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Comparison of genetic gains per year for carcass traits among breeding programs in the Japanese Brown and the Japanese Black cattle[1]

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ABSTRACT: The breeding program for beef cattle in Japan has changed dramatically over 4 decades. Visual judging was done initially, but progeny testing in test stations began in 1968. In the 1980s, the genetic evaluation program using field records, so-called on-farm progeny testing, was first adopted in Oita, Hyogo, and Kumamoto prefectures. In this study, genetic trends for carcass traits in these 3 Wagyu populations were estimated, and genetic gains per year were compared among the 3 different beef cattle breeding programs. The field carcass records used were collected between 1988 and 2003. The traits analyzed were carcass weight, LM area, rib thickness, s.c. fat thickness, and beef marbling standard number. The average breeding values of reproducing dams born the same year were used to estimate the genetic trends for the carcass traits. For comparison of the 3 breeding programs, birth years of the dams were divided into 3 periods reflecting each program. Positive genetic trends for beef marbling standard number were clearly shown in all populations. The genetic gains per year for all carcass traits were significantly enhanced by adopting the on-farm progeny testing program. These results indicate that the on-farm progeny testing program with BLUP is a very powerful approach for genetic improvement of carcass traits in Japanese Wagyu beef cattle.

Key words: beef cattle, carcass trait, genetic trend, Japanese Black, Japanese Brown

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INTRODUCTION

In the past, there were many small and horned cattle used for plowing in Japan. One hundred years ago, foreign breeds were imported from Europe and crossed with the native cattle only from 1900 to 1908. In order to standardize the conformation and quality, a registration system was organized in each prefecture around 1918. Finally, cattle raised in various prefectures were classified into 4 breeds, the Japanese Black, the Japanese Brown, the Japanese Shorthorn, and the Japanese Polled, from 1948 to 1957. These 4 breeds comprise the so-called Wagyu.

The Wagyu had been used as draft animals initially but became increasingly important as beef animals since around 1960. Visual judging was adopted initially as a means for improvement of the cattle (Habu, 1973); then performance and progeny testing in test stations for meat productivity were established in 1968.

After the BLUP method (Henderson, 1973, 1974) was proposed, a genetic evaluation program using carcass records collected at carcass markets was investigated, the so-called on-farm progeny testing program (Sasaki et al., 1976; Sasaki and Iwaisaki, 1980; Sasaki and Sasae, 1988). The effectiveness of the on-farm program was clarified for small-scale conditions of fattening farms by Sasaki (1992). In collaboration with these studies, the on-farm program was first adopted for the Japanese Black populations in Oita (in 1983) and Hyogo (in 1987) prefectures, and for the Japanese Brown population in Kumamoto prefecture (in 1987).

The breeding program for beef cattle in Japan has changed dramatically and become more sophisticated during the past 4 decades. The objectives of this study were to estimate genetic trends for carcass traits in the Japanese Black and the Japanese Brown populations,

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Table 1. Results of significance testing for the fattening period and the slaughter age as covariates included in the mathematical models for 5 carcass traits in the Japanese Brown (Kumamoto prefecture) and the Japanese Black (Oita and Hyogo prefectures)

	Carcass trait[1]				
Covariate effect	CWT	LMA	RT	SFT	BMS
Japanese Brown (Kumamoto)					
Fattening period: linear	***	***	***	***	***
Fattening period: quadratic	NS[2]	***	***	***	NS
Slaughter age: linear	***	***	***	***	***
Slaughter age: quadratic	***	***	***	***	NS
Japanese Black (Oita)					
Fattening period: linear	***	***	***	***	***
Fattening period: quadratic	***	***	***	*	*
Slaughter age: linear	***	*	***	**	***
Slaughter age: quadratic	***	*	***	**	***
Japanese Black (Hyogo)					
Fattening period: linear	***	***	***	***	***
Fattening period: quadratic	NS	NS	NS	NS	NS
Slaughter age: linear	***	***	***	***	*
Slaughter age: quadratic	***	***	***	NS	***

[1]CWT = carcass weight, LMA = LM area, RT = rib thickness, SFT = s.c. fat thickness, and BMS = beef marbling standard number.
[2]NS = not significant.
*$P < 0.05$. **$P < 0.01$. ***$P < 0.001$.

and to compare genetic gains per year among the 3 different breeding programs that were based on visual judging, progeny testing in test stations, or on-farm progeny testing with BLUP.

MATERIALS AND METHODS

Genetic trends and gains were estimated from carcass records of Japanese Brown fattened in Kumamoto and Japanese Black steers and heifers, fattened in Oita and Hyogo prefectures. The fattened animals were shipped to various carcass markets from 1988 to 2003, where they were slaughtered and their carcasses evaluated. The recording systems in these prefectures had collected carcass records for a few years before 1988, but they were not used for this analysis because the Japanese Meat Grading System was completely changed in 1988 (JMGA, 1988). The data were edited to connect across subclasses such that each market-year subclass had 50 or more animals and each farm had 10 or more animals for the two Japanese Black populations (in Oita and Hyogo). For the Japanese Brown population (in Kumamoto), each market-year subclass had 100 or more animals and each farm had 20 or more animals. The reason each subclass had more Japanese Brown animals is that there was less connection among subclasses. The final numbers of animals were 52,475, 48,045, and 26,397 for Kumamoto, Oita, and Hyogo, respectively. There were 49, 89, and 39 market-year subclasses; 205, 332, and 165 farms; and 227, 228, and 112 sires for Kumamoto, Oita, and Hyogo, respectively.

The carcass records used were carcass weight (**CWT**), LM area (**LMA**), rib thickness (**RT**), s.c. fat thickness (**SFT**), and beef marbling standard number (**BMS**, 1 to 12 classes). The LMA, RT, SFT, and BMS were measured at the 6th to 7th rib section. The BMS was classified using the plastic-made Beef Marbling Standards with numbers 1 to 12; number 12 was the most highly marbled (JMGA, 1988).

Data were analyzed by the REML method using the MTDFREML programs (Boldman et al., 1995), and genetic and environmental variances were estimated within a prefecture. The BLUP option in the programs using the estimated variance components was chosen to predict the breeding values of animals with a single trait model. Sex, market-year, and farm were considered fixed effects. Fattening period and slaughter age were also considered as up to quadratic covariates. The fattening period denotes the period from the start of fattening to shipping to market for each animal. Among these fixed effects, only significant effects were included in the mathematical model for each analysis. Significance testing was done with the GLMTEST program (Moriya et al., 1998). Results of significance testing are shown in Table 1 for the covariates. The other fixed effects were all significant ($P < 0.001$). Random effects included additive genetic effect of the individuals; that is, the animal model was adopted. The equation for the linear model was

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

in which $\mathbf{y}$ is the vector of the records for each carcass trait; β is the vector of the fixed effects; and $\mathbf{a}$ is the vector of the random individual additive genetic effects with incidence matrices $\mathbf{X}$ and $\mathbf{Z}$, and $\mathbf{e}$ is the vector of the environmental effect. Local convergence in the

Table 2. Averages of the accuracy for the predicted breeding values of dams

Population	Period[2]	No. of dams	Dams with records, %	Carcass trait[1]				
				CWT	LMA	RT	SFT	BMS
Japanese Brown (Kumamoto)	P_I	2,501	0.2	0.38	0.37	0.37	0.39	0.40
	P_{II}	31,762	54.4	0.60	0.59	0.58	0.61	0.62
	P_{III}	12,536	95.8	0.69	0.68	0.68	0.71	0.71
Japanese Black (Oita)	P_I	2,656	0.0	0.20	0.21	0.19	0.22	0.22
	P_{II}	16,617	39.1	0.49	0.50	0.48	0.51	0.51
	P_{III}	22,466	89.9	0.66	0.66	0.65	0.67	0.68
Japanese Black (Hyogo)	P_I	1,482	0.2	0.28	0.29	0.27	0.28	0.30
	P_{II}	15,572	54.9	0.56	0.57	0.56	0.56	0.59
	P_{III}	10,186	90.0	0.67	0.68	0.67	0.68	0.70

[1]CWT = carcass weight, LMA = LM area, RT = rib thickness, SFT = s.c. fat thickness, BMS = beef marbling standard number (classes 1 to 12).

[2]P_I, P_{II}, and P_{III} are the periods of visual judging, test station, and on-farm programs, respectively.

MTDFREML programs was declared when the variance of –2 times the log likelihood in the simplex was less than 10^{-8}. Restarts were done to increase the chance of finding a global maximum rather than a local maximum; convergence was declared when the (co)variance estimates did not change after the 15th decimal point under the threshold value.

The genetic trend was estimated according to the approach applied by Blair and Pollak (1984). In each of our 3 populations, pedigree of the animals was traced back to the ancestors born in the 1950s. The total numbers of animals included in the analyses were 114,098, 91,027, and 56,202 for the cases of Kumamoto, Oita, and Hyogo, respectively. The average breeding value of reproducing dams born the same year was considered to represent the genetic level of a particular year. The genetic gain per year within a given period was estimated by linear regression of the genetic level on the year of birth of dams.

The beef cattle breeding systems historically adopted in Japan have been changed as follows. Initially, visual judging based on ideal type for each breed was adopted with the belief that animals with good visual quality (i.e., soft and elastic hide, fine and soft hair, fine textured horn, and clean-cut face) would produce high quality (marbled) beef. In 1968, a central testing system in test stations was adopted within each prefecture for both performance and progeny testing of the young bulls. The outline of this system is as follows: 1) Candidate bulls produced from planned matings using superior sires and dams based on visual judging were gathered and performance-tested in a test station (112 d after weaning); 2) Based on their growing ability, selected young bulls were test-mated with ordinary cows, and their progeny (8 to 10 animals) was performance-tested (364 d); 3) Bulls were selected based on their carcass records. Initially, the primary concern in beef markets was carcass quality traits for the Japanese Black and growth traits for the Japanese Brown. In the late 1980s, the 3 prefectures (Oita, Hyogo, and Kumamoto) began on-farm progeny testing based on BLUP within each prefecture by establishing the recoding systems that collect carcass records from carcass markets and pedigree records from registry associations. Under this program, all sires and dams of the steers and heifers shipped to the carcass markets were simultaneously evaluated. Therefore, planned matings using the superior sires and dams based on predicted breeding values became available for the production of candidate bulls. Furthermore, on-farm culling for reproducing dams based on breeding values also became available. Now on-farm progeny testing has become popular and has been adopted in many prefectures. At present, the primary concern changed to carcass quality for both Wagyu breeds.

For comparison of the 3 breeding programs, birth years of the dams were divided into 3 periods ($\mathbf{P_I}$, $\mathbf{P_{II}}$, and $\mathbf{P_{III}}$) that reflected the programs based on visual judging, progeny testing in test stations, and on-farm progeny testing with BLUP, respectively. As progeny testing in test stations began throughout Japan in 1968, P_I is before 1968 for all 3 prefectures. On the other hand, the on-farm progeny testing began in 1983 in Oita and in 1987 in Kumamoto and Hyogo. Thus, in Oita, P_{II} was between 1968 and 1982, and P_{III} was after 1982. In Kumamoto and Hyogo, P_{II} was between 1968 and 1986, and P_{III} was after 1986. The number of reproducing dams, percentage of the dams with records, and averages of accuracies for predicted breeding values of dams that were used for estimation of genetic gains in the 3 periods are shown in Table 2.

RESULTS

Characteristics of Carcass Traits

Mathematical means for carcass traits, the fattening period, and the slaughter age are shown in Table 3. Japanese Black cattle have been well known as highly marbled beef in Japan. Japanese Black showed greater BMS than Japanese Brown, but with a longer fattening period and older slaughter age ($P < 0.001$). There also were variations between the 2 Japanese Black populations. The slaughter ages were approximately 29.5 and

Table 3. Averages and SD for carcass traits and periods at the slaughter age with the fattening period in the Japanese Brown (Kumamoto) and in the Japanese Black (Oita and Hyogo prefectures)

	Japanese Brown				Japanese Black					
	Kumamoto				Oita				Hyogo	
	Steer		Heifer		Steer		Heifer		Steer	
Item	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
No. of records	37,866		14,609		36,618		11,427		26,397	
Carcass weight, kg	441.5	43.6	404.9	40.5	431.9	45.0	382.2	43.2	382.1	39.9
LM area, cm^2	49.2	6.0	47.4	5.5	49.6	7.2	48.3	7.2	49.0	6.9
Rib thickness, mm	70.7	7.6	69.7	7.4	70.9	7.9	68.5	8.3	67.6	7.6
S.c. fat thickness, mm	24.7	8.0	27.8	8.7	27.2	9.3	30.6	9.7	20.8	6.3
BMS[1]	3.4	1.3	3.2	1.2	5.7	2.2	4.9	2.0	6.4	2.2
Fattening period, d	446.4	46.6	463.2	51.2	603.6	52.8	596.0	61.0	693.4	54.7
Slaughter age, d	737.8	50.5	769.1	53.3	879.7	57.4	890.3	64.5	965.9	55.3

[1]Beef marbling standard number (1 to 12).

32.2 mo in Oita and Hyogo, respectively. The Japanese Black steers in Hyogo were characterized by thinner SFT and smaller CWT than those in Oita ($P < 0.001$). The growth performance of the steers in Oita was superior to Hyogo. Unlike Japanese Black, Japanese Brown cattle are well known for growth performance. Their CWT was heavier but with a shorter fattening period than the Japanese Black cattle ($P < 0.001$), as shown in Table 3. Estimates of heritability for the 5 carcass traits analyzed are shown in Table 4. Variations in heritabilities were also recognized among the 3 populations, but moderate to high heritabilities were obtained for all carcass traits.

Genetic Trends

Genetic trends estimated by averaging predicted breeding values of reproducing dams born the same year are shown in Figure 1 for the 5 carcass traits in Wagyu. The most prominent feature in genetic trends was recognized in BMS, where all 3 prefectures showed a positive trend in the progression of averaged breeding values of the reproducing dams. In the Japanese Black (both in Oita and Hyogo), positive genetic trends for BMS began in approximately 1978. In Japanese Brown, the positive genetic trend began in approximately 1988.

A positive trend for LMA was clearly apparent only in Oita. The clear trend for LMA was similar to the trend for BMS. In CWT and RT, the genetic trends became positive after beginning on-farm progeny testing, except for CWT in Hyogo. Surprisingly, a negative trend for CWT was apparent in Hyogo. Hyogo is also notable in a negative (i.e., desirable) trend for SFT; it improved just after beginning progeny testing in test stations in 1968.

Table 4. Estimates of heritability for carcass traits

	Carcass trait[1]				
Population	CWT	LMA	RT	SFT	BMS
Japanese Brown (Kumamoto)	0.44	0.44	0.42	0.57	0.56
Japanese Black (Oita)	0.46	0.48	0.40	0.53	0.56
Japanese Black (Hyogo)	0.50	0.54	0.47	0.50	0.64

[1]CWT = carcass weight, LMA = LM area, RT = rib thickness, SFT = s.c. fat thickness, and BMS = beef marbling standard number.

Genetic Gains per Year

Genetic gains per year during periods P_I, P_{II}, and P_{III} were estimated as shown in Table 5. Genetic gain per year during the period of visual judging (P_I) was small and not significantly different from zero for all traits analyzed in all 3 prefectures with few exceptions.

Genetic gains in periods after beginning progeny testing in test stations (P_{II}) were generally significantly different from zero for most traits in the 3 prefectures but their directions were not desirable in many cases (e.g., CWT in Hyogo, RT in Oita, SFT in Kumamoto and Oita). Both BMS and LMA were improved in the desired direction in all prefectures.

After adopting on-farm progeny testing (P_{III}), genetic changes of all carcass traits were significant and in desirable directions, except for CWT, RT, and SFT in Hyogo.

Comparison of Genetic Gains Among Periods

Comparison among the 3 periods (i.e., among P_I, P_{II}, and P_{III}) indicates that genetic improvement of all carcass traits was significantly enhanced in P_{III} in all 3 prefectures except for SFT in Hyogo, which had already improved greatly during P_{II} (Table 5; Figure 1).

DISCUSSION

Originally, Japanese Black and Japanese Brown cattle were improved and established from the same native cattle in Japan. Now, however, meat productivity is quite different between the Japanese Brown and Black cattle as well as between the 2 Japanese Black popula-

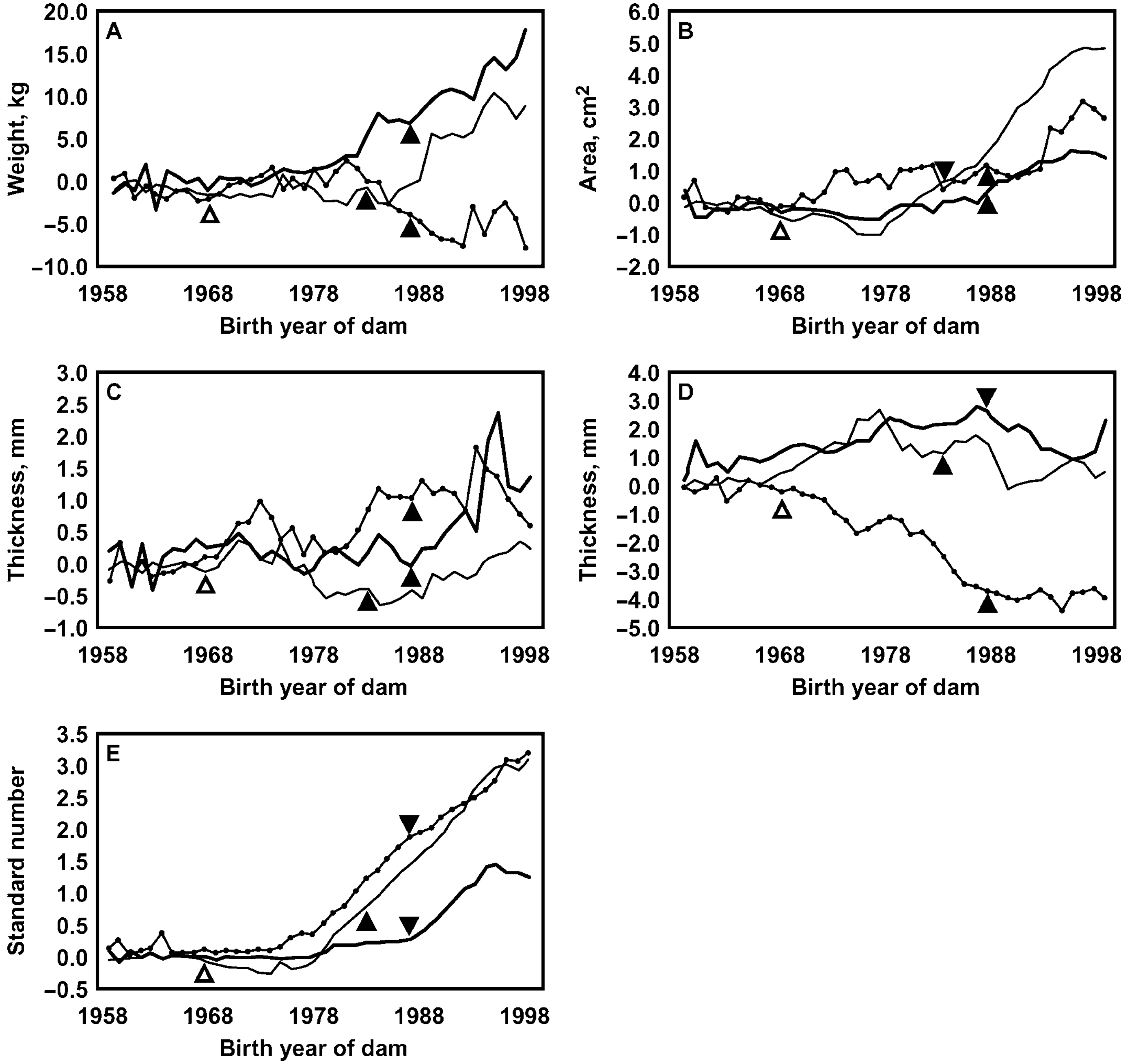

Figure 1. Genetic trends for carcass weight (A), LM area (B), rib thickness (C), s.c. fat thickness (D), and beef marbling standard number (E) by birth year of dams for the Japanese Brown in Kumamoto (thick line), and for the Japanese Black in Oita (thin line) and in Hyogo (thin line with dot) prefectures. The beginning of the progeny testing program in test stations is indicated by △. The beginning of the on-farm progeny testing program based on BLUP is indicated by ▲.

tions as shown in Table 3. During establishment of the Wagyu breeds, the Japanese Black were affected differently from prefecture to prefecture by different foreign breeds (e.g., the Swiss Brown, the Aberdeen Angus, the Devon, etc.). Japanese Brown seemed to be affected more by Simmental when foreign breeds were imported and crossed with the native cattle 100 years ago. The differences in characteristics of their performance among prefectures, and even in the Japanese Black, may reflect which foreign breeds they were crossed with and the breeding programs applied in their subsequent breeding history.

Visual judging had been initially adopted as a means of improving Wagyu. This might be the same as in other countries (Harrison et al., 1940; Yapp, 1959; Beeson et al., 1970), but the following point was quite unique in Wagyu. Visual quality traits were used in indirect selection for meat quality traits including beef marbling (Takahashi, 1985). Our results clearly show the ineffectiveness of the indirect selection applied in P_I (Table

Table 5. Genetic gains per year estimated as the regression coefficient of the predicted breeding values of dams born the same year for 5 carcass traits in the Japanese Brown and the Japanese Black

Period[2]	Carcass trait[1] CWT, kg/yr	LMA, cm^2/yr	RT, mm/yr	SFT, mm/yr	BMS, class/yr
	Japanese Brown (Kumamoto)				
P_I	−0.025 ± 0.066^x	0.026 ± 0.026^x	**0.086** ± 0.031^x	0.031 ± 0.048^x	0.000 ± 0.007^x
P_{II}	**0.480** ± 0.013^y	**0.027** ± 0.005^x	−0.002 ± 0.005^y	**0.083** ± 0.005^x	**0.019** ± 0.005^y
P_{III}	**0.747** ± 0.036^z	**0.125** ± 0.005^y	**0.184** ± 0.006^z	**−0.159** ± 0.009^y	**0.131** ± 0.005^z
	Japanese Black (Oita)				
P_I	−0.145 ± 0.078^x	**−0.036** ± 0.016^x	0.000 ± 0.015^x	0.014 ± 0.028^x	0.000 ± 0.006^x
P_{II}	−0.048 ± 0.026^x	**0.059** ± 0.007^x	**−0.057** ± 0.007^y	**0.028** ± 0.007^x	**0.058** ± 0.007^y
P_{III}	**0.980** ± 0.024^y	**0.347** ± 0.007^y	**0.061** ± 0.007^z	**−0.087** ± 0.008^y	**0.176** ± 0.008^z
	Japanese Black (Hyogo)				
P_I	−0.095 ± 0.067^x	−0.056 ± 0.036^x	0.018 ± 0.032^{xy}	0.000 ± 0.031^x	−0.011 ± 0.012^x
P_{II}	**−0.055** ± 0.019^x	**0.034** ± 0.004^y	**0.031** ± 0.004^x	**−0.179** ± 0.004^y	**0.102** ± 0.002^y
P_{III}	0.040 ± 0.040^y	**0.218** ± 0.009^z	0.005 ± 0.008^y	−0.012 ± 0.007^x	**0.122** ± 0.003^z

x–z Within a column and population, regression coefficients without a common superscript letter differ ($P < 0.05$).

[1] CWT = carcass weight, LMA = LM area, RT = rib thickness, SFT = s.c. fat thickness, and BMS = beef marbling standard number (classes 1 to 12). Bold denotes that the regression coefficient is different from zero ($P < 0.05$).

[2] P_I, P_{II}, and P_{III} are the periods of visual judging, test station, and on-farm programs, respectively.

5). Iwaisaki et al. (1984) also investigated genetic correlations between these visual quality traits and carcass traits, and clarified that they are generally very low and negligible.

Aiming at improvement of carcass traits in Wagyu, the progeny testing program was then proposed by breeders, but a question remained. Which would be the better testing system, in test stations or an on-farm system? In 1965, only 4.6% of slaughtered cattle carcasses were evaluated, and carcass records could not be collected at that time. Then the central testing system in test stations was adopted for performance and progeny testing in 1968, but the system was adopted within each prefecture. Therefore, numbers of progeny-tested bulls in each prefecture were very small, and the total number of bulls progeny-tested in 1992 was 78 at all 25 test stations in Japan (Sasaki, 2001).

Progeny testing in test stations improved only a few traits (Table 5). Among them, BMS in 2 Japanese Black populations and CWT in the Japanese Brown were most notable. Interestingly, positive trends for BMS in Japanese Black and CWT in Japanese Brown began simultaneously around 1978 (Figure 1), which was about 10 yr after beginning performance and progeny testing in test stations. The difference in breeding objectives applied in P_{II} for each breed would result in positive trends appearing in different traits (BMS in Japanese Black and CWT in Japanese Brown). Beef marbling in Japanese Brown would be recognized as an important objective in the late 1970s. For BMS in Japanese Brown, a small genetic gain was seen during the 1980s (Figure 1).

In Hyogo prefecture, a negative but desirable trend was clearly seen in SFT during P_{II}. In addition, a negative (i.e., undesirable) trend was recognized in CWT. Hyogo prefecture is famous for the production of highly marbled beef with thin s.c. fat, so-called Kobe beef. It is important to note that carcass weight should be smaller than 450 kg to be certified as Kobe brand beef at the carcass market in Kobe city (KBCPC, 1984). This rule might affect the negative genetic trend for CWT in Hyogo. Considering the moderate to high heritabilities for these traits in the 2 Japanese Black populations (Oita and Hyogo, Table 4), the difference of the trends for SFT and CWT between these populations would reflect the difference of the selection criteria applied in each prefecture.

Around 1980, more than 40% of animals slaughtered at abattoirs were graded, and carcass records become available and could be used for their sire and dam evaluations. Then the possibility of on-farm (field) progeny testing for carcass traits of beef cattle was proposed and its usefulness was clarified for small-scale conditions in Japan (Sasaki et al., 1986; Sasaki and Sasae, 1988; Sasaki, 1992). The on-farm progeny testing program based on BLUP began in 1983 in Oita and in 1987 in Kumamoto and Hyogo.

The genetic gains achieved during P_{III} (Figure 1 and Table 5) suggest that on-farm progeny testing would effectively enhance the genetic improvement of all carcass traits of Wagyu populations when it is applied. Because progeny testing in test stations was continued after on-farm progeny testing began, genetic improvement in P_{III} may reflect the summation of genetic improvements achieved by both programs. Even considering that point, genetic gains achieved in P_{III} are generally much larger than those achieved in P_{II}. In addition, the realized directions for genetic change in P_{III} are generally preferable to P_{II}.

The percentages of reproducing dams with records (i.e., their steers or heifers) are above 90% in P_{III} but less than 50% in P_{II} (Table 2), suggesting that some breeding dams were included in the dams in P_{II}. This might lead to an upward bias in predicted breeding values of dams in P_{II} because these breeding dams would be expected to be superior to average dams. Assuming the presence of an upward bias, our results for the differences of genetic gains between P_{II} and P_{III} in Table 5 could be downwardly biased. If we could get an unbiased result for P_{II}, differences in genetic gains between P_{II} and P_{III} could be larger than our current results.

Only a few estimates of genetic trends for carcass traits of beef cattle have been reported so far (Wilson et al., 1993; Wheeler et al., 1996; MacNeil et al., 1999). In dairy cattle, there were several studies reporting that genetic gain per year for milk production and milk fat production were enhanced by adopting BLUP evaluation (Powell and Wiggans, 1991; Meinert et al., 1992; Nizamani and Berger, 1996). The desirable genetic improvements clearly shown in P_{III} in the Wagyu would therefore be an important observation in the studies of beef cattle breeding.

IMPLICATIONS

The present results indicate that an on-farm progeny testing program combined with best linear unbiased genetic prediction is very powerful for genetic improvement of carcass traits in beef cattle. After the on-farm program began, predicted breeding values for the reproducing dams became available to farmers. The enhanced genetic gains during the period when on-farm progeny testing and genetic evaluation were combined must be partially caused by the effective selection of reproducing dams based on predicted breeding values.

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