Effect of direct and indirect selection criteria for efficiency of gain on profitability of Japanese Black cattle selection strategies[1]

A. K. Kahi*[2] and H. Hirooka†

*Animal Breeding and Genetics Group, Department of Animal Sciences, Egerton University, 20115 Egerton, Kenya; and †Laboratory of Animal Husbandry Resources, Division of Applied Biosciences, Graduate School of Agriculture, Kyoto University, 606 8502 Kyoto, Japan

ABSTRACT: The objective of this study was to determine the effect of use of residual feed intake (RFI) and the blood concentration of IGF-I (IGF) as selection criteria for efficiency of gain on profitability of Japanese Black cattle selection strategies with restricted test capacity. A breeding objective that integrated the cow-calf and feedlot segments was considered. Selection strategies were defined that differed in whether information on IGF and RFI during performance testing (RFIpt) was used to make selection decisions and in the number of animals measured for IGF. In all strategies, sires were selected from the proportion chosen during the first selection stage (performance testing), modeling a 2-stage selection process. The effect on genetic gain and profitability of variations in test capacity, of the genetic correlations of IGF with marbling score (MS) and RFIpt, and nonzero economic values for and, hence, inclusion of RFI of the cow and feedlot animals in the breeding objective was examined. Additional genetic gain and profitability were generated when information on IGF concentration and RFIpt in the performance-tested young bulls was included in the selection criteria. Profit per cow was optimal when measurement of IGF and RFIpt were incorporated together in the selection index. Increasing test capacity resulted in an increase in genetic gain in all strategies, and profit per cow was optimal in all strategies when 900 places were available for performance testing. Profit per cow was more sensitive to changes in the genetic correlation between IGF and MS than between IGF and RFIpt, especially when more animals were measured for IGF, or else the favorable relationship between IGF and MS had no significant effect on profit per cow. Additional genetic gain and profitability were generated in each strategy when RFI of the cow and feedlot animals were included in the breeding objective with nonzero economic values. These results may be used to provide guidance to Japanese Black cattle breeders and, in the absence of more breed-specific information, may also have application in other Japanese beef breeds.

Key words: breeding program design, carcass trait, insulin-like growth factor I, Japanese Black cattle, residual feed intake, selection strategy

J. Anim. Sci. 2007. 85:2401–2412
doi:10.2527/jas.2006-713

INTRODUCTION

Residual feed intake (**RFI**) has been identified as a direct selection criterion for the improvement of efficiency of gain (G:F, which is the reciprocal of the commonly used term feed efficiency; Archer et al., 1999, 2001). In Japanese Black cattle, genetic parameters for, and genetic relationships between, RFI and BW, weight gains, and carcass traits have been estimated, and opportunity exists for improvement of efficiency of gain (Hoque et al., 2006a,b). Determination of RFI requires accurate measurements of DMI, BW, and weight gains on individual animals over a period. This is expensive, and, therefore, it would be beneficial for the beef industry in Japan to identify and test alternative selection criteria that can be measured easily and cheaply and are correlated with BW, weight gains, efficiency of gain, RFI, and carcass traits.

There is evidence that the blood concentration of IGF-I (IGF) polypeptide hormone that regulates growth and cellular metabolism during all developmental stages is correlated to BW, weight gains (Davis et al. 1995),

[1]We thank Kyoto University, Kyoto, Japan, for provision of facilities and the Japan Society for the Promotion of Science for funding this study. This paper was written when A. K. Kahi was at the Laboratory of Animal Husbandry Resources, Division of Applied Biosciences, Graduate School of Agriculture, Kyoto University, Kyoto, Japan.
[2]Corresponding author: a.kahi@incip.org
Received October 31, 2006.
Accepted June 1, 2007.

efficiency of gain, RFI (Johnston et al., 2002), and carcass traits (Johnston et al., 2001). There is potential to use IGF as a physiological marker and indirect selection criterion for improvement of RFI in herds of cattle. It is possible to improve RFI by selecting for lower IGF concentration without significantly affecting BW and weight gains (Davis and Simmen, 2006).

Genetic improvement of RFI will help reduce feed costs, which are major determinants of profitability in livestock production enterprises. It is of interest to determine whether inclusion of direct and indirect selection criteria for feed intake would improve the efficiency of Japanese Black cattle breeding programs.

The objective of this study was to determine via a model study the effect of use of direct and indirect selection criteria for feed intake on profitability of Japanese Black cattle selection strategies with restricted test capacity.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from existing databases.

Breeding Objective and Selection Criteria

In this study, the actual beef cattle breeding objective in Japan was considered. Beef production systems are separated into 2 segments (cow-calf and feedlot), which are integrated, because the feedlot segment depends on the cow-calf segment for animals to be fattened for slaughter. Inherent inefficiency of beef production may result from separation of objectives by production segment, which may differ from overall industry objectives (MacNeil and Newman, 1994). Therefore, breeding objectives developed for integrated systems (Hirooka et al., 1998a,b) should meet the goals of both segments and were adopted in this study. Traits in the breeding goal included (Hirooka et al., 1998a,b; Hirooka and Sasaki, 1998) birth weight (**BWT**, kg), weaning weight (**WWT**, kg), mature weight (**MWT**, kg), ADG during the feedlot period (**DG**, kg/d), LM area (**LMA**, mm^2), rib thickness (**RT**, mm), s.c. fat thickness (**SFT**, mm), and marbling score (**MS**). Economic values for traits of the breeding objectives, representing values of unit changes in traits, whereas other traits are unchanged, were derived from the estimates reported by Hirooka et al. (1998b) and Hirooka and Sasaki (1998) and are presented in Table 1.

Records available for use as selection criteria included information on BWT, WWT, MWT, DG, daily gain during performance testing (ADG, g/d), LMA, RT, SFT, and MS. Measurements of LMA, RT, SFT, and MS were taken at the sixth-seventh-rib section in Japan (Sasaki, 2001). This was done on the left side of the cold beef carcass. The LMA was measured by grid approximation. The RT is the distance between the LM and pleura membrane measured halfway between the rib ends. Carcass quality was also evaluated based on a visual standard of marbling. The MS was measured by scoring based on the Beef Marbling Standards, which range from 1 to 12, with number 12 being the best (Japan Meat Grading Association, 1988). In addition to information on these traits, it was assumed that records on RFI and IGF concentrations were available for use as direct and indirect selection criteria, respectively, for feed intake. The RFI is the difference between the actual feed intake and the expected feed requirements for body maintenance and production (Arthur et al., 2001). In this study, the selection criterion was RFI during performance testing (**RFIpt**).

The IGF is synthesized and secreted primarily by the liver and is found circulating in the plasma bound to 1 of 6 binding proteins, which keep the levels of IGF relatively stable (Murphy et al., 1987; Hossner et al., 1997). The IGF concentrations were measured during performance testing at 9 mo of age. The genetic correlations among IGF measurements at different ages ranged from 0.86 to 1.00, indicating that the same genetic mechanisms are involved in determining IGF concentrations at different ages (Davis and Simmen, 1997, 2006; Moore et al., 2005).

Sires in Japan are usually selected based on breeding values estimated using BLUP under an animal model (Sasaki et al., 2006). In this study, sires were selected based on a selection index. Best linear unbiased prediction optimally uses all of the available records on the individual and its relatives, while simultaneously adjusting for environmental effects, such that the accuracy of the predicted breeding values is maximized. Wray and Hill (1989) showed that selection indices can be used to approximate selection on BLUP-EBV under an animal model. Therefore, selection index theory remains a useful tool for approximating the accuracy of BLUP selection and predicting selection response. The method used in the current study will also provide a good approximation of response to BLUP selection.

Breeding Structure

The Japanese Black cattle breeding structure was modeled using the computer program ZPLAN (Karras et al., 1997). The breeding structure was similar to that described by Kahi and Hirooka (2005) and consisted only of 1 tier, in agreement with the current Japanese situation, in which there is no differentiation in the levels of performance and pedigree recording, because breeding occurs in the whole population. Breeding was by AI using semen from progeny-tested bulls with a conception rate of 50% (Hirooka et al., 1998a). Genetic gain was generated in the whole population, in which bull and female selection and production of slaughter progeny are the main activities. Replacement bulls and females were selected on indices that included all available information at the time of selection.

A total population size of 500,000 breeding cows was considered. This is the approximate population size for

Table 1. Assumed economic values (v) for breeding objective traits, phenotypic standard deviations (σ_p), heritabilities (along the diagonal), and genetic (below diagonal) and phenotypic (above diagonal) correlations among and between selection criteria and traits in the breeding objective

Trait[1]	v, ¥	σ_p	BWT	WWT	MWT	DG	MS	LMA	RT	SFT	ADG	RFIc	RFIf	RFIpt	IGF
BWT, kg	–1,267.80	3.46	**0.43**	0.43	0.30	0.20	–0.02	–0.03	–0.03	–0.04	0.16	0.00	0.00	–0.04	–0.07
WWT, kg	76.95	18.40	0.52	**0.30**	0.37	0.21	–0.04	0.29	0.29	0.04	0.31	0.00	0.00	–0.13	–0.15
MWT, kg	109.92	54.00	0.42	0.44	**0.50**	0.10	0.00	0.16	0.16	0.08	0.08	0.00	0.00	–0.15	0.13
DG, g/d	85.20	98.00	0.27	0.26	0.11	**0.41**	0.10	0.19	0.19	0.18	0.71	0.00	0.00	–0.11	–0.21
MS, score	19,603.00	2.01	0.21	–0.11	0.00	0.05	**0.56**	0.30	0.24	0.00	–0.01	0.00	0.00	–0.42	–0.45
LMA, mm^2	204.63	70.85	–0.03	0.15	0.12	0.16	0.27	**0.46**	0.33	0.00	0.21	0.00	0.00	–0.38	–0.26
RT, mm	2,500.26	8.00	–0.03	0.15	0.12	0.16	0.25	0.26	**0.38**	0.21	0.38	0.00	0.00	–0.49	–0.26
SFT, mm	925.19	7.51	–0.03	0.03	0.07	0.15	–0.03	–0.05	0.11	**0.46**	–0.11	0.00	0.00	–0.23	–0.06
ADG, g/d	—	160.00	0.13	0.26	0.07	0.60	–0.01	0.17	0.32	–0.09	**0.34**	0.00	0.00	0.15	–0.17
RFIc, kg	–2,195.00	1.43	–0.07	–0.20	–0.20	–0.10	–0.13	–0.13	–0.16	–0.16	–0.10	**0.23**	0.00	0.00	0.00
RFIf, kg	–2,212.00	0.96	–0.07	–0.20	–0.20	–0.10	–0.13	–0.13	–0.16	–0.16	–0.10	0.43	**0.25**	0.00	0.00
RFIpt, kg	—	0.96	–0.03	–0.10	–0.05	–0.12	–0.33	–0.29	–0.38	–0.18	–0.12	0.36	0.52	**0.25**	0.21
IGF, ng/mL	—	6.87	–0.16	0.11	0.07	–0.16	–0.35	–0.20	–0.20	0.25	–0.13	0.13	0.13	0.16	**0.32**

[1]BWT = birth weight; WWT = weaning weight; MWT = mature weight; DG = daily gain during the feedlot period; MS = marbling score; LMA = LM area; RT = rib thickness; SFT = s.c. fat thickness; ADG = daily gain during performance testing; RFIc = residual feed intake of cows; RFIf = residual feed intake of feedlot animals; RFIpt = residual feed intake during performance testing.

the Japanese Black cattle in Japan (Sasaki, 2001). The average calving and annual cow survival rates (including both death and culling) were assumed to be 85 and 92%, respectively. The calf survival rate from birth to weaning was assumed to be 98%, whereas the proportion of male and females calves that were suitable for breeding was 0.80 and 0.90, respectively. Male calves from planned matings were preselected based on BW for performance testing in a central station. The average age of male calves at the beginning of performance testing was 210 d (7 mo), and they were tested for 112 d. The total test capacity available for performance testing was 500, whereas the survival rate during performance testing was assumed to be 90%.

Bulls were selected in a 2-stage selection process. Twenty percent of the young bulls selected in the first stage were test-mated with average cows, and their progeny performance was tested for carcass traits (Sasaki, 2001). After a waiting period of 4 yr, 45 bulls were selected from the progeny-tested young bulls based on the carcass records of 25 progeny and information from relatives. The bulls were 5 yr old at the birth of their progeny, with a productive lifetime of 9 yr and a survival rate of 92%. The proportion of bull dams was assumed to be 5% of the total population. The age at first calving and the productive lifetime of cows was 2 and 7 yr, respectively. The replacement rate was assumed to be 33% for breeding females and 20% for breeding males (Mukai, 1994). Calves not used for replacements were shipped to calf markets for fattening and slaughter. Their carcass traits were evaluated at carcass markets. The number of records used to select sires and dams using a selection index was determined by these biological parameters.

Selection Pathways

At the end of performance testing, a proportion of young bulls to breed sires was selected based on their growing ability. Depending on the selection strategy under investigation, this included information on IGF and RFIpt. The selected bulls were used to produce both bulls and cows (bulls to breed sires and bulls to breed dams). In addition, these bulls were used to produce slaughter progeny. There was 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 bulls to breed sires, bulls to breed dams, and slaughter progeny. Selection of cows also occurred to breed sires, dams, and slaughter progeny. The intensities of selection were equal for dams and slaughter progeny.

Input Parameters

The ZPLAN program uses economic, statistical, and genetic and phenotypic parameters to calculate the annual genetic gain for the breeding objective, genetic gain for single traits, and returns on investment adjusted for costs (profit) using gene-flow and selection index methodology (Karras et al., 1997). In addition, the program calculates selection indices for breeding animals and applies order statistics to obtain adjusted selection intensities for populations with finite sizes. These calculations assume that parameters and selection strategies remain unchanged during the investment period. Archer et al. (2004) outlined the changes made to the ZPLAN code to calculate response from 2-stage selection following the procedure of Wade and James (1996). The assumed variable costs incurred in the breeding population of 500,000 cows are shown in Table 2. The variable costs were directly related to performance and pedigree recording and were applied to the complete population. These costs affect profitability of the breeding scheme but not genetic response. Costs were based on Hirooka et al. (1998a,b) and when missing for the Japanese situation were based on Kahi et al. (2003).

Table 2. Variable costs incurred in a breeding population of 500,000 cows and the average time of cost occurrences in years

Cost element	Cost, ¥	Year
Identification, pedigree recording, electronic data processing, etc., costs per cow	1,000	2.00
Birth weight	320	0
Weaning weight	200	0.49
Mature weight	200	3.00
Carcass traits	1,500	2.18
Residual feed intake	13,500	0.88
Insulin-like growth factor 1	1,800	0.75
Performance testing per bull	1,000,000	0.88
Subsidy for a progeny on farm	38,000	1.00
Waiting period/(bull yr)	850,000	5.00
AI cost per cow	20,000	1.15

Genetic and phenotypic parameters were derived from studies with Japanese Black cattle when available (Oikawa et al., 2000; Oyama et al., 2004; Hoque et al., 2006a,b). When not available, they were derived from other studies on other beef breeds (Koots et al., 1994a,b; Johnston et al., 2001; Maiwashe et al., 2002). In situations in which estimates of phenotypic, but not genetic, correlations were found and vice versa, the phenotypic and genetic correlations were assumed to be equal (Koots et al., 1994a,b). Information on covariances between IGF and other traits of economic importance in Japanese Black cattle are unavailable. Therefore, parameters involving IGF were obtained from Johnston et al. (2001, 2002), Moore et al. (2005), and Davis and Simmen (2006). The resulting genetic and phenotypic variance-covariance matrices were nonpositive definite. Bending was applied to find positive definite variance-covariance matrices that were a minimum distance from the nonpositive definite matrices (Henshall and Meyer, 2002). The genetic and phenotypic parameters used are presented in Table 1.

Selection Strategies and Index Information

Selection strategies were defined that differed in whether information on IGF and RFIpt was used to make selection decisions and in the number of animals measured for IGF. The base scenario (strategy 1) simulated the current situation in which neither IGF nor RFI are recorded. The selection criteria were those currently used in Japan. During performance testing, a proportion of young bulls to breed sires is selected based on their ability to grow, plus information on weights and carcass traits from their relatives. The other selection paths are also selected based on information on weights and carcass traits from relatives. The criteria therefore included measurements on ADG, DG, BWT, WWT, MWT in females retained for replacement in the herd, LMA, RT, SFT, and MS. All other selection strategies included measurements available in strategy 1, as well as any additional measurements.

In this study, measurement of IGF concentration was only done in males, because increased costs to measure IGF in females would not be compensated for by increased gain in the breeding objective (Kahi et al., 2003; Wood et al., 2004). Strategies 2 and 3 considered measurement at the first stage of selection of IGF and RFIpt, respectively, in bulls. Strategy 4 had both IGF and RFIpt measured during performance testing. In strategies 2 and 4, the assumption was that information on IGF concentration was available on the individual and on the sires for relevant selection pathways and that this had only previously been available for selection of sires. Strategies 5 and 6 were similar to strategies 2 and 4, respectively, but assumed that all male animals were measured for IGF and that relevant selection pathways had previously been selected under this same structure.

In all selection strategies, selection was based on the best index for the available criteria, and sires were selected from the proportion selected after performance testing (first selection stage). For all selection pathways, information sources included records on individuals, paternal half-sibs, sire, dam, and half-sibs of the sire and dam. In addition, for sires, information sources included records on carcass traits of progeny. Table 3 shows the number of records and information sources for indices used to select sires and dams.

Effect of Variations in Test Capacity, Genetic Correlations of IGF with MS and RFI, and Nonzero Economic Values for RFI

The effect of variation in test capacity, of genetic correlations of IGF with MS and RFI, and of nonzero economic values for RFI were investigated for all relevant selection strategies. The test capacity varied from 200 to 2,000 places. The aim was to determine the optimal capacity needed in the Japanese Black cattle breeding program that incorporates direct and indirect measures of efficiency of gain. The genetic correlations of IGF with MS and RFIpt were based on literature values from other beef cattle breeds. An overestimation of the expected response from selection based on a selection index will arise from sampling error of genetic parameters used in constructing an index (Hazel, 1943). Sensi-

Table 3. Number of records and information sources used to select sires and dams

Information sources in each selection group[1]	Number of records and selection criteria[2]										
	BWT	WWT	MWT	DG	MS	LMA	RT	SFT	ADG	IGF	RFIpt
Bulls for performance testing (ySS)											
IND	1	1	—	—	—	—	—	—	1	1	1
PHS – males, not for replacement	478	478	—	478	478	478	478	478	—	478	—
PHS – females, not for replacement	337	337	—	337	337	337	337	337	—	—	—
Sires (SS, SD, and SP)											
IND	1	1	—	—	—	—	—	—	1	1	1
PHS – males, not for replacement	478	478	—	478	478	478	478	478	—	478	—
PHS – males, for replacement	4	4	—	—	—	—	—	—	4	4	4
PHS – females, not for replacement	337	337	—	337	337	337	337	337	—	—	—
Progeny	25	25	—	25	25	25	25	25	—	—	—
Dams (DS, DD, and DP)											
IND	1	1	1	—	—	—	—	—	—	—	—
PHS – males, not for replacement	478	478	—	478	478	478	478	478	—	—	—
PHS – females, not for replacement	337	337	—	337	337	337	337	337	—	—	—
PHS – females, for replacement	150	150	150	—	—	—	—	—	—	—	—
Extra information for all groups											
Sire	1	1		—	—	—	—	—	1	1	1
Dam	1	1	1	—	—	—	—	—	—	—	—
HSS – males	956	956		956	956	956	956	956	—	956	—
HSS – females, not for replacement	674	674		674	674	674	674	674	—	—	—
HSS – females, for replacement	300	300	300	—	—	—	—	—	—	—	—
HSD – males	956	956		956	956	956	956	956	—	956	—
HSD – females, not for replacement	674	674		674	674	674	674	674	—	—	—
HSD – females, for replacement	300	300	300	—	—	—	—	—	—	—	—

[1]IND = the individual; PHS = paternal half-sibs; HSD and HSS = half-sibs of the dam and sire; ySS = young bulls to breed sires; SS = bulls to breed sires; SD = bulls to breed dams; SP = bulls to breed slaughter progeny; DS = cows to breed sires; DD = cows to breed dams; DP = cows to breed slaughter progeny.

[2]Numbers of records are calculated from figures for cow-to-bull ratio, cow and calf survival rates, and culling rate. BWT = birth weight; WWT = weaning weight; MWT = mature weight; DG = daily gain during the feedlot period; MS = marbling score; LMA = LM area; RT = rib thickness; SFT = s.c. fat thickness; ADG = daily gain during performance testing; RFIpt = residual feed intake during performance testing. Measurements of IGF apply to strategies 2, 4, 5, and 6; measurements of RFIpt apply to strategies 3, 4, and 6.

tivity of profitability to changes in the genetic correlations of IGF with MS and RFIpt were investigated. Alternative correlations were examined within the parameter space, because larger variations in correlations would have resulted in a nonpositive definite genetic covariance matrix. This would have necessitated further bending of the matrix, making comparisons of sensitivity difficult. The basis for the sensitivity analysis is that correlation estimates will likely change if estimated in the Japanese Black cattle breed. Such changes will have an effect on the profitability of beef production enterprises in Japan, because carcass value is primarily determined by the degree of marbling (Hirooka and Groen, 1999) and feed cost is a major cost determinant (Hoque et al., 2006a).

The breeding objective comprises breeding values and economic values for traits that directly influence either income or costs of the production enterprise. Currently, the breeding objective in Japan is aimed mainly at output traits, with little emphasis placed on reducing inputs. In this case, the economic values for traits associated with inputs (e.g., feed intake) are zero, and, for that matter, the assumption is that such traits are not included in the breeding objective. However, feed costs are the single largest expense in most beef production enterprises, and it is important to estimate the actual economic value of feed intake and test its effect on profitability at the industry level. All simulations were repeated assuming nonzero economic values for RFI of cow (**RFIc**) and RFI of feedlot animals (**RFIf**). The economic values (v) for RFIc and RFIf were calculated in yens (**¥**)·kg^{-1}·day^{-1} and were derived using the following equation:

$$v = -(EI_i \times p_i \times 18.4 \times q_i)/PRC, \quad [1]$$

where EI_i = the GE intake in MJ; p_i = the price of feed in ¥ per MJ of ME; 18.4 = the conversion factor of the metabolizability of the GE of a feed at maintenance to dietary ME values (AFRC, 1993); q_i = the metabolizability of feed; and PRC = the mean length of the reproductive cycle of a cow in days (2,435 d). The first PRC is defined as the interval from replacement to weaning of the first calf. The growing period is included in the first PRC. For second and later reproductive cycles, PRC is defined as the interval from weaning of 1 calf to weaning of the next calf. The EI_i for cows and feedlot animals in MJ was 113,000 and 119,000, respectively (Hirooka

Table 4. Index accuracy, annual monetary genetic gain in the breeding objective, and costs, returns, and profit per cow in the population for the different selection strategies

Selection strategy[1]	Index accuracy	Annual genetic gain, ¥/100	Costs per cow, ¥/100	Returns per cow in the population, ¥/100	Profit per cow in the population, ¥/100
1	0.702	81.70	151.79	827.62	675.83
2	0.706	82.17	151.81	832.28	680.47
3	0.708	82.46	151.91	835.16	683.25
4	0.710	82.69	151.93	837.49	685.56
5	0.707	82.37	158.62	834.30	675.68
6	0.711	82.86	158.74	839.19	680.45

[1]Strategy (Str) 1 = base scenario with young bulls being selected based on their ability to grow during performance testing, plus information on growth (ADG during the feedlot period), weights (birth weight, weaning weight, and mature weight of females retained for replacement in the herd), and carcass traits (marbling score, LM area, rib thickness, and s.c. fat thickness) from their relatives; other selection pathways were also selected based on information on weights and carcass traits from relatives; Str 2 = Str 1 criteria plus information on concentration of IGF-I measured at 9 mo of age during performance testing; Str 3 = Str 1 criteria plus measurement of residual feed intake during performance testing; Str 4 = a combination of Str 2 and 3; Str 5 = Str 2 criteria, plus assumption that information on concentration of IGF-I was available for all males and that relevant selection pathways had previously been selected under this same structure; Str 6 = Str 4 criteria plus the assumption made for Str 5.

et al., 1998a). Correspondingly, p_i in ¥ per MJ of ME was 4.51 and 4.10. The q_i was assumed to be 0.57 and 0.6 for cows and feedlot animals, respectively. No information is available on covariances of RFIc and RFIf with other traits in Japanese Black cattle. Genetic and phenotypic parameters involving RFIc and RFIf were obtained from Kahi et al. (2003). The economic values and genetic and phenotypic parameters involving RFIc and RFIf are also presented in Table 1. Sensitivity of profitability to changes in the genetic correlations of IGF with MS and RFIpt, and of IGF and MS with RFIc and RFIf, was investigated when RFI was included in the breeding objective with nonzero economic values.

RESULTS AND DISCUSSION

Annual Monetary Genetic Gain, Returns, and Profit per Cow and Contribution of Breeding Objective Traits to Returns

The index accuracy, annual monetary genetic gain and costs, returns, and profit per cow varied according to the selection strategy (Table 4). Strategy 1 had the lowest and strategy 6 the highest index accuracies, annual monetary genetic gains, costs, and returns per cow in the population. The profit per cow was lowest (¥67,568) in strategy 5 and highest (¥68,556) in strategy 4. A comparison of strategies 1 and 2 shows that additional genetic gain and profitability were generated when information on IGF in the performance-tested young bulls was included in the selection criteria. Inclusion of IGF in the selection criteria provides a breeder with a possible method to select for efficiency of gain without the cost of measuring feed intake. Use of IGF allows for earlier selection of bulls, but the influence of decreased generation intervals on genetic gain and profitability were not modeled in this study.

The difference in profit per cow between strategies 1 and 2 was smaller than between strategies 1 and 3. This emphasizes the importance of information on RFI from the performance-tested young bulls to overall profitability of a beef herd. Inclusion of IGF in the selection criteria, though useful to the selection of more profitable animals, will not be as profitable as RFI selection, the costs associated with measuring feed intake notwithstanding. Additional genetic gain and profitability was generated when both IGF and RFI (strategy 4) were additional criteria measured for the breeding program. This indicates that additional costs associated with measurement of IGF and feed intake will have little effect on profitability and therefore on their implementation as selection criteria. The increase in costs to measure both IGF and RFI would be compensated for by increased genetic gain in the breeding objective. In Japan, young bulls are selected because of their growing ability during performance testing, which is a less desirable strategy both genetically and economically, because this may result in bulls of potential merit for carcass traits being culled based on the performance test (Hirooka et al., 1998c). Thus, there is a need to include information on feed intake either alone or coupled with IGF as additional selection criteria during performance testing. The genetic correlations of IGF with RFI and carcass traits is desirable, and use of these traits during selection of young bulls will ensure that genetically superior candidates are not selected against early in the selection process.

Strategy 2 can be compared with strategy 5, because the difference between these strategies was in the number of animals on which IGF measurement is taken. Similarly, strategy 4 can be compared with strategy 6. The annual genetic gain and returns per cow were greater in strategies 5 and 6 than in strategies 2 and 4, respectively. However, the costs associated with measuring IGF in strategies 5 (¥15,862) and 6 (¥15,874) had high effect on profit and, therefore, on the implementation of these strategies in a breeding program for Japanese Black cattle. The increase in costs to measure IGF in all males would not be compensated for by the increased gain in the objective. This is contrary to other studies, which have reported greater profitability in strategies in which more animals were measured for IGF (Kahi et al., 2003; Wood et al., 2004). Those studies also reported over 7.6% greater (relative to the base scenario) profitability in strategies that included measurement of RFI. This study reported a difference of 1.5% (Table 4). The lower differences in this study are apparently due to differences in the genetic and economic parameters used and the number of traits included in the selection criteria (in both selection stages) and breeding objective. Further, the difference could also be due to differences in population size and breeding structure and, hence, number of selection pathways modeled, breeds, number of animals measured for IGF and RFI in different selection stages, and information available during each selection stage. Because of the importance of sire selection to genetic response and profitability, the major causes of differences could be associated with sire selection pathways and are related to the number of animals measured for IGF and RFI and in which selection stage information on IGF and RFI was included in the selection criteria.

In the studies by Kahi et al. (2003) and Wood et al. (2004), number of animals measured for IGF in the first stage of selection, which occurred immediately after weaning, was not restricted, and measurement of IGF was used as a screening test in a 2-stage selection procedure to identify animals to test for RFI. Measurement of RFI was done postweaning in the second stage of selection. In this study, the number of sires measured for IGF and RFI was restricted, and these traits were selection criteria in the first stage of selection. The second stage of selection was based on progeny testing, in which bulls were selected based on the carcass records on progeny and information from relatives. Therefore, in this study, the increase in profitability as a result of measurement of IGF and RFI was small, because the increase in costs associated with measuring these traits was only compensated for by the limited gain in the breeding objective as a result of improvements in traits, especially carcass traits, and greater accuracy of first-stage selection. In the studies by Kahi et al. (2003) and Wood et al. (2004), an increase in profitability also came from improvements in traits and greater accuracy of first- and second-stage selection and from a decrease in the number of animals needing to be placed into feed tests in the second stage of selection and increased returns from lower feed costs.

Recording of feed intake that is used to calculate RFI is expensive, and, therefore, a 2-stage selection policy has been used by previous authors (Kahi et al., 2003; Archer et al., 2004; Wood et al., 2004). In this policy, potential breeding animals are first evaluated for production traits of interest or even for physiological or genetic markers for efficiency of gain, after which selected individuals are tested for efficiency of gain (Arthur and Herd, 2005). As described above, this 2-stage selection policy is different from the one applied in the current study. This study has demonstrated that evaluating animals for production traits of interest and physiological markers for efficiency of gain, and testing for efficiency of gain in the same selection stage, yielded additional benefits over and above the benefits from strategies that did not include testing for efficiency of gain. Results of the current study assume conditions in which the performance test capacity is limited. Caution is consequently needed in extrapolating from these results to conditions under which the performance test capacity is not restricted, and progeny testing, especially for carcass traits, is not applied in the second stage of selection.

Table 5 shows returns from annual genetic gain in individual traits in the breeding objective for the different selection strategies. The returns were greatest for MS and lowest for BWT for all selection strategies. Inclusion of IGF and RFIpt in the selection criteria in strategies 2 to 6 resulted in increased returns from annual genetic gain in carcass traits. The genetic relationships assumed between most carcass traits and RFIpt and IGF in this study were favorable (Table 1). When unfavorable genetic relationships exist between traits of high economic value, collection of sufficient information on these traits through progeny testing is important, because accurate information on both traits enables selection of outlier animals that do not follow the general antagonistic relationship (Archer and Barwick, 2001; Archer et al., 2004). In this study, information on carcass traits was collected through progeny testing, and this further led to positive returns for carcass traits.

Effect of Variation in Test Capacity and of the Genetic Correlations of IGF with MS and RFIpt

Figure 1 shows the effect of varying the test capacity on genetic gain and profit per cow. Only results for strategies 1, 2, 3, and 4 are presented. Increasing the test capacity increased the value of genetic gain in all strategies, and the differences between strategies were small at greater test capacities. Improvements in genetic gain at high test capacities came from an increase in selection intensities in the second stage of selection, greater accuracy of first- and second-stage selection, and improvement in individual traits. In contrast, profit per cow increased with increase in test capacity, reaching an optimum at 900 places, and then decreased as the test capacity increased to 2,000. The effect of test capacity on profitability came not only from an increase in selection intensities in the second stage of selection and greater accuracy of first- and second-stage selection but also from an increase in the number of animals for

Table 5. Returns (¥/100) from annual genetic gain in individual traits in the breeding objective for the different selection strategies

Selection strategy[2]	Traits[1]							
	BWT	WWT	MWT	DG	MS	LMA	RT	SFT
1	–13.35	1.28	14.10	30.77	525.45	108.84	147.78	12.75
2	–13.39	1.25	13.53	30.67	529.47	109.27	148.05	13.42
3	–13.08	1.22	13.79	31.22	528.69	110.01	150.17	13.15
4	–13.13	1.21	13.46	31.13	530.99	110.17	150.11	13.53
5	–13.40	1.24	14.04	30.78	530.86	109.38	148.17	13.23
6	–13.16	1.21	13.91	31.17	532.41	110.23	150.08	13.34

[1]BWT = birth weight; WWT = weaning weight; MWT = mature weight; DG = daily gain during the feedlot period; MS = marbling score; LMA = LM area; RT = rib thickness; SFT = s.c. fat thickness.

[2]Strategy (Str) 1 = base scenario with young bulls being selected based on their ability to grow during performance testing, plus information on growth (ADG during the feedlot period), weights (birth weight, weaning weight, and mature weight of females retained for replacement in the herd), and carcass traits (marbling score, LM area, rib thickness, and s.c. fat thickness) from their relatives; other selection pathways were also selected based on information on weights and carcass traits from relatives; Str 2 = Str 1 criteria, plus information on concentration of IGF-I measured at 9 mo of age during performance testing; Str 3 = Str 1 criteria, plus measurement of residual feed intake during performance testing; Str 4 = a combination of Str 2 and 3; Str 5 = Str 2 criteria, plus assumption that information on concentration of IGF-I was available for all males and that relevant selection pathways had previously been selected under this same structure; Str 6 = Str 4 criteria plus the assumption made for Str 5.

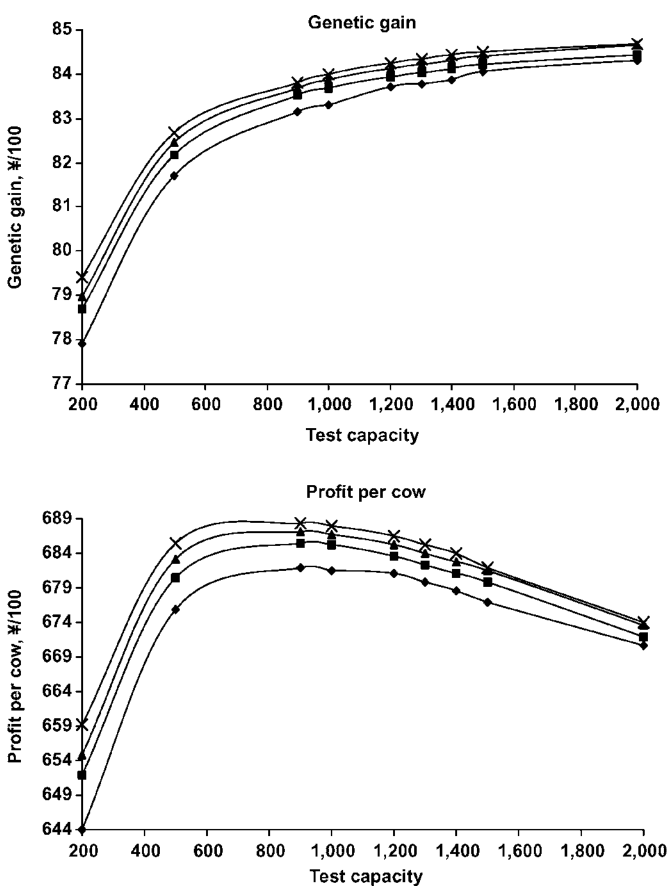

Figure 1. Effect of varying the test capacity on annual genetic gain and profit per cow under selection strategies 1 (◆), 2 (■), 3 (▲), and 4 (x).

IGF measurement needing to be placed into feed tests, as well as reduced returns from greater measurement costs.

This result suggests that the optimal test capacity in the Japanese Black cattle breeding program incorporating direct and indirect measures of efficiency of gain is 900 places. In Japan, Kahi and Hirooka (2005) reported an optimal test capacity from 900 to 1,000 places when direct and indirect measures of efficiency of gain were not incorporated into the breeding program. This study should serve as an encouragement for the beef industry in Japan to increase the number of young bulls that are performance-tested. Usually, the cost of measurement is of lesser importance when considered across the whole breeding program, especially where application of relatively expensive measurements is targeted to animals likely to be most influential on the population (Archer et al., 2004). However, the importance of a large increase in cost to the breeding program should not be underestimated, because this can be a significant barrier to adoption of beneficial technologies in breeding (Kahi et al., 2003).

Table 6 shows the sensitivity of profit per cow to changes in genetic correlations of IGF with MS and RFIpt for strategies 4 and 6. In strategy 4, the profit per cow was not sensitive to changes in the genetic correlations between IGF and RFIpt. Similarly, strategy 6 was not sensitive to changes in the genetic correlation between IGF and RFIpt, but only when the genetic correlation between IGF and MS was from –0.45 to 0.20. Strategy 4 was less sensitive to changes in the genetic correlation between IGF and MS than strategy 6. In strategy 4, the change in sign of the genetic correlations between IGF and MS resulted in very small effects on profit per cow. In contrast, these changes resulted in larger effects on profit per cow in strategy 6, a strat-

Table 6. Sensitivity of profit per cow (¥) to changes in genetic correlations of IGF-I (IGF)with marbling score (MS) and residual feed intake during performance testing (RFIpt) under strategies 4 and 6

Correlation with IGF		Selection strategy[1]	
MS	RFIpt	Strategy 4	Strategy 6
–0.45	–0.10	686.74	679.61
–0.45	0.10	686.75	680.91
–0.45	0.20	686.76	681.00
–0.45	0.45	686.76	681.28
–0.20	–0.10	683.26	679.07
–0.20	0.10	683.26	679.32
–0.20	0.20	683.26	679.46
–0.20	0.45	683.26	679.91
0.20	–0.10	683.57	682.94
0.20	0.10	683.55	683.35
0.20	0.20	683.54	683.61
0.20	0.45	683.53	683.28
0.45	–0.10	687.54	689.74
0.45	0.10	687.50	690.34
0.45	0.20	687.49	690.74
0.45	0.45	687.47	692.10

[1]Strategy (Str) 4 = young bulls were selected based on their ability to grow during performance testing and information on concentration of IGF-I measured at 9 mo of age and residual feed intake, plus information on growth (ADG during the feedlot period), weights (birth weight, weaning weight, and mature weight of females retained for replacement in the herd), and carcass traits (marbling score, LM area, rib thickness, and s.c. fat thickness) from their relatives; other selection pathways were also selected based on information on weights and carcass traits from relatives; Str 6 = Str 4 criteria, plus assumption that information on concentration of IGF-I was available for all males and that relevant selection pathways had previously been selected under this same structure.

egy that assumed all males were measured for IGF. This study has shown that genetic correlations between IGF and MS are more important than correlations between IGF and RFIpt, especially when more animals are measured for IGF. With little information on IGF, the favorable relationship between IGF and MS will not have a significant effect on profit per cow. Use of reliable estimates of genetic correlations is important to avoid over- or underestimating the expected response to selection.

Effect of Nonzero Economic Values for RFI

The index accuracy, annual monetary genetic gain and costs, and returns and profit per cow in the population for the different selection strategies are shown in Table 7. In all selection strategies, there was a moderate increase in genetic gain and costs, as well as in returns and profit per cow, when the economic value for RFI was nonzero. A comparison of Tables 4 and 7 indicates that the increase ranged from ¥108 to ¥114 for genetic gain and ¥1,100 to ¥1,154 for return and profit per cow in the population. Table 8 shows returns from annual genetic gain in individual traits in the breeding objective for the different selection strategies. The returns from all traits in the breeding objective are worth examining, particularly the returns from the highly valued MS. Results presented in Tables 5 and 8 show that nonzero economic values for RFI make little difference in returns from all traits apart from MS, which had lower returns in this case. This result implies that when RFI is included in the breeding objective, the lower returns from MS would be compensated for by increased gain in the objective associated mainly with improvements in RFIc and RFIf.

The sensitivity of profit per cow to changes in the genetic correlations of IGF with MS and RFIpt in strategies 4 and 6, when RFI was included in the breeding objectives, is not presented, because the trends were similar to those reported in Table 6. Table 9 shows the sensitivity of profit per cow to changes in genetic correlations of IGF with MS, RFIc, and RFIf for strategies 4 and 6 when RFI is included in the breeding objective. Both strategies were less sensitive to variation in the genetic correlations of IGF with RFIc and RFIf. In contrast, these strategies were more sensitive to variation in the genetic correlations of MS with RFIc and RFIf. This sensitivity stresses the importance of knowing the genetic variances for RFIc and RFIf and covariance with MS under conditions in Japan, where the degree of marbling and feed costs determine the overall efficiency of beef production enterprises. To our knowledge, information on genetic variances for RFIc and RFIf and covariance with MS for the Japanese Black breed is currently not available.

Feed cost is the single largest expense in most commercial beef production enterprises, and efforts at genetic improvement of efficiency of gain will help reduce these costs (Arthur et al., 2004). Theoretically, genetic improvement of efficiency of gain will have the additional benefit of reducing greenhouse emissions by livestock, leading to improved environmental sustainability (Arthur and Herd, 2005). Koch et al. (1963) first proposed RFI as a trait to be used for the improvement of efficiency of gain. However, whether feed intake is expressed as actual or residual for inclusion in selection indices has no effect on the outcome for a given breeding objective, provided appropriate genetic parameters are used (Kennedy et al., 1993). Therefore, both approaches are appropriate. In Japanese Black cattle, RFI has been recommended as a direct selection criterion for improvement of efficiency of gain (Hoque et al., 2006a), and it was therefore appropriate to use an index containing RFI.

In this study, IGF was used as an indicator trait that is predictive of RFI, and its usefulness in reducing costs and selection of more profitable animals was demonstrated. Selection should be directed toward reduced IGF to produce more efficient cattle with reduced RFI values (Davis and Simmen, 2006). For the Japanese beef industry to benefit fully from breeding programs aimed at improving the efficiency of feed utilization, there is need to include RFI in the breeding objective

Table 7. Index accuracy, annual monetary genetic gain in the breeding objective and costs, and returns and profit per cow in the population for the different selection strategies when residual feed intake is included in the breeding objective with a nonzero economic value

Selection strategy[1]	Index accuracy	Annual genetic gain, ¥/100	Costs per cow, ¥/100	Returns per cow in the population, ¥/100	Profit per cow in the population, ¥/100
1	0.702	82.78	151.79	838.63	686.83
2	0.706	83.26	151.81	843.36	691.55
3	0.708	83.60	151.91	846.70	694.79
4	0.710	83.82	151.93	849.00	697.08
5	0.707	83.46	158.62	845.35	686.73
6	0.711	83.98	158.74	850.65	691.91

[1]Strategy (Str) 1 = base scenario with young bulls being selected based on their ability to grow during performance testing, plus information on growth (ADG during the feedlot period), weights (birth weight, weaning weight, and mature weight of females retained for replacement in the herd), and carcass traits (marbling score, LM area, rib thickness, and s.c. fat thickness) from their relatives; other selection pathways were also selected based on information on weights and carcass traits from relatives; Str 2 = Str 1 criteria, plus information on concentration of IGF-I measured at 9 mo of age during performance testing; Str 3 = Str 1 criteria, plus measurement of residual feed intake during performance testing; Str 4 = a combination of Str 2 and 3; Str 5 = Str 2 criteria, plus assumption that information on concentration of IGF-I was available for all males and that relevant selection pathways had previously been selected under this same structure; Str 6 = Str 4 criteria, plus the assumption made for Str 5.

and use IGF and RFI test data separately or together to estimate RFI breeding values. The use of IGF measurements must be preceded by accurate estimation of breed-specific estimates of variances and covariances between IGF and growth and carcass traits under conditions in Japan. This study provides a reasonable basis for general guidelines on the inclusion of IGF and RFI measurement in Japanese beef cattle breeding programs.

In conclusion, the results presented here indicate that even when the test capacity is restricted, it would be profitable for Japanese Black cattle breeders to incorporate measurement of IGF concentration and RFI in the selection of young bulls during performance testing to identify animals to be progeny-tested. Profit was maximized when measurements of IGF concentration and RFI were incorporated together in the selection index and when 900 places were available for performance testing. Inclusion of RFI in the breeding objective with nonzero economic value is important under conditions in Japan. However, this should be preceded by accurate estimation of variances of, and covariances

Table 8. Returns (¥/100) from annual genetic gain in individual traits in the breeding objective for the different selection strategies when residual feed intake is included in the breeding objective with a nonzero economic value

Selection strategy[2]	Trait[1]									
	BWT	WWT	MWT	DG	MS	LMA	RT	SFT	RFIc	RFIf
1	–13.54	1.50	14.84	31.15	522.94	109.06	147.87	13.53	6.61	4.65
2	–13.58	1.47	14.26	31.04	526.97	109.48	148.15	14.20	6.67	4.70
3	–13.24	1.44	14.48	31.58	525.74	110.15	150.22	13.92	7.14	5.27
4	–13.29	1.42	14.16	31.49	528.12	110.34	150.18	14.30	7.09	5.19
5	–13.59	1.46	14.76	31.14	528.35	109.59	148.27	14.01	6.65	4.69
6	–13.32	1.42	14.60	31.52	529.48	110.39	150.16	14.12	7.07	5.18

[1]BWT = birth weight; WWT = weaning weight; MWT = mature weight; DG = daily gain during the feedlot period; MS = marbling score; LMA = LM area; RT = rib thickness; SFT = s.c. fat thickness; RFIc = residual feed intake of cows; RFIf = residual feed intake of feedlot animals.

[2]Strategy (Str) 1 = base scenario with young bulls being selected based on their ability to grow during performance testing, plus information on growth (ADG during the feedlot period), weights (birth weight, weaning weight, and mature weight of females retained for replacement in the herd), and carcass traits (marbling score, LM area, rib thickness, and s.c. fat thickness) from their relatives; other selection pathways were also selected based on information on weights and carcass traits from relatives; Str 2 = Str 1 criteria, plus information on concentration of IGF-I measured at 9 mo of age during performance testing; Str 3 = Str 1 criteria, plus measurement of residual feed intake during performance testing; Str 4 = a combination of Str 2 and 3; Str 5 = Str 2 criteria, plus assumption that information on concentration of IGF-I was available for all males and that relevant selection pathways had previously been selected under this same structure; Str 6 = Str 4 criteria plus the assumption made for Str 5.

Table 9. Sensitivity of profit per cow to changes in genetic correlations of concentration of IGF-I (IGF) with residual feed intake (RFI) of the cow (RFIc) and feedlot animals (RFIf) and of marbling score (MS) with RFIc and RFIf for strategies 4 and 6 when RFI is included in the breeding objective with a nonzero economic value

Correlation with IGF		Selection strategy[1]	
RFIc	RFIf	Strategy 4	Strategy 6
–0.20	–0.20	697.01	692.69
–0.20	–0.10	697.02	692.57
–0.20	0.20	697.03	692.25
–0.20	0.45	697.06	692.02
–0.10	–0.20	697.02	692.52
–0.10	–0.10	697.02	692.41
–0.10	0.20	697.04	692.11
–0.10	0.45	697.06	691.92
0.20	–0.20	697.04	692.09
0.20	–0.10	697.06	692.01
0.20	0.20	697.11	691.80
0.20	0.45	697.17	691.68
0.45	–0.20	697.10	691.83
0.45	–0.10	697.13	691.77
0.45	0.20	697.21	691.64
0.45	0.45	697.29	691.58
Correlation with MS		**Selection strategy[1]**	
RFIc	RFIf	Strategy 4	Strategy 6
–0.45	–0.35	707.78	702.85
–0.45	–0.20	705.37	700.40
–0.45	0.20	699.03	693.90
–0.45	0.25	698.24	693.09
–0.20	–0.35	702.12	697.07
–0.20	–0.20	699.74	694.64
–0.20	0.20	693.45	688.22
–0.20	0.25	692.69	687.42
0.20	–0.35	693.20	687.95
0.20	–0.20	690.87	685.57
0.20	0.20	684.72	679.28
0.20	0.25	683.95	678.50
0.45	–0.35	687.71	682.34
0.45	–0.20	685.41	679.99
0.45	0.20	680.46	673.79
0.45	0.25	679.70	673.02

[1]Strategy (Str) 4 = performance testing of young bulls selected based on their ability to grow and information on concentration of IGF-I measured a 9 mo of age and residual feed intake, plus information on growth (ADG during the feedlot period), weights (birth weight, weaning weight, and mature weight of females retained for replacement in the herd), and carcass traits (marbling score, LM area, rib thickness, and s.c. fat thickness) from their relatives; other selection pathways were also selected based on information on weights and carcass traits from relatives; Str 6 = Str 4 criteria, plus assumption that information on concentration of IGF-I was available for all males and that relevant selection pathways had previously been selected under this same structure.

between, RFI and growth and carcass traits. These results apply to the Japanese Black breed but, in the absence of more breed-specific information, may also have application in other beef breeds.

LITERATURE CITED

AFRC. 1993. Energy and Protein Requirements of Ruminants. Agric. Food Res. Counc., CAB Int., Wallingford, UK.

Archer, J. A., and S. A. Barwick. 2001. An analysis of investment in advanced breeding program designs for beef cattle. Proc. Assoc. Adv. Anim. Breed. Genet. 14:465–468.

Archer, J. A., S. A. Barwick, and H.-U. Graser. 2004. Economic evaluation of beef cattle breeding schemes incorporating performance testing of young bulls for feed intake. Aust. J. Exp. Agric. 44:393–404.

Archer, J. A., E. C. Richardson, R. M. Herd, and P. F. Arthur. 1999. Potential for selection to improve efficiency of feed use in beef cattle: A review. Aust. J. Agric. Res. 50:147–161.

Arthur, P. F., J. A. Archer, D. J. Johnston, R. M. Herd, E. C. Richardson, and P. F. Parnell. 2001. Genetic and phenotypic variance and covariance components for feed intake, efficiency of gain, and other postweaning traits in Angus cattle. J. Anim. Sci. 79:2805–2811.

Arthur, P. F., and R. M. Herd. 2005. Efficiency of feed utilization by livestock – Implications and benefits of genetic improvement. Can. J. Anim. Sci. 85:281–290.

Arthur, P. F., R. M. Herd, D. J. Johnston, K. Moore, and H.-U. Graser. 2004. Incorporating information on plasma IGF concentration in genetic improvement strategies for efficiency of gain in beef cattle. Can. J. Anim. Sci. 84:769. (Abstr.)

Davis, M. E., M. D. Bishop, N. H. Park, and R. C. M. Simmen. 1995. Divergent selection for blood serum insulin-like growth factor 1 concentration in beef cattle. I. Nongenetic effects. J. Anim. Sci. 73:1927–1932.

Davis, M. E., and R. C. M. Simmen. 1997. Genetic parameter estimates for serum insulin-like growth factor I concentration and performance traits in Angus beef cattle. J. Anim. Sci. 75:317–324.

Davis, M. E., and R. C. M. Simmen. 2006. Genetic parameter estimates for serum insulin-like growth factor I concentrations, and body weight and weight gains in Angus beef cattle divergently selected for serum insulin-like growth factor I concentration. J. Anim. Sci. 84:2299–2308.

Hazel, R. N. 1943. The genetic basis for constructing selection indexes. Genetics 28:476–490.

Henshall, J. M., and K. Meyer. 2002. "PDMATRIX" – Programs to make matrices positive definite. Communication 28-12 in Proc. 7th World Congr. Genet. Appl. Livest. Prod., Montpellier, France.

Hirooka, H., and A. F. Groen. 1999. Effects of production circumstances on expected responses for growth and carcass traits to selection of bulls in Japan. J. Anim. Sci. 77:1135–1143.

Hirooka, H., A. F. Groen, and J. Hillers. 1998a. Developing breeding objectives for beef cattle production. 1. A bio-economic simulation model. Anim. Sci. 66:607–621.

Hirooka, H., A. F. Groen, and J. Hillers. 1998b. Developing breeding objectives for beef cattle production. 2. Biological and economic values of growth and carcass traits in Japan. Anim. Sci. 66:623–633.

Hirooka, H., A. F. Groen, and M. Matsumoto. 1998c. Genetic parameters for growth and carcass traits in Japanese Brown cattle estimated from field records. J. Anim. Sci. 74:2112–2116.

Hirooka, H., and Y. Sasaki. 1998. Derivation of economic weights for carcass traits in Japanese Black cattle from field records. J. Anim. Breed. Genet. 115:27–37.

Hoque, M. A., P. F. Arthur, K. Hiramoto, and T. Oikawa. 2006a. Genetic relationship between different measures of efficiency of gain and its component traits in Japanese Black (Wagyu) bulls. Livest. Sci. 99:111–118.

Hoque, M. A., P. F. Arthur, K. Hiramoto, and T. Oikawa. 2006b. Genetic parameters for carcass traits of field progeny and their relationship with efficiency of gain traits of their sire population for Japanese Black cattle. Livest. Sci. 100:251–260.

Hossner, K. L., R. H. McCusker, and M. V. Dodson. 1997. Insulin-like growth factors and their binding proteins in domestic animals. Anim. Sci. 64:1–15.

Japan Meat Grading Association. 1988. New Beef Grading Standards [in Japanese]. Jpn. Meat Grading Assoc., Tokyo, Japan.

Johnston, D. J., R. M. Herd, M. J. Kadel, H.-U. Graser, P. F. Arthur, and J. A. Archer. 2002. Evidence of IGF-1 as a genetic predictor of efficiency of gain traits in beef cattle. Proc. 7th World Congr. Genet. Appl. Livest. Prod. 31:257–260.

Johnston, D. J., R. M. Herd, A. Reverter, and V. H. Oddy. 2001. Heritability of IGF-1 in beef cattle and its association with growth and carcass traits. Proc. Assoc. Adv. Anim. Breed. Genet. 14:164–166.

Kahi, A. K., S. A. Barwick, and H.-U. Graser. 2003. Economic evaluation of Hereford cattle breeding schemes incorporating direct and indirect measures of feed intake. Aust. J. Agric. Res. 54:1039–1055.

Kahi, A. K., and H. Hirooka. 2005. Genetic and economic evaluation of Japanese Black (Wagyu) cattle breeding schemes. J. Anim. Sci. 83:2021–2032.

Karras, E., E. Niebel, H.-U. Graser, H. Bartenschlager, and G. Nitter. 1997. ZPLAN. A computer program to optimise livestock selection schemes. Univ. Hohenheim, Stuttgart, Germany.

Kennedy, B. W., H. H. J. van der Werf, and T. H. E. Meuwissen. 1993. Genetic and statistical properties of residual feed intake. J. Anim. Sci. 71:3239–3250.

Koch, R. M., L. A. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. J. Anim. Sci. 22:486–494.

Koots, K. R., J. P. Gibson, C. Smith, and J. W. Wilton. 1994a. Analyses of published genetic parameter estimates for beef production traits. 1. Heritability. Anim. Breed. Abstr. 62:309–338.

Koots, K. R., J. P. Gibson, and J. W. Wilton. 1994b. Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. Anim. Breed. Abstr. 62:825–853.

MacNeil, M. D., and S. Newman. 1994. Selection indices for Canadian beef production using specialized sire and dam lines. Can. J. Anim. Sci. 8:95–99.

Maiwashe, A. N., M. J. Bradfield, H. E. Theron, and J. B. van Wyk. 2002. Genetic parameter estimates for body measurements and growth traits in South African Bonsmara cattle. Livest. Prod. Sci. 75:293–300.

Moore, K. L., D. J. Johnston, H.-U. Graser, and R. Herd. 2005. Genetic and phenotypic relationships between insulin-like growth factor (IGF-I) and net feed intake, fat, and growth traits in Angus beef cattle. Aust. J. Agric. Res. 56:211–218.

Mukai, F. 1994. Genetic evaluation and selection methods for carcass traits in Japanese Black cattle. Jpn. J. Zootech. Sci. 65:890–905.

Murphy, L. J., G. I. Bell, and H. G. Friesen. 1987. Tissue distribution of insulin-like growth factor I and II messenger ribonucleic acid in the adult rat. Endocrinology 120:1279–1282.

Oikawa, T., T. Sanehira, K. Sato, Y. Mizuguchi, H. Yamamoto, and M. Baba. 2000. Genetic parameters for growth and carcass traits of Japanese Black (Wagyu) cattle. Anim. Sci. 71:59–64.

Oyama, K., T. Katsuta, K. Anada, and F. Mukai. 2004. Genetic parameters for reproductive performance of breeding cows and carcass traits of fattening animals in Japanese Black (Wagyu) cattle. Anim. Sci. 78:195–201.

Sasaki, Y. 2001. Beef cattle breeding and its trends in Japan. Asian-australas. J. Anim. Sci. 14:111–122.

Sasaki, Y., T. Miyake, C. Gaillard, T. Oguni, M. Matsumoto, M. Ito, T. Kurahara, Y. Sasae, K. Fujinaka, S. Ohtagaki, and T. Dougo. 2006. Comparison of genetic gains per year for carcass traits among breeding programs in the Japanese Brown and Japanese Black cattle. J. Anim. Sci. 84:317–323.

Wade, C. M., and J. W. James. 1996. Optimal allocation of resources considering two sexes and selection in two stages. Genet. Sel. Evol. 28:3–21.

Wray, N. R., and W. G. Hill. 1989. Asymptotic rates of response from index selection. Anim. Prod. 49:217–227.

Wood, B. J., J. A. Archer, and J. H. J. van der Werf. 2004. Response to selection in beef cattle using IGF-1 as a selection criterion for residual feed intake under different Australian breeding objectives. Livest. Prod. Sci. 91:69–81.