

Effects of Production Circumstances on Expected Responses for Growth and Carcass Traits to Selection of Bulls in Japan

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ABSTRACT: Economic values of growth and carcass traits in Japanese beef cattle for production systems with various types of integration of levels/stages (cow-calf and feedlot segments and the integrated system) and production circumstances (including 20% higher genetic levels of the traits, management, and economic alternatives) were used to examine responses to selection. Discounted economic values with interest rates of 0, 4.2 (Japanese average), and 8.4% were obtained to investigate the effect of discounting on selection efficiency. Traits considered were daily gain in the feedlot, marbling score, birth weight, weaning weight, and mature weight. The effects of discounting were small. Correlated responses

to selection were not always economically favorable for all situations. Selecting bulls for the base situation (i.e., the typical biological and economic conditions for the production of Japanese Black cattle) resulted in negative genetic changes in weaning weight and mature weight in the feedlot segment. Higher genetic levels of daily gain and weaning weight affected efficiency of selection. Although effects of management and economic alternatives on responses to selection were generally small, lighter market weight influenced responses to selection. The results indicate that predicted correlated responses to selection are sensitive to production systems and some production circumstances.

Key Words: Economics, Selection Responses, Beef Production, Breeding

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Introduction

A formal definition of the breeding objective is the primary step for designing integrated breeding programs (Harris, 1970; Harris and Newman, 1994). Incorrect definition of the breeding objective may lead to genetic change in the wrong direction, resulting in economic deterioration of the population (James, 1982b). Development of breeding objectives for beef cattle has received increasing attention (Ponzoni and Newman, 1989; Newman et al., 1992; MacNeil and Newman, 1994; Nitter et al., 1994; Amer et al., 1996).

Hirooka et al. (1998b) estimated biological and economic values of growth and carcass traits in Japanese Black cattle, using a bioeconomic model developed by Hirooka et al. (1998a). They reported that these values were sensitive to breeding objectives (biological vs economic efficiency), production systems (cow-calf vs feedlot vs the integrated system) and

management alternatives (Hirooka et al., 1998b). In Japan, selection of bulls in beef breeds is practiced at official government-owned testing stations. Approximately 400 candidate bulls are performance- and progeny-tested every year, and approximately 10% of the bulls are selected to be used as proven sires all over Japan. Nevertheless, there are no definite breeding objectives and selection criteria. Consequently, only a meat quality trait (i.e., marbling score) has been strongly emphasized in selecting beef bulls, because carcass value is primarily determined by degree of marbling in Japanese markets. In fact, domestic production of highly marbled beef has received emphasis by Japanese consumers, who prefer such beef for certain dishes (e.g., *sukiyaki* and *shabu-shabu*).

The goals for this study were 1) to calculate selection indices and genetic responses for selection of bulls in the official breeding program in Japan and 2) to examine the effects of using different economic values on indices and genetic responses to selection. The genetic responses to selection given the breeding structure in Japan were obtained using economic values derived from a bioeconomic model (Hirooka et al., 1998a,b).

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Materials and Methods

Breeding Goal

In Japan, breeding programs are organized per prefecture, and the official performance and progeny testing of bulls are carried out at testing stations (Namikawa, 1992). In the performance testing program, candidate bull calves aged 6 to 7 mo (200 to 300 kg) are given ad libitum access to a concentrate mixed with 10% chopped rice straw by weight in individual pens for 112 d, and, in the progeny testing program, 8 to 10 steer calves of a candidate bull are group-fed for 364 d (Namikawa, 1992). Genetic improvement in commercial herds is fully dependent on the bull selection by prefectural governments. In this study, the breeding objective was economic efficiency, defined as the ratio of returns to costs.

Aggregate genotype traits considered to influence economic efficiency were birth weight (**BWT**), weaning weight (**WWT**), mature weight (**MWT**), daily gain during the feedlot period (**DG**), and marbling score (**BMS**). In Japan, marbling is measured at the sixth-seventh rib section and classified using beef marbling standards (so-called BMS) with scores 1 to 12; 12 being the most desirable and indicating the highest degree of marbling. The traits were aggregated to a formal breeding objective (Hazel, 1943) using discounted economic values: $H = \mathbf{a}'\mathbf{g}$ where H is the aggregate genotype or breeding objective, \mathbf{g} is a 5×1 vector with the genetic superiorities of 5 traits (i.e., BWT, WWT, MWT, DG, and BMS), and \mathbf{a} is a 5×1 vector of discounted economic values calculated as $\mathbf{c}'\mathbf{v}$,

with \mathbf{c} being a 5×5 matrix with cumulative discounted expressions as diagonal elements and \mathbf{v} being a 5×1 vector with economic values of the traits. The same procedure was used in Groen (1990).

Economic Values

A bioeconomic model for beef production was used to simulate cow-calf and feedlot segments and the integrated (cow-calf + feedlot) system for Japanese Black cattle in Japan and to develop breeding objectives for each system (Hirooka et al., 1998a). In Japan, beef production systems are separated into two different segments (i.e., cow-calf and feedlot segments) in practice, or organizationally in the integrated system. The feedlot segment is independent of the cow-calf segment, and each of these segments has its own breeding objective. The base situation was chosen to represent the typical biological and economic conditions for the production of Japanese Black cattle in Japan. Detailed descriptions of the production circumstances are presented in Hirooka et al. (1998a,b). Economic values (Table 1) were derived from changes in the economic efficiency as a consequence of one unit change in each trait (Groen, 1989; Hirooka et al., 1998b). The base genetic levels of DG and BMS for males and BWT, WWT, and MWT for females were set to be .72 kg/d, 6, 28 kg, 164 kg, and 480 kg, respectively (Hirooka et al., 1998a,b). It was assumed that improvement of a trait for one sex led to equal improvement of the same trait for the other sex (Hirooka et al., 1998b). Alternatives for genetic levels of the traits, management, and economic options were

Table 1. Economic values^a for different systems and alternatives

System and alternatives ^c	Selected trait ^b				
	DG	BMS	BWT	WWT	MWT
BASE					
EE _{CC}	0	0	-6.38	3.46	.34
EE _{FL}	271.54	64.19	.59	-2.38	.09
EE _{IN}	232.51	53.50	-3.46	.21	.30
Alternatives					
+20% DG	-25.56	51.22	-3.69	-.66	.27
+20% BMS	230.72	53.50	-3.80	.16	.29
+20% BWT	196.03	52.11	-4.17	.24	.30
+20% WWT	2.26	50.52	-2.51	-.57	.31
+20% MWT	236.83	53.57	-3.16	.29	.26
MAXRECY	209.61	48.43	-4.35	.22	.44
FIXAGE	474.28	53.50	-3.48	1.02	.33
FIXFAT	194.16	53.45	-3.13	.13	.88
FIXWT	-198.44	38.00	-2.24	-1.58	.19
FEEDPR	141.13	34.76	-2.11	-.08	.18

^aThe values in this table have been multiplied by 1,000.

^bDG = daily gain of steers in feedlot systems; BMS = beef marbling score; BWT = birth weight of females; WWT = weaning weight of females; and MWT = mature weight of females.

^cEE = economic efficiency; CC = cow-calf segment; FL = feedlot segment; IN = integrated system; MAXRECY = reducing maximum reproductive cycle (from 6 to 4); FIXAGE = marketing at a constant age; FIXFAT = marketing at a constant carcass fat percentage; FIXWT = marketing at a lighter slaughter weight; and FEEDPR = doubled concentrate price.

studied in the integrated system (Hirooka et al., 1998b). The alternative genetic levels of the traits were +20% deviations of each trait (DG, BMS, BWT, WWT, and MWT) from the base levels (**BASE**) for the trait. Five alternative management and economic systems were used: 1) reducing maximum reproductive cycle (**MAXRECY**), 2) marketing at a constant age (**FIXAGE**), 3) marketing at a constant carcass fat percentage (**FIXFAT**), 4) marketing at lower slaughter weight (**FIXWT**), and 5) doubled feed price (**FEEDPR**).

Cumulative Discounted Expression

Cumulative discounted expressions were calculated using the computer program Gflow (Brascamp, 1978). In the program, the cumulative discounted expression is derived as

$$\mathbf{c}_{lt} = \sum_{i=0}^t \mathbf{h}\mathbf{m}_{li}\delta^i \quad [1]$$

where t is time horizon, l is selection path, \mathbf{h} is the incidence vector that specifies frequencies by which age classes contribute to (phenotypic) expression of a traits, \mathbf{m}_{li} specifies the relative contribution of the initial set of genes in the selected animals (through selection path l) to the genes of animals in this age class at time i , and δ^i is the factor that discounts future revenues to a base year ($i = 0$). The total number of rows in \mathbf{h} and \mathbf{m} are equal to the total number of age classes over tiers and sexes within tiers considered in the gene flow. In this study, a reproduction tier with nine male and seven female age classes, and a production tier with two male age classes were considered. The time horizon defined the period over which future expression of genes by offspring of the initial set of selected animals was evaluated. A 25-yr time horizon was considered in this study.

The incidence vectors were defined according to production and reproduction levels and replacement times. In this study, incidence vectors accounted for only proportional numbers of animals within an age class, because the relative level of expression in an age class was already considered in calculating economic values (Hirooka et al., 1998b). Because the number of reproducing males (sires) was very small due to use of AI, only expression of BWT and WWT were considered in cows (dams) and feedlot animals. The incidence vectors for BWT and WWT contained .28 for age class 10 (1-yr-old cows) and .72 for age class 17 (1-yr-old feedlot animals). The ratio (.28:.72) was given according to the ratio of replacement heifers and feedlot animals (steers and feedlot heifers). Because expression of DG and BMS was in the production tier (steers and feedlot heifers) only, the incidence vectors for DG and BMS contained a nonzero element .72 for age-class 18 (2-yr-old feedlot animals). The incidence

vector for MWT contained .12, .09, and .08 for cows at 5, 6, and 7 yr (the sum of the elements was .28).

Because expressions of genes were not exactly at the end of the age-classes (1-yr duration), the additional time adjustment discounts revenue from the last day of the age-class to the average moment of expression (in an age-class). The two traits, BMS and DG, were measured at approximately 600 d of age in the official progeny testing program and weaning age of bulls was 180 d. Thus, additional time adjustments for DG (or BMS) and WWT were $(600 - 730)/730 = -.178$ and $(180 - 365)/365 = -.51$, respectively.

Cumulative discounted expressions differed between the selection path l ; selected individuals were sires to breed sires, dams to breed dams, dams to breed sires, or dams to breed dams (path SS, SD, DS, and DD, respectively). In calculating \mathbf{m}_{li} , first an initial \mathbf{n}_{l0} vector was defined, with one nonzero element equal to 1, indicating that the initial matings were performed with selected individuals in that age-class (in a certain tier and sex) and that these selected individuals represent 100% of their own genes. In matrix algebra, the relevant transmission of genes can be described as follows (Brascamp, 1978; Jiang et al., 1999):

$$\mathbf{n}_{li} = \mathbf{Q}\mathbf{n}_{l(i-1)} \quad [2]$$

$$\mathbf{m}_{li} = \mathbf{R}\mathbf{n}_{l(i-1)} + (\mathbf{R} + \mathbf{Q})\mathbf{m}_{l(i-1)} \quad [3]$$

$$\mathbf{R} = \sum_{l=1}^s \mathbf{R}_l \quad [4]$$

where \mathbf{R} describes the process of reproduction and \mathbf{Q} describes aging. The elements in \mathbf{R} denote the relative contribution of parents to the genes of the youngest animals (per sex per tier) one time period later, and the elements in \mathbf{Q} are either zero or one, where the ones denote the aging (per sex per tier) up to the eldest age-class. Equation [2] describes the aging of the initial set of genes of selected individuals (the initial set of genes will be lost after selected individuals reached the eldest age-class), and Eq. [3] describes the flow of (offspring) genes through the population age-classes by reproduction and aging.

$$\mathbf{R} = \begin{bmatrix} \mathbf{R}_{SS} & \mathbf{R}_{DS} & \mathbf{0} \\ \mathbf{R}_{SD} & \mathbf{R}_{DD} & \mathbf{0} \\ \mathbf{R}_{SP} & \mathbf{R}_{DP} & \mathbf{0} \end{bmatrix}$$

where \mathbf{R}_{SS} is a 9×9 matrix, \mathbf{R}_{SD} is a 7×9 matrix, \mathbf{R}_{SP} is a 1×9 matrix, with all zero elements except for the elements (1,5), (1,6), (1,7), (1,8), and (1,9) being .021, .125, .125, .125, and .104, respectively; \mathbf{R}_{DS} is a 9×7 matrix, \mathbf{R}_{DD} is a 7×7 matrix, and \mathbf{R}_{DP} is a 1×7 matrix, with all zero elements except for the elements (1,2), (1,3), (1,4), (1,5), (1,6), and (1,7) being .111, .103, .92, .080, .062, and .051, respectively.

Table 2. Phenotypic standard deviation (σ_p), heritability (h^2), and phenotypic (below diagonal) and genetic (above diagonal) correlations used

Trait ^a	σ_p	h^2	DG	BMS	BWT	WWT	MWT
DG	.098 ^b	.41 ^b	—	.05 ^h	.35 ^g	.39 ^g	.17 ^g
BMS	2.01 ^c	.19 ^d	.10 ^h	—	.31 ^g	-.17 ^g	0 ^g
BWT	3.46 ^e	.43 ^e	.20 ^g	-.02 ^g	—	.78 ^g	.62 ^g
WWT	18.4 ^e	.30 ^e	.12 ^g	-.04 ^g	.52 ^g	—	.66 ^f
MWT	54.0 ^f	.50 ^f	.10 ^g	0 ^g	.34 ^g	.37 ^g	—

^aDG = daily gain of steers in feedlot systems; BMS = beef marbling score; BWT = birth weight of females; WWT = weaning weight of females; MWT = mature weight of females.

^bK. Moriya (personal communication).

^cH. Hirooka (unpublished data).

^dFukuhara et al. (1989).

^eSasaki (1980).

^fKoots et al. (1994a).

^gKoots et al. (1994b).

^hYang et al. (1985).

In this study, the cumulative discounted expression used was obtained as the sum of the cumulative discounted expressions in the three sire paths: sire to son (**SS**), sire to daughter (**SD**), and sire to slaughter progeny (**SP**). In the current Japanese situation, there is no differentiation in the use of selected bulls as sires of young bulls, replacement cows, and slaughter progeny. Therefore, intensities of selection were equal for the three paths.

The discounting factor was calculated according to Smith (1978):

$$\delta^i = \left(\frac{1}{1+q} \right)^i \quad [5]$$

$$q = \frac{r-k}{1+k} \quad [6]$$

where q is the inflation-free interest rate, r is the (uncorrected) interest rate, and k is the inflation rate. In this study, long-term prime lending rates and consumer price index were used as r and k , respectively (Statistical Bureau, 1998). Average q for the period of 1986 to 1995 in Japan was .042 (4.2%). Two alternative discount rates (0 and 8.4%) were assumed to investigate the effects of discount rates on selection efficiencies.

Index Calculations

In Japan, selection takes place among bulls completing progeny testing. Information on BWT and WWT was assumed to be available for the candidate bull and his progeny. The use of 10 progeny per bull was assumed here in accordance with the official progeny test program in Japan (Namikawa, 1992). It was also assumed that DG and BMS of a candidate's progeny were known, and MWT was recorded for the candidate's dam.

Phenotypic and genetic parameters are shown in Table 2. Estimates of genetic parameters were ob-

tained from studies with Japanese Black cattle when available. When parameters for Japanese Black cattle were not found, estimates for other beef breeds were chosen.

Selection index weights (\mathbf{b}_j) for the j^{th} situation were calculated for different breeding objectives, production systems, and management alternatives as $\mathbf{b}_j = \mathbf{P}^{-1} \mathbf{G} \mathbf{a}_j$, where \mathbf{P} is a matrix with variances and covariances between observations and \mathbf{G} is a matrix with covariances between observations and breeding values of traits in the breeding goal (Hazel, 1943). Consistency of the matrices used was tested using the procedure of Foulley and Ollivier (1986).

The genetic gain achieved by one round of selection on the index for bulls for the j^{th} situation (\mathbf{g}_j) was calculated as $\mathbf{g}_j = .5 (i \mathbf{b}_j \mathbf{G} / s_I)$, where i is the selection intensity and s_I is the standard deviation of the index = $(\mathbf{b}_j' \mathbf{P} \mathbf{b}_j)^{.5}$.

In this study, it was assumed that 40 bulls were selected from 400 candidate bulls in the official breeding program, resulting in the proportion of selected animals of 10%. The selection intensity was adjusted for small population size following the method of Burrows (1972): $i = i_\infty - (N - n) / [2n (N + 1) i_\infty]$, where $i_\infty = .8 + .41 \ln (1/p - 1)$ as given by Smith (1969), where p is the proportion of selected animals, and N and n are the number of tested and selected bulls, respectively.

The correlations among indices ($r_{II'}$) were calculated as (James, 1982a) $r_{II'} = \mathbf{b}_j' \mathbf{P} \mathbf{b}_{j'} / [\mathbf{b}_j' \mathbf{P} \mathbf{b}_j] (\mathbf{b}_{j'}' \mathbf{P} \mathbf{b}_{j'})^{.5}$, where $j \neq j'$. The $r_{II'}$ represents the relative response of selection (i.e., efficiency of selection).

Results

Calculated cumulative discounted expressions per generation path are shown in Table 3. There were differences between selection paths, originating partially from differences between initial moment of gene

Table 3. Cumulative discounted expression of traits per selection path for different discount rates

Selection path	Selected trait ^a				
	DG	BMS	BWT	WWT	MWT
Discount rate = 0%					
SS ^b	.400	.400	.434	.434	.114
SD	.435	.435	.463	.463	.262
SP	.360	.360	.360	.360	.000
Sum	1.195	1.195	1.257	1.257	.376
Discount rate = 4.2%					
SS	.183	.183	.210	.205	.048
SD	.213	.213	.241	.236	.134
SP	.247	.247	.267	.261	.000
Sum	.643	.643	.718	.702	.182
Discount rate = 8.4%					
SS	.088	.088	.106	.102	.022
SD	.111	.111	.133	.128	.073
SP	.173	.173	.200	.192	.000
Sum	.372	.372	.439	.422	.095

^aDG = daily gain of steers in feedlot systems; BMS = beef marbling score; BWT = birth weight of females; WWT = weaning weight of females; MWT = mature weight of females.

^bSelection path of sires: SS = sire to son; SD = sire to daughter; SP = sire to slaughter progeny.

introduction and the moment of first expression of genes in the population (Groen, 1990). The differences between traits arose from different incidence of future expression of genetic superiority. For example, the cumulative discounted expression was higher for weaning weight (WWT) than for mature weight (MWT), the difference becoming more pronounced at higher interest rate. The gene flow method increases the relative importance of traits expressed early in the life of animals (see also Ponzoni and Newman, 1989).

Table 4 shows the genetic gains per generation achieved by one round of index selection and accuracy of selection (r_{HI}) in the integrated system, when original and discounted economic values with different discounting were compared. In general, selection responses were greatest when economic values were

calculated without discounting, and the responses were smaller for traits, except BMS, with discounting at a greater rate.

Table 5 shows the genetic gains per generation achieved by one round of index selection for each different production system. The selection responses in all traits, except BMS, were greatest in the cow-calf segment. Correlated responses of BMS to selection were large in the feedlot segment and the integrated systems, but the response was negative in the cow-calf segment. The genetic changes in WWT and MWT were negative in the feedlot segment.

Correlations among indices for the same breeding objectives in different production systems are also given in Table 5. The correlation of indices between the feedlot segment and the integrated systems was

Table 4. Correlated responses to one round of selection with indices using economic values derived from different methods, accuracy of selection (r_{HI}), and correlations between an index derived with a discount rate at 4.2% and alternative indices ($R_{II'}$) in the integrated system

Index ^a	Selected trait ^b					r_{HI}	$R_{II'}$
	DG	BMS	BWT	WWT	MWT		
I_v	15.1	.45	.92	1.07	5.69	.65	.99
I_0	13.4	.46	.73	.10	2.69	.64	1.00
$I_{4.2}$	13.2	.46	.70	-.01	2.36	.64	—
$I_{8.4}$	13.0	.46	.68	-.11	2.06	.64	1.00

^a I_v = index derived with original economic values without considering discount rate; I_0 = index derived with economic values calculated with the discounted gene flow method with discount rate equal to 0%; $I_{4.2}$ = as I_0 , but with discount rate at 4.2%; $I_{8.4}$ = as I_0 , but with discount rate at 8.4%.

^bDG = daily gain of steers in feedlot systems; BMS = beef marbling score; BWT = birth weight of females; WWT = weaning weight of females; MWT = mature weight of females (but the units for DG are grams).

Table 5. Responses to one round of selection, accuracy of selection (r_{IH}), and correlations (r_{II}) with an index derived assuming different production systems (cow-calf, feedlot, and integrated), and in relation to production levels and alternative management systems (assuming integrated production systems)

System and alternative ^b	Selected trait ^a					r_{IH}	r_{II}^c
	DG	BMS	BWT	WWT	MWT		
BASE							
CC	18.7	-.18	1.01	6.37	16.09	.74	-.26
FL	3.4	.45	.18	-2.51	-4.37	.65	.93
IN	13.2	.46	.70	-.01	2.36	.64	—
Alternative							
+20% DG	-8.2	.45	.03	-3.20	-5.40	.65	.83
+20% BMS	12.5	.46	.65	-.26	1.65	.64	1.00
+20% BWT	11.0	.47	.62	-.43	1.32	.63	1.00
+20% WWT	-4.6	.47	.24	-2.40	-3.12	.65	.89
+20% MWT	14.5	.46	.86	.80	4.70	.65	1.00
MAXRECY	13.9	.45	.75	.23	2.98	.65	1.00
FIXAGE	26.4	.37	1.03	2.32	7.41	.68	.91
FIXFAT	12.3	.47	.83	.54	4.37	.65	.99
FIXWT	-21.9	.34	-.52	-5.01	-10.48	.71	.51
FEEDPR	10.5	.47	.57	-.68	.63	.64	1.00

^aDG = daily gain of steers in feedlot systems; BMS = beef marbling score; BWT = birth weight of females; WWT = weaning weight of females; MWT = mature weight of females (but the units for DG are grams).

^bCC = cow-calf segment; FL = feedlot segment; IN = integrated system; MAXRECY = reducing maximum reproductive cycle (from 6 to 4); FIXAGE = marketing at a constant age; FIXFAT = marketing at a constant carcass fat percentage; FIXWT = marketing at a lighter slaughter weight; FEEDPR = doubled concentrate price.

^cCorrelations between an index derived with the integrated system in BASE and indices in alternative circumstances.

high (.925), but the correlation of indices between the cow-calf segment and the integrated systems was relatively low and negative (-.260).

The genetic gains from one round of selection for alternative genetic levels of the traits, accuracy of selection (r_{IH}), and correlations among indices (r_{II}) between base genetic levels and alternative levels for +20% deviation of each trait for economic objectives in the integrated system are given in Table 5. Higher genetic levels of DG and WWT affected efficiency of selection. A 20% higher genetic level of DG or WWT provided negative correlated responses to selection for DG, WWT, and MWT.

Effects of management alternatives are also given in Table 5. The genetic gains in all traits except BMS were negative under alternative FIXWT, and correlated responses in all traits under alternatives MAXRECY and FEEDPR were almost the same as those under the BASE system. The correlations of indices between BASE and FIXWT were relatively low (.505). In all remaining situations, the correlations never fell below .90.

Discussion

The aim of this study was to investigate expected responses for growth and carcass traits to selection of bulls in Japan and to quantify influences of production

systems, genetic levels of the traits, and management and economic alternatives on correlated responses in growth and carcass traits to one round of selection. It should be noted that the results presented here depend on the economic values derived by Hirooka et al. (1998b).

In this study, economic efficiency (return/costs) was used rather than the profit expressed by return minus costs. Harris (1970) stated that breeding objectives may be described by combining return and costs in three ways: profit, economic efficiency (return/costs), and the inverse ratio (costs/return). Smith et al. (1986) concluded that economic efficiency is a more appropriate basis for estimating economic values. Ponzoni (1988) showed that under some conditions the way in which the return and costs are combined (profit vs economic efficiency) has a negligible effect on selection decision.

Correlations between indices derived from original economic values (v) and discounted economic values (a) were high, indicating that the effect of discounting on selection efficiency is small. Ponzoni (1986) and Newman et al. (1992) found correlations above .99 between indices from different methods of calculating economic values in Merino sheep and beef cattle in New Zealand, respectively, and Ponzoni and Newman (1989) reported a wide range of correlations between the indices in Australian beef cattle. These differences among the studies may be caused by differences of

assumed age distribution each year, size and sign of genetic correlations, and life span. Groen et al. (1997) mentioned that ignoring cumulative discounted expression did not lead to optimum genetic responses. Groen et al. (1997) also pointed out that the cumulative discounted expression were especially useful when combining different groups of traits in the breeding objectives (e.g., milk production, beef production, and functional traits). Ponzoni and Newman et al. (1989) recommended use of discounting in estimating economic values even if the effects are small, because it reflects differences in time of trait expression.

An important result of this study was the observed low correlation for the indices suitable for the cow-calf segment and the integrated system, although the results in this study indicated that correlated responses to selection for the integrated system are similar to those for the feedlot system (Table 5). MacNeil and Newman (1994) pointed out that inherent inefficiency of beef production may result from separation, by the production segment, of objectives from overall industry objectives. Under such situations, the breeding objectives for the integrated systems would be taken to meet the demand of both segments (i.e., cow-calf and feedlot). It should be noted, however, that this is true only when market prices used to transfer commodities (i.e., animals) between production segments strongly deviate from true costs (Brascamp et al., 1985; Jiang et al., 1998).

As mentioned before, degree of marbling is the most important trait in Japan from an economic point of view. The BMS changed in the wrong direction in the cow-calf segment from an economic point of view (Table 5). The undesirable changes in BMS may result in very low correlations between indices for the cow-calf segment and the integrated system (or the feedlot segment). Likewise, the correlated responses in economically important traits such as WWT and MWT were negative in the feedlot segment. The results indicate that a large genetic gain for BMS may sacrifice genetic gains for the other traits.

When genetic levels of DG and WWT were raised, correlated responses to selection for DG considerably decreased and efficiency of selection decreased approximately 10 to 20%. This indicates that influences of genetic levels of DG and WWT on economic values and correlated responses to selection are nonlinear. The nonlinearity of genetic levels of traits was also reported by Groen (1989) and Hirooka et al. (1998b). When there are nonlinear effects of genetic levels of traits on responses to selection, two alternatives to solution have been considered. The first alternative is use of a quadratic index when the effects are quadratic (Wilton et al., 1968). The second alternative is development of optimum linear selection indices for multiple generations (Itoh and Yamada, 1988; Pasternak and Weller, 1993; Groen et al., 1994; Dekkers et

al., 1995). Groen et al. (1994) and Dekkers et al. (1995) used a general derivative-free search algorithm and optimum control methods to derive the linear optimum indices, respectively.

With exceptions, correlations between the BASE system and each management and economic alternative were considerably high. However, it is indicated that decreasing the market weight (FIXWT) led to negative genetic gains in all traits, except BMS, and rather different types of animals may be created by selecting to satisfy the marketing situation. Although the marketing strategy is generally supported because of higher biological efficiency and reduction of production costs, selection based on the economic values in this strategy gave negative responses for all growth traits and relatively small gains for BMS. This may reflect negative economic values of DG, BWT, and WWT. There were moderate differences of selection responses among slaughter end points (BASE vs FIXAGE vs FIXFAT). Under constant-age marketing (FIXAGE), daily gain was expected to increase more than under other situations, resulting from the large economic value of the trait in the market situation. Correlated responses of growth traits (BWT, WWT, and MWT) were larger under FIXAGE and FIXFAT. Smith et al. (1983) showed that selection based on economic values for marketing by age gave low to moderate responses for other marketing situations with marketing at a fixed weight for pork production. Nevertheless, the difference may disappear when management variable is optimized (Wilton and Goddard, 1996). More discussion on this topic is in a previous paper (Hirooka et al., 1998b).

Ponzoni and Newman (1989) and Newman et al. (1992) reported effects of removal of the traits on selection efficiency. With current central progeny testing programs of bulls in Japan, only DG and BMS for progeny of candidate bulls have been measured among traits used in this study. When only the two traits were assumed to be measured, genetic responses to one round of selection were 14.5 g, .40, .48 kg, .06 kg and 1.36 kg for DG, BMS, BWT, WWT, and MWT, respectively, and accuracy of selection (r_{HI}) was .584. This result shows that there was a moderate loss of selection efficiency of 9% ($.584/.641 \times 100 = 91.9\%$). This indicates the importance of taking measurements of traits considered in this study.

There is a continuing consumer demand for marbled beef in Japan. In integrated systems, the genetic gains of BMS achieved were positive in all production circumstances in this study. However, if in the future Japanese consumers discriminate against animal fat due to health problems, then the economic advantage of producing marbled beef may disappear. At that time, the economic value of BMS will become zero, or even negative. Consequently, selection may be conducted based on biological breeding objectives. For example, when biological values for the integrated

systems obtained by Hirooka et al. (1998b) (2,607.54, 0, -20.85, .03, and 2.76 for DG, BMS, BWT, WWT, and MWT, respectively) were used to compute selection index, genetic responses to one round of selection were 38.8 g, -.04, .67 kg, 3.85 kg, and 8.36 kg for DG, BMS, BWT, WWT, and MWT, respectively. The genetic gains for three growth traits (DG, WWT, and MWT) were larger than those based on economic values used in this study. Land (1981) suggested that, although current breeding programs aim to fulfill demands of society by defining breeding objectives in economic terms, the objectives may alter, particularly as a result of social change. Therefore, he emphasized the need for genetic flexibility and proposed the development of strains with divergent biological characteristics as a supplement to existing improvement methods. Conversely, Ponzoni and Davis (1989) concluded that economic selection indices have advantages over biological ones because they enable monitoring of changes in components and updating of objectives. Further research should be focused on the trade-off between economic objectives and biological diversification of beef cattle breeding in Japan.

In this study, genetic parameters assumed were taken from Japanese Black and other breeds of beef cattle. The set assumed was tested on consistency. In general, resulting genetic responses are sensitive to assumed parameters (Smith, 1983). But such sensitivity tests were outside the scope of this paper.

Implications

Economic evaluation of breeding programs is the most important process in identifying optimal breeding strategies. This process depends on defined breeding objectives and breeding structures. Japanese breeding programs can provide significant annual genetic gains for beef marbling, which is the most important trait in Japan, as long as economic breeding objectives are defined in integrated systems. However, the results also show that the responses to selection for the traits are sensitive to production systems and some production circumstances.

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