of the image analysis traits is illustrated in Figure 1, and details of these traits are as follows.

First, to specify the muscle to be analyzed, a border line (line width is 1 pixel) of the muscle was semiautomatically drawn and manually corrected using an image analysis program developed by Kuchida et al. (1997; Figure 1a). Next, the following procedures were used to calculate each image analysis trait:

FAR: M-LONG and M-TRAP with a border line (Figure 1a) were binarized as lean and fat using the image analysis program. The FAR was calculated by dividing all pixels of the fat image (Figure 1b) by those of M-LONG or M-TRAP;

OCM: The binarized image (Figure 1b) was thinned with 5 rounds (Figure 1c), and the hairline was removed (Figure 1d) using the image analysis program, to pick up rough marbling particles. The OCM was calculated by dividing all pixels of fat after thinning and removing the hairline (Figure 1d) by all pixels of the fat image (Figure 1b). A high OCM value indicates a muscle with many rough marbling particles; and

MMC: This trait was calculated by dividing the pixels of the largest marbling particle in the fat image after thinning and removing the hairline (Figure 1d) by all pixels of the fat image (Figure 1b). An extremely large marbling particle is not usually preferred, and the OCM is undetectable. A high MMC value indicates the existence of extremely large marbling particle(s) in the muscle.

Statistical Analysis

Genetic parameters were estimated for 6 carcass traits (CW, REA, RT, SFT, YE, and MS), as well as 4 image analysis traits in M-LONG and M-TRAP (MA, FAR, OCM, and MMC). Components of variance and

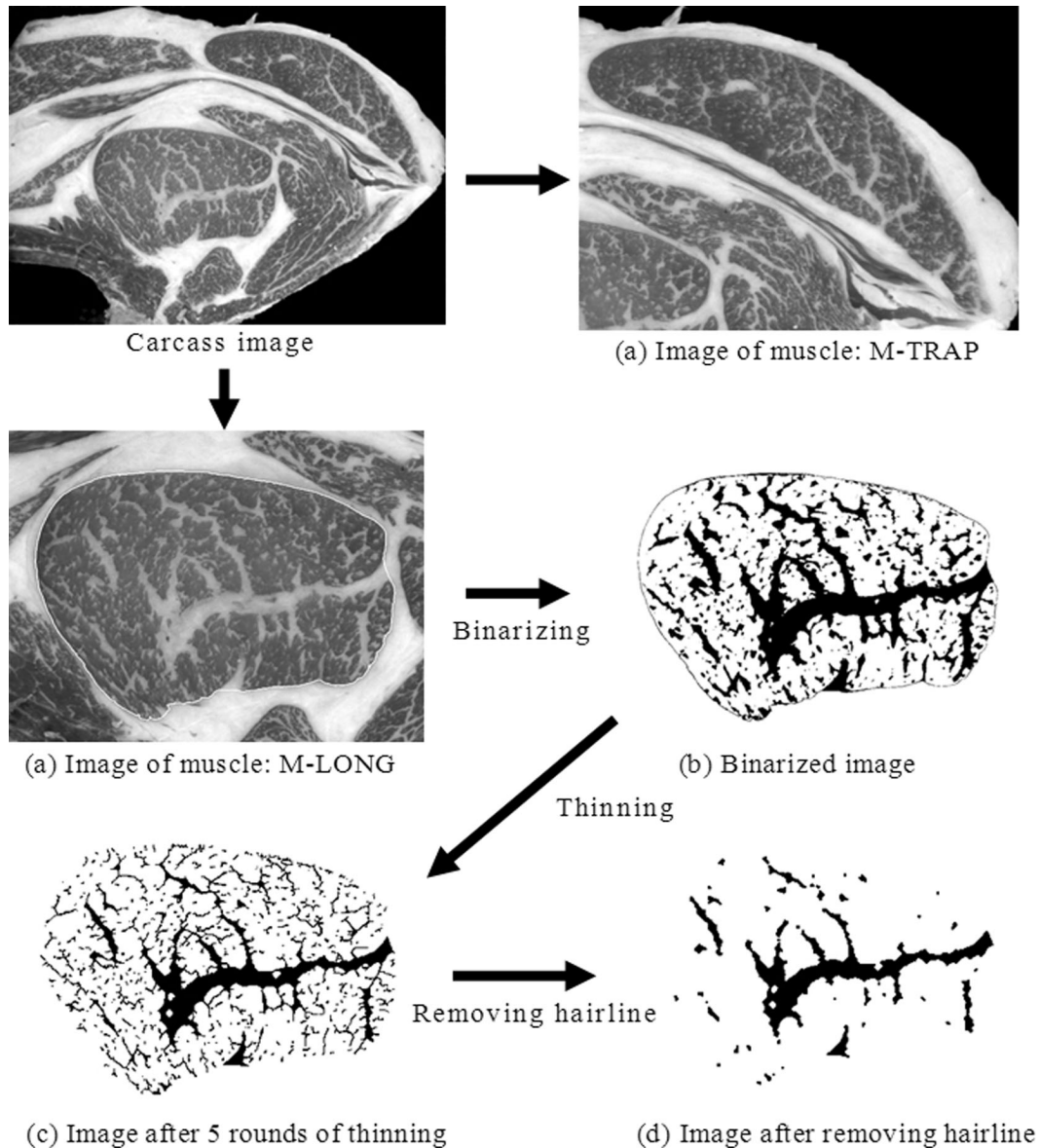


Figure 1. Detailed flow of image analysis to calculate coarseness of marbling particles. M-LONG = *M. longissimus thoracis* and M-TRAP = *M. trapezius*.

heritability estimates for these traits were computed with a single-trait animal model. Genetic and phenotypic correlations among these traits were estimated using bivariate animal models for carcass traits and image analysis traits in M-LONG, carcass traits and image analysis traits in M-TRAP, and image analysis traits in M-LONG and M-TRAP. Computations were conducted using the AIREMLF90 program (Misztal et al., 2002). A total of 10,889 pedigree records were traced back 3 generations. Unknown parents groups, which were based on the sex of unknown parents and the birth year of the animal, and the inbreeding coefficient of the animal were considered. The inbreeding coefficient was considered because although the average inbreeding coefficient in the current study was $1.1 \pm 2.1\%$, which was lower than the $21.7 \pm 4.41\%$ and $6.8 \pm 5.05\%$ reported by Shojo et al. (2006) for Japanese Black cattle

in Hyogo and Tottori prefectures, a high inbreeding coefficient (more than 10%; the maximum was 28.1%) was recognized in several animals. The animal model used in this analysis was

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{a} + \mathbf{W}\mathbf{f} + \mathbf{e},$$

where \mathbf{y} is the vector of records, $\boldsymbol{\beta}$ is the vector of fixed effects (87 subclasses for the dates at carcass market, 12 subclasses for slaughter age in months), \mathbf{a} is the vector of random additive genetic effect, \mathbf{f} is the vector of random fattening farm effect, and \mathbf{e} is the vector of residual effect. The \mathbf{X} , \mathbf{Z} , and \mathbf{W} denote the incidence matrices relating \mathbf{y} to $\boldsymbol{\beta}$, \mathbf{a} , and \mathbf{f} . The size of most herds in this study was small. In this case, Oikawa and Sato (1996, 1997) reported that a model with random herd effect is more advantageous than a model with a fixed

Table 1. Summary of basic statistics for slaughter age, inbreeding coefficient, and carcass and image analysis traits in Japanese Black steers (n = 2,925)

Trait	Mean	SD	Minimum	Maximum
Slaughter age, mo	29.6	1.8	24.6	37.1
Inbreeding coefficient, %	1.1	2.1	0.0	28.1
Carcass trait				
Carcass weight, kg	445.0	48.0	257.0	609.0
Ribeye area (REA), cm ²	56.8	7.8	31.0	88.0
Rib thickness (RT), cm	7.6	0.9	4.6	11.0
Subcutaneous fat thickness (SFT), cm	2.3	0.7	0.6	5.8
Yield estimate (YE), %	74.2	1.3	69.3	78.4
Beef marbling score (MS), 1 to 12	5.5	2.4	2.0	12.0
Image analysis trait				
<i>M. longissimus thoracis</i> (M-LONG)				
Muscle area (MA), cm ²	52.3	7.2	29.2	80.0
Fat area ratio (FAR), %	39.3	7.9	14.2	64.5
Overall coarseness of marbling particle (OCM)	19.6	5.0	4.9	39.6
Coarseness of maximum marbling particle (MMC)	4.8	2.7	0.7	26.6
<i>M. trapezius</i> (M-TRAP)				
Muscle area (MA), cm ²	46.6	8.4	18.9	84.1
Fat area ratio (FAR), %	36.3	7.5	15.1	60.3
Overall coarseness of marbling particle (OCM)	18.9	4.5	3.2	35.8
Coarseness of maximum marbling particle (MMC)	5.4	2.4	0.8	21.3

herd effect. Hence, fattening farm effect was treated as a random effect.

RESULTS AND DISCUSSION

Descriptive statistics of the data set are given in Table 1. Means and SD for FAR for M-LONG and M-TRAP in image analysis traits were $39.3 \pm 7.9\%$ and $36.3 \pm 7.5\%$, respectively. Generally, intramuscular fat of Japanese Black cattle is larger than that of other breeds. For example, the proportion of marbling flecks areas in ribeye (i.e., it corresponds to FAR for M-LONG) were reported to be $6.3 \pm 2.2\%$ by Yang et al. (2006) for German Holstein and Charolais crossbreed cattle at the age of 18 mo.

Variance of fattening farms, additive genetic variance, residual variance, proportion of phenotypic variance due to fattening farm variance, and heritability estimates (\pm SE) for carcass and image analysis traits are shown in Table 2.

Heritability estimates (\pm SE) for carcass traits were moderate to high in CW, REA, RT, SFT, YE, and MS (0.37 ± 0.05 , 0.43 ± 0.06 , 0.39 ± 0.05 , 0.22 ± 0.04 , 0.38 ± 0.06 , and 0.59 ± 0.06 , respectively). Heritability estimates for CW corresponded with 0.45 and 0.38 reported by Shojo et al. (2006) for Japanese Black cattle in Hyogo and Tottori prefectures, Japan, and 0.37 by Hirooka et al. (1996) for Japanese Brown cattle. However, the estimate for CW was lower than 0.49 by Splan et al. (2002) for crossbred cattle and 0.55 by Riley et al. (2002) for Brahman cattle. Heritability estimates for REA were similar to 0.44 by Riley et al. (2002), whereas the estimate for REA was little lower than those (0.48 to 0.61) in the literature for Japanese Black cattle (Kawada et al., 2003; Shojo et al., 2006) and that by Splan et al. (2002) for crossbred cattle (0.58). Heritability esti-

mates for MS corresponded with those by Kawada et al. (2003) and Shojo et al. (2006) for Japanese Black cattle (0.49 to 0.66), while they were higher than 0.40 by Hirooka et al. (1996) for Japanese Brown cattle, 0.35 by Splan et al. (2002) for crossbred cattle and 0.44 by Riley et al. (2002) for Brahman cattle. Though there are differences in breed, number of records, and effects in model, MS for Japanese Black cattle is highly heritable compared with that for other breeds.

In M-LONG, heritability estimates (\pm SE) of MA, FAR, OCM, and MMC for image analysis traits were 0.46 ± 0.06 , 0.59 ± 0.06 , 0.47 ± 0.06 , and 0.20 ± 0.05 . In M-TRAP, they were 0.47 ± 0.06 , 0.57 ± 0.07 , 0.49 ± 0.07 , and 0.13 ± 0.04 , respectively. Contrary to heritability estimates for image analysis traits, Osawa et al. (2004b) reported that heritability estimates for the ribeye in Japanese Black cattle shipped between April 2000 and March 2002 to the same market as the current study were 0.57, 0.34 and 0.09 for FAR, OCM, and MMC, respectively. Although estimates for OCM and MMC were higher than those by Osawa et al. (2004b), FAR showed a similar tendency. Moreover, Osawa et al. (2004a) reported the following heritability estimates for MA and FAR in M-LONG and M-TRAP for 404 Japanese Black steers in progeny testing slaughtered at 21 mo of age: (0.59 and 0.61 for M-LONG, 0.55 and 0.62 for M-TRAP, respectively.) The estimate for FAR corresponded with that by Osawa et al. (2004a), but it was lower for MA. Although FAR in both muscles were highly heritable as with MS, MMC in both muscles showed low heritability. An extremely large marbling particle might be distributed in the muscle at random, and its appearance on the sixth and seventh rib would be incidental if some large marbling particles exist in the muscle.

Table 2. Variance of fattening farms (σ_f^2), additive genetic variance (σ_a^2), residual variance (σ_e^2), proportion of phenotypic variance due to fattening farm variance (Pf), and heritability estimates (h^2) for carcass and image analysis traits

Trait	σ_f^2	σ_a^2	σ_e^2	Pf	$h^2 \pm SE$
Carcass trait ¹					
CW	333.05	827.34	1,105.70	0.15	0.37 \pm 0.05
REA	4.55	27.12	31.34	0.07	0.43 \pm 0.06
RT	0.08	0.27	0.33	0.12	0.39 \pm 0.05
SFT	0.06	0.11	0.35	0.11	0.22 \pm 0.04
YE	0.17	0.67	0.91	0.09	0.38 \pm 0.06
MS	0.78	3.34	1.57	0.14	0.59 \pm 0.06
Image analysis trait ²					
M-LONG					
MA	3.66	25.20	25.84	0.07	0.46 \pm 0.06
FAR	8.02	32.84	14.72	0.14	0.59 \pm 0.06
OCM	1.87	12.08	11.86	0.07	0.47 \pm 0.06
MMC	0.22	1.53	5.75	0.03	0.20 \pm 0.05
M-TRAP					
MA	3.09	32.12	33.65	0.04	0.47 \pm 0.06
FAR	4.72	30.29	18.56	0.09	0.57 \pm 0.07
OCM	0.42	10.55	10.57	0.02	0.49 \pm 0.07
MMC	0.03	0.80	5.23	0.01	0.13 \pm 0.04

¹CW = carcass weight; REA = ribeye area; RT = rib thickness; SFT = subcutaneous fat thickness; YE = yield estimate; and MS = beef marbling score.

²M-LONG = *M. longissimus thoracis*; M-TRAP = *M. trapezius*; MA = muscle area; FAR = fat area ratio; OCM = overall coarseness of marbling particle; and MMC = coarseness of maximum marbling particle.

To investigate the influence of fattening farms for each trait, the variance ratios of the fattening farm variance to the phenotypic variance were compared. The results for CW (0.15), MS (0.14), RT (0.12), and SFT (0.11) in carcass traits and FAR for M-LONG (0.14) and M-TRAP (0.09) in image analysis traits were similar to those reported by Shojo et al. (2006) for Japanese Black cattle in Hyogo and Tottori prefectures, Japan (CW: 0.14 and 0.09, MS: 0.09 and 0.07, RT: 0.09 and 0.08, and SFT: 0.07 and 0.06), suggesting that these traits were strongly influenced by different environments: in this case, fattening farm.

Genetic and phenotypic correlations among carcass traits and image analysis traits are shown in Table 3. Genetic and phenotypic correlations between MS and FAR for M-TRAP were moderate to high (0.62 and 0.51), but those correlations between MS and FAR for M-LONG were very highly positive (0.97 and 0.92). The high correlations between MS and FAR in M-LONG may have been caused by the beef carcass grading system for MS in Japan, an evaluation method that focuses mainly on M-LONG using the Beef Marbling Standard based on the ratio of marbling of M-LONG (JMGA, 1988). Genetic correlations between MS and OCM for M-LONG and M-TRAP were low to moderate and positive (0.66 and 0.23, respectively). That is, emphasis on marbling could increase not only the marbling ratio in muscles but also undesirable rough marbling particles.

For M-LONG, genetic correlations of FAR, OCM, and MMC with SFT were low and negative (-0.21 , -0.11 , and -0.03 , respectively). Genetic correlations of these traits with SFT for M-TRAP also showed a similar tendency for M-LONG (-0.19 , -0.15 , and -0.28 , respec-

tively). Many literature estimates showed low to moderate positive genetic correlations of marbling with fat thickness. For example, the genetic correlation between marbling score and fat thickness were reported as 0.56 by Riley et al. (2002) for Brahman cattle and 0.26 by Pariacote et al. (1998) for American Shorthorn Beef Cattle. Moreover, genetic correlations between marbling score and fat thickness adjusted to age and weight end points were 0.34 and 0.35 (Ríos-Utrera et al., 2005) for purebred and composite steers, respectively, and 0.17 and 0.18 (Shanks et al., 2001) for Simmental and percentage Simmental cattle, respectively. However, Kawada et al. (2003) reported that genetic correlation between MS and SFT were low and negative in Japanese Black cattle (-0.24). Hirooka et al. (1996) reported a low and negative genetic correlation (-0.12) in Japanese Brown cattle. Therefore, the improvement of increasing marbling in muscles for Wagyu would not increase the subcutaneous fat thickness, indicating that those traits are genetically independent.

Genetic (phenotypic) correlations among image analysis traits between M-LONG and M-TRAP are shown in Table 4. These correlations between M-LONG and M-TRAP were moderate to high for MA (0.38), FAR (0.52), OCM (0.39), and MMC (0.60). The estimates for MA and FAR reported by Osawa et al. (2004a) were moderate and positive (0.35 and 0.39, respectively), similar to those of the current study. Genetic correlations of OCM and MMC with FAR for M-LONG were 0.69 and 0.29, respectively, and those for M-TRAP with FAR of M-LONG were 0.22 and -0.07 , respectively. These estimates corresponded with correlations of OCM and MMC with MS (Table 3). Thus, genetic relation-

Table 3. Genetic (phenotypic) correlations between carcass traits and image analysis traits in each muscle

Trait	Carcass trait ¹											
	CW		REA		RT		SFT		YE		MS	
Image analysis trait ²												
M-LONG												
MA	0.35	(0.45)	0.97	(0.91)	0.27	(0.33)	-0.18	(-0.10)	0.84	(0.70)	0.46	(0.43)
FAR	0.17	(0.15)	0.34	(0.37)	0.51	(0.27)	-0.21	(-0.02)	0.48	(0.34)	0.97	(0.92)
OCM	0.17	(0.28)	0.34	(0.34)	0.41	(0.34)	-0.11	(0.12)	0.41	(0.22)	0.66	(0.43)
MMC	0.33	(0.12)	0.29	(0.08)	0.33	(0.12)	-0.03	(0.07)	0.22	(0.02)	0.18	(0.01)
M-TRAP												
MA	0.34	(0.47)	0.38	(0.41)	0.49	(0.48)	0.06	(0.10)	0.32	(0.25)	0.41	(0.31)
FAR	0.28	(0.19)	0.21	(0.13)	0.49	(0.24)	-0.19	(0.09)	0.32	(0.07)	0.62	(0.51)
OCM	-0.11	(0.16)	-0.02	(0.01)	0.18	(0.26)	-0.15	(0.16)	0.16	(-0.04)	0.23	(0.17)
MMC	0.05	(0.08)	-0.16	(-0.02)	0.27	(0.14)	-0.28	(0.10)	0.09	(-0.04)	0.04	(0.04)

¹CW = carcass weight; REA = ribeye area; RT = rib thickness; SFT = subcutaneous fat thickness; YE = yield estimate; and MS = beef marbling score.

²M-LONG = *M. longissimus thoracis*; M-TRAP = *M. trapezius*; MA = muscle area; FAR = fat area ratio; OCM = overall coarseness of marbling particle; and MMC = coarseness of maximum marbling particle.

ships between degree of marbling in M-LONG and M-TRAP were not strong. If muscles other than M-LONG are improved, objective and detailed evaluation of these muscles may be necessary.

For both muscles, genetic correlations between OCM and MMC were high (M-LONG: 0.85 and M-TRAP: 0.93). This may be because both muscles include the largest marbling particle that represents the overall coarseness of the meat. Hence, MMC with lower heritability can be indirectly improved by selecting OCM.

The degree of marbling in M-LONG is an important factor economically. However, it is visually evaluated, and a more objective evaluation method is necessary. In addition, it may be desirable to grade muscles other than the ribeye because they also influence carcass prices. The image analysis traits for M-LONG and M-TRAP evaluated in the current study are more detailed and objective than the traditional beef carcass grading system and could potentially become an economically effective indicator. Additionally, the factors that heritability estimates of image analysis traits were moderate

to high, genetic relationships between marbling score and coarseness of marbling particles were undesirable, and genetic relationships between M-LONG and M-TRAP were not strong lead to the conclusion that both muscles need to be considered separately for improvement. Thus, image analysis in various muscles for carcass evaluation could lead to more useful and accurate genetic evaluation.

The estimates of genetic parameters found in this study could be useful in the design of breeding programs for the improvement of various muscles in Japanese Black cattle. Heritability estimates of most image analysis traits for M-LONG and M-TRAP in Japanese Black cattle were moderate to high, indicating that objective evaluations with image analysis of carcass cross section could be useful as an alternative to the current subjective grading system. The improvement with emphasis on marbling would lead to the rough marbling particles. Moderate genetic correlations between M-LONG and M-TRAP were estimated using image analysis. Therefore, the M-TRAP should also be evaluated and included

Table 4. Genetic (above diagonal) and phenotypic (below diagonal) correlations among image analysis traits¹ in each muscle

Trait	M-LONG				M-TRAP			
	MA	FAR	OCM	MMC	MA	FAR	OCM	MMC
M-LONG								
MA		0.36	0.39	0.24	0.38	0.16	-0.08	-0.26
FAR	0.35		0.69	0.29	0.32	0.52	0.22	-0.07
OCM	0.36	0.50		0.85	0.31	0.30	0.39	0.21
MMC	0.08	0.05	0.61		0.26	0.18	0.57	0.60
M-TRAP								
MA	0.41	0.26	0.22	0.03		0.45	0.26	0.34
FAR	0.08	0.50	0.15	0.00	0.39		0.69	0.50
OCM	0.00	0.19	0.31	0.18	0.31	0.43		0.93
MMC	-0.03	0.05	0.18	0.12	0.11	0.11	0.65	

¹M-LONG = *M. longissimus thoracis*; M-TRAP = *M. trapezius*; MA = muscle area; FAR = fat area ratio; OCM = overall coarseness of marbling particle; and MMC = coarseness of maximum marbling particle.

in the breeding program for meat quality for more efficient improvements in the future.

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