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journal or publication title	Tohoku journal of agricultural research
volume	58
number	1/2
page range	31-41
year	2007-11
URL	http://hdl.handle.net/10097/40430

Tohoku Journal of Agricultural Research
Vol. 58 No. 1-2, November 2007
Printed in Japan

Estimation of Genetic Gain on Growth and Carcass Traits over Direct and Index Selection for Growth and Feed Efficiency of Japanese Black Cattle by computer simulation

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(Received, 17, April, 2007)

Summary

A simulation study was performed for performance traits on 740 bulls and carcass traits on 1,774 progeny in Japanese Black cattle to compare the efficiency of direct and index selection. Performance traits included average daily gain (*ADG*), final body weight (*BWF*), metabolic body weight (*MWT*), feed intake (*FI*), feed conversion ratio (*FCR*) and residual feed intake (*RFI*). Progeny traits were carcass weight (*CWT*), rib eye area (*REA*), rib thickness (*RBT*), subcutaneous fat thickness (*SFT*), marbling score (*MSR*), meat quality grade (*MQG*), meat color (*MCL*) and fat color (*FCL*). Direct selection for *BWF* has resulted larger increase in *ADG* than direct selection for *ADG* itself. Correlated responses in *CWT*, *REA*, *RBT* and *MSR* were higher, while in *SFT* was lower over selection against *RFI* than those against *FCR*. Improvement in *ADG* or *BWF* resulting positive correlated responses in *MSR* and *SFT*, indicating that selection for rapid gain may favor fatter animals. This study provides evidence that selection against *RFI* might be better than that of *FCR* for getting better responses in carcass traits. On the other hand, *BWF* was better than *ADG* to be included in selection program for either in aggregate index (economic) selection or single trait selection to achieve better correlated responses.

Key words: Direct and index selection, growth, feed efficiency, simulation

Response to selection, and hence achieving breeding goals, is largely dependent on the genetic and phenotypic parameters and economic weights used. Economic values vary with the definition of breeding objectives and with the

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production systems and circumstances involved and are to be modified to consider the change of future market demands (Hill, 1974). The economic values for growth and carcass traits in Japanese Black cattle have been estimated (Hirooka et al., 1998). However, no literature is found to estimate the correlated responses on growth and carcass traits over selection for aggregate indexes using economic values of component traits, which are needed to maximize breeding efficiency.

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. Many beef cattle improvement schemes are based on some measure of growth. The perceived benefits of selecting for faster growing cattle include the ability of stock to grow meat production and to use feed more efficiently. By eating more, by utilizing feed more efficiently, or by some combinations of the two, animals can grow faster (Roberts, 1981). Residual feed intake (*RFI*) is the trait derived from the combination of feed consumption and production traits and the weights of its component traits are determined by biological variances. However, profitability will be maximized when index weights on feed intake, growth and other traits are determined by both biological and economic parameters as aggregate index. The aim of this study was to compare the efficiency of direct selection for growth traits with ratio and linear index traits and also with aggregate indexes using different economic values for the component traits for improving growth and carcass traits. The comparison was made by estimating the expected genetic change in growth and carcass traits to one generation of selection for either direct or as aggregate indexes by computer simulation.

Materials and Methods

Data structure

The data used in this study were collected in Japan on 740 Japanese Black bulls at the test station of Okayama Prefecture Animal Industry Centre and on 1,774 of their progeny (1,281 steers and 493 heifers) at 19 feedlot operations, where progeny fattening were being conducted. For this study, data on animals tested from 1971-2004 were used. In order to estimate genetic parameters for the traits measured, a pedigree file was constructed. Pedigrees of the recorded bulls were traced back to three generations and, including the tested animals, totaled 8,938.

Bull performance

Seventy seven bulls were tested for 140 days and the remaining 663 bulls for 112 days at test station. The bull calves, collected from designated farms, were within the age limit of 7-8 months and body weight of 200-300 kg. The feeding and management of bulls have been performed as described by Hoque et al.

(2006b). Cohort was defined as a group of bulls of same birth date and introduced to the test station on the same day and managed together. The mean age of bulls at the finish of test was 345 days. The studied traits were average daily gain (*ADG*), metabolic body weight (*MWT*), body weight at finish (*BWF*), daily feed intake (*FI*), feed conversion ratio (*FCR*) and *RFI*. The *RFI* was calculated using following equation :

$$RFI = FI - \beta_w \times MWT - \beta_g \times ADG$$

where genetic regression coefficient, $\begin{bmatrix} \beta_w \\ \beta_g \end{bmatrix} = \boldsymbol{G}^{-1}\boldsymbol{c}$; $\boldsymbol{G}$ = genetic covariance matrix of two production traits (*MWT* and *ADG*) ; and $\boldsymbol{c}$ = vector of the genetic covariance of *FI* with production traits estimated using the residual maximum likelihood (*REML*) method. The detail description for obtaining the studied traits and statistical procedure for estimating covariance components have been described by Hoque et al. (2006b). The phenotypic variances, heritabilities and correlations among growth and feed efficiency traits estimated by them (Hoque et al., 2006b) for the same data set are summarized in Table 1, which have been used in the simulation of this study.

Aggregate indexes were calculated by different combinations using different economic values for *FI* with *ADG* or *BWF* (Table 2). The economic weight was calculated as to change the trait of interest by a unit amount, relative to the mean of the trait, and to determine the change in the cost of production, assuming that all other traits remain fixed at their current levels. The feed cost was assumed to be 30,000 yen per tone and there was an overhead cost of 60 yen per day. The detail procedure for calculating economic values for these traits has been described by Cameron (1997). The correlated responses in performance and carcass traits to one generation of selection using these combinations were estimated by simulation.

Table 1. Phenotypic variance (V_p), heritabilities (h^2) and correlations among performance traits

Traits	V_p	$h^2 \pm$SE	†Correlations					
			ADG	*BWF*	*MWT*	*FI*	*RFI*	*FCR*
ADG	0.071	0.20±0.10		0.95±0.10	0.96±0.09	0.87±0.08	−0.18±0.20	−0.58±0.24
BWF	796.13	0.47±0.10	0.49		0.97±0.08	0.88±0.11	−0.04±0.15	−0.52±0.25
MWT	14.69	0.49±0.09	0.36	0.89		0.74±0.15	−0.07±0.14	−0.57±0.25
FI	1.30	0.34±0.11	0.56	0.55	0.55		0.61±0.10	0.34±0.15
RFI	0.92	0.25±0.10	−0.13	−0.18	−0.18	0.59		0.62±0.11
FCR	0.89	0.15±0.04	−0.52	0.11	0.14	0.40	0.76	

†genetic and phenotypic correlations are above and below the diagonal, respectively

Table 2. Economic values for growth and FI in different combinations of aggregate indexes

Traits	*ADG*	*BWF*	*FI*
Combination 1	307.40	–	−33.66
Combination 2	307.40	–	−25.25 (25% decreased)
Combination 3	307.40	–	−42.08 (25% increased)
Combination 4	–	2.14	−33.66
Combination 5	–	2.14	−25.25 (25% decreased)
Combination 6	–	2.14	−42.08 (25% increased)

Progeny performance

Beef production systems in Japan are generally divided into two operations, a cow-calf operation and feedlot operation. Calves produced from the mating between tested bulls of the test station and dams of the cow-calf operation are sold at 8–10 months of age at calf markets and purchased by feedlot farmers. Feeding and management of tested progeny at feedlot operation were adopted as described by Hoque et al. (2006a). Cohort in progeny was a group of animals of same sex born in same season (spring, summer, autumn or winter) of the year and managed in the same feedlot operation. Progeny under this study were slaughtered at the end of feedlot operation at the mean age of 864 days. Traits measured in progeny were carcass weight (*CWT*), rib eye area (*REA*), rib thickness (*RBT*), subcutaneous fat thickness (*SFT*), marbling score (*MSR*), meat quality grade (*MQG*), meat color (*MCL*) and fat color (*FCL*). All these progeny traits were measured as described by Hoque et al. (2006a). The estimated phenotypic and genetic parameters for carcass traits and their genetic correlations with growth and feed efficiency traits estimated by our previous study (Hoque et al., 2006a) for the same

Table 3. Phenotypic variance (V_p) and heritabilities (h^2) for carcase traits and their genetic correlations with performance traits

Traits	V_p	$h^2 \pm$SE	Genetic correlations				
			ADG	*BWF*	*FI*	*RFI*	*FCR*
CWT	1838.92	0.70±0.07	0.53±0.03	0.42±0.21	0.42±0.29	−0.53±0023	−0.41±0.36
REA	48.57	0.47±0.06	0.42±0.22	0.65±0.20	0.98±0.02	−0.45±0.29	−0.18±0.34
RBT	48.16	0.45±0.06	0.20±0.22	0.47±0.24	0.12±0.28	−0.58±0.25	−0.26±0.29
MSR	7.64	0.33±0.06	0.28±0.17	0.60±0.22	−0.20±0.31	−0.50±0.31	−0.54±0.32
MQG	0.48	0.35±0.06	0.11±0.25	0.34±0.26	0.26±0.29	−0.26±0.23	−0.43±0.24
SFT	16.59	0.34±0.06	0.45±0.24	0.23±0.18	0.25±0.17	−0.27±0.20	−0.61±0.39
MCL	0.13	0.15±0.03	0.87±0.03	0.19±0.33	0.55±0.38	−0.28±0.27	−0.59±0.27
FCL	0.05	0.02±0.31	0.41±0.24	0.46±0.21	0.94±0.10	−0.51±0.38	−0.70±0.21

data set are shown in Table 3, which have also been used in the simulation.

Simulation

The simulation study was performed using SelAction (Rutten and Bijma, 2002) computer program. Response to selection was predicted based on selection index theory (Wray and Hill, 1989). A total of 1800 progeny, 20 sires and 600 dams were used in this simulation. In existing Japanese Black breeding, 20-30 bull calves are selected for performance test from approximately 200 bull calves on the basis of heavier body weight. After performance testing, four bulls are selected as candidate young bulls for progeny testing. Assumed that no selection is practiced in cowherd but only a few cows are culled each year on the basis of their health and reproductive performance. Thus, the selected proportion for sire and dam were assumed to be 0.02 and 0.9, respectively. A hierarchical mating structure where dams are nested within sires and random mating of selected animals was applied in SelAction program. Features of SelAction and the theoretical background have been described by Rutten and Bijma (2002). The genetic model for each trait was $P=A+E$, where P was the phenotype, A was the breeding value and E was the individual environmental component. P, A, and E were assumed to follow an approximate normal distribution. The breeding goal was the sum of the selected traits weighted by their respective values, $H=\boldsymbol{a}'\boldsymbol{v}$, where $\boldsymbol{a}$ was the vector of breeding values and $\boldsymbol{v}$ was a vector of economic values for selected traits. Traits in the index and in the breeding goal were allowed to be different traits. Index weights were determined as $\boldsymbol{b}=\boldsymbol{P}^{-1}\boldsymbol{G}\boldsymbol{v}$, where the (co)variance matrix of the information sources, $\boldsymbol{P}=\mathrm{Var}(\boldsymbol{x})$, and $\boldsymbol{G}$ was the covariance matrix of information sources and breeding goal traits as $\boldsymbol{G}=\mathrm{Cov}(\boldsymbol{x}, \boldsymbol{a})$. Genetic selection differentials for each trait and for the breeding goal were determined as in Villanueva et al. (1993). Prediction of the rate of inbreeding was based on the long-term genetic contribution theory (Wray and Thompson, 1990). The equations that SelAction used were a multi-trait analogy of the equations given in Woolliams and Bijma (2000).

Results

Simulated responses (or correlated responses) in performance traits and percent of inbreeding to one generation of selection for growth or feed efficiency traits are presented in Table 4. Direct selection for *BWF* has resulted more increase in *ADG* than direct selection for *ADG* itself, because estimated heritability for *ADG* was low (0.20) and for *BWF* was moderate (0.47), and the genetic correlation between *BWF* and *ADG* was high (0.95). *RFI* and *FCR* favorably decreased with increasing *ADG* and *BWF*. Selection against *RFI* would lead to a larger reduction in *FI* and slightly lower increase in growth traits

Table 4. Simulated responses (or correlated responses) in performance traits to one generation of selection for growth or against feed efficiency traits

Selected traits	*ADG* (kg)	*BWF* (kg)	*MWT* (kg)	*FI* (kg)	*RFI* (kg)	*FCR* (kg)	Inbreeding (%)
↑ *ADG* (kg)	0.059	9.040	1.267	0.285	−0.045	−0.104	0.765
↑ *BWF* (kg)	0.079	13.458	1.811	0.407	−0.085	−0.132	0.819
↓ *FI* (kg)	−0.063	−10.409	−1.214	−0.408	−0.243	−0.076	0.805
↓ *RFI* (kg)	0.012	2.505	0.101	−0.280	−0.275	−0.122	0.783
↓ *FCR* (kg)	0.021	3.164	0.453	−0.098	−0.137	−0.159	0.742

↑, upward selection ; ↓, downward selection

Table 5. Simulated correlated responses on carcass traits to one generation of selection for growth or against feed efficiency traits

Selected traits	*CWT* (kg)	*REA* (cm^2)	*RBT* (mm)	*MSR* (No.)	*MQG* (No.)	*SFT* (mm)	*MCL* (No.)	*FCL* (No.)
↑ *ADG* (kg)	9.354	0.987	0.458	0.219	0.022	0.526	0.060	0.006
↑ *BWF* (kg)	10.484	2.168	1.522	0.663	0.097	0.380	0.018	0.010
↓ *FI* (kg)	−9.214	−2.883	−0.342	−0.194	−0.065	−0.363	−0.047	−0.180
↓ *RFI* (kg)	11.418	1.140	1.432	0.421	0.057	0.340	0.021	0.009
↓ *FCR* (kg)	6.381	0.373	0.525	0.372	0.076	0.628	0.036	0.010

↑, upward selection ; ↓, downward selection

(*ADG*, *BWF* and *MWT*) than selection against *FCR*. Selection for lowering *FI* has resulted in decreasing growth traits. The highest and lowest coefficients of inbreeding were obtained to selection for *BWF* and against *FCR*, respectively.

Simulated correlated responses in carcass traits to selection for growth or feed efficiency traits after one generation of selection are shown in Table 5. Effects of increased *BWF* were higher on carcass traits than effects of increasing *ADG*. Selection against *RFI* has resulted in favorably positive correlated responses in *CWT*, *REA*, *RBT* and *MSR*. Improvement in *CWT* and *MSR* resulting from one generation of selection for *BWF* were smaller than corresponding responses to selection against *RFI*. Selection against *FCR* has resulted lower correlated responses in these traits and higher correlated response in undesirable *SFT* than those with selection against *RFI*. Selection for growth or feed efficiency traits has resulted weak correlated responses in *MQG*, *MCL* and *FCL*. It was observed that *CWT*, *REA*, *RBT* and *SFT* decreased with decreasing *FI*.

Table 6 shows the correlated responses in growth and feed efficiency traits by one generation of selection using different combinations of aggregate indexes with economic values for *ADG* or *BWF* and modified economic values for *FI*. In general, correlated responses in growth and feed efficiency traits were lower when

Table 6. Simulated correlated responses in performance traits to one generation of selection using different combinations of aggregate indexes

Economic selection	*ADG* (kg)	*BWF* (kg)	*MWT* (kg)	*FI* (kg)	*RFI* (kg)	*FCR* (kg)	Total merit (yen)
Combination 1	0.063	9.786	1.328	0.320	0.003	−0.078	8.449
Combination 2	0.067	10.539	1.376	0.364	0.069	−0.041	11.288
Combination 3	0.049	7.355	1.103	0.208	−0.123	−0.142	6.265
Combination 4	0.078	13.379	1.806	0.402	−0.095	−0.137	15.115
Combination 5	0.080	13.611	1.816	0.419	−0.060	−0.119	18.540
Combination 6	0.074	12.774	1.760	0.366	−0.149	−0.165	11.928

Table 7. Simulated correlated responses on carcass traits to one generation of selection using different combinations of aggregate indexes

Economic selection	*CWT* (kg)	*REA* (cm^2)	*RBT* (mm)	*MSR* (No.)	*MQG* (No.)	*SFT* (mm)	*MCL* (No.)	*FCL* (No.)
Combination 1	9.829	1.352	0.463	0.161	0.031	0.527	0.061	0.009
Combination 2	10.259	1.857	0.457	0.072	0.042	0.513	0.061	0.012
Combination 3	7.950	0.241	0.424	0.315	0.015	0.496	0.055	0.002
Combination 4	10.386	2.108	1.542	0.683	0.097	0.375	0.017	0.010
Combination 5	10.695	2.284	1.470	0.612	0.098	0.390	0.021	0.011
Combination 6	9.707	1.788	1.629	0.785	0.094	0.345	0.010	0.007

combinations considered *ADG* with *FI* (first three combinations) than *BWF* with *FI* (last three combinations). Selection responses in growth traits as well as total merit were highest when aggregate index was calculated by economic value for *BWF* with 25% decreased value for *FI* (combination 5).

Table 7 shows the correlated responses in carcass traits by one generation of selection using different combinations of aggregate indexes. The selection responses in all carcass traits, except *SFT* and *MCL*, were greater when aggregate indexes were calculated considering *FI* with *BWF* (last three combinations) than *FI* with *ADG* (first three combinations). The correlated responses for *CWT*, *REA* and *MQG* were greatest when index value was calculated by economic value for *BWF* with 25% decreased value for *FI* (combination 5).

Discussion

Improvement of *RFI* has favorable correlated responses in *ADG* and *BWF* but slightly lower than those to selection against *FCR* from one generation of selection in this study. The favorable correlated responses in *ADG* and *BWF* to selection against *RFI* in the present study are in agreement with the reports by

Richardson et al. (1998) and our previous study (Hoque et al., 2006a). Richardson et al. (1998) noted that steer progeny of low *RFI* (higher feed efficiency) parents grew faster than steers of high *RFI* (lower feed efficiency) parents. Hoque et al. (2006a) estimated positive correlated response in body weight of progeny tested at the test station resulting from selection against *RFI* of their sire population and concluded that selection to lower *RFI* would result in heavier progeny at finish (614 days of age) than selection to lower *FCR*.

Slight differences in estimated coefficients of inbreeding to selection for growth or feed efficiency traits are in agreement with the findings of Oikawa et al. (1997) who showed in their simulation study that heritabilities for and genetic correlation between traits had little effect on inbreeding coefficients but number of selected sires had large effect on it. In other study, Oikawa et al. (2002) estimated coefficient of inbreeding using effective population size (Falconer, 1989) based on 30 males and 600 females to be 0.394, which was slightly lower than the values of the present study. These differences may have resulted from the difference in the number of males used in the simulation and unequal genetic contribution of the ancestry of the animals due to selection.

Most reports on cattle slaughtered prior to maturity indicate that correlated responses in carcass composition to selection for *ADG* are either non-significant or very small (Koch, 1978). Present study has shown that correlated responses in *SFT* and *MSR* were positive to selection for *ADG* or *BWF*, indicating that selection for rapid gain may actually favor fatter animals. Simulated correlated response in *CWT* was highest to selection against *RFI*, which indicates that the use of *RFI* in selection program was more efficient for increasing *CWT* than the use of other studied traits. Weak correlated responses in *MQG*, *MCL* and *FCL* were found to selection for any growth or feed efficiency traits. These results are partially in agreement with the reports by Richardson et al. (1998), who concluded that there were no differences ($p > 0.05$) in visual scores for meat and fat color between carcass from the high efficiency (low *RFI*) and low efficiency (high *RFI*) steers. However, they also observed a small reduction in subcutaneous fat thickness in response to a single generation of selection against *RFI*.

Marbling is the most important trait from an economic point of view in Japan because domestic consumers prefer marbled beef to lean beef. In the European countries, biological efficiency of lean production is the most important breeding objective (Simm et al., 1986). Consumer discrimination against animal fat will probably increase in these countries because of reports on the relationship between the level of consumption of saturated fat in human diets and incidence of geriatric diseases. Simm et al. (1986) proposed selection indexes to improve the efficiency of lean beef production. Conversely, in Japan, it is impractical for focusing the improvement of lean beef production, because Japanese consumers traditionally prefer marbled beef to lean beef. Estimated correlated responses indicating that downward selection of *RFI* (lowering excessive intake of feed) would lead to higher increase in beef marbling than those to selection against either *FCR* or aggregate indexes using different economic values for component traits. The correlated responses in *MSR* of progeny tested at the test station with selection against *RFI* and *FCR* of their sire population were reported to be 0.131 and 0.236, respectively for the same breed (Hoque et al., 2006a), which were lower than those of the present results.

Considering the origin of secondary traits, *FCR* is expressed as a ratio, whereas *RFI* is a linear index. Direct selection on the ratio is complicated by the disproportionate nature by which selection pressure is exerted on the component traits. Linear selection index place a predetermined amount of selection pressure in the traits of interest and therefore a predictable amount of genetic change should result (Arthur et al., 2001). Gunsett (1984) compared the efficiency of direct selection for a two-component trait with a linear index trait derived from the same two components and concluded that the use of linear index increases selection responses as compared with direct selection on the ratio trait. *RFI* is the trait derived from the linear combination of feed consumption and production traits and our study has shown that *RFI* correlated favorably stronger with carcass weight and beef marbling than those of *FCR* with them. The correlated response in undesirable *SFT* was higher to selection against *FCR* than that to selection against *RFI*. These results indicate that the selection program in Japanese Black breed should include *RFI* to obtain heavier carcass and simultaneous improvement of beef marbling, and *RFI* might be better than that of *FCR* to be included in selection program for getting better responses in carcass traits.

The weights of economic value for *FI* affected correlated responses on growth (Table 6) and carcass traits (Table 7). The correlated responses in growth and carcass traits were larger when *FI* was combined with *BWF* instead of *ADG*, might be due to estimated higher heritability for *BWF* than that for *ADG*. The correlated responses in the growth traits, *CWT* and *MSR* were higher when combination 5 was considered for calculating aggregate index, suggesting that including of *BWF* and 25% decreased value for *FI* were better than other combinations of aggregate indexes used in study. Concomitant comparisons of these selections using aggregate indexes with different economic values for *FI* are not found in literature to compare the fact of this study. In this study, no simple solution was found for choosing direct or economic (aggregate index) selection. However, the results of this study suggest that *BWF* was better than *ADG* to be included in selection program for either in aggregate indexes or single trait selection to achieve better correlated responses.

Conclusion

Larger direct and correlated responses in growth and carcass traits were estimated to selection for *BWF* as a single trait or included in aggregate index selection than *ADG*, which encourages the inclusion of final body weight (345 days of age) in the selection program. Downward selection for *RFI* would lead to higher increase in beef marbling than those to selection against either *FCR* or aggregate indexes using different economic values for growth and feed intake. Given the associated problems with selection for ratio traits (*FCR*) and the fact that the correlated responses in *CWT*, *REA*, *RBT* and *MSR* were higher with selection against *RFI* than those against *FCR*, selection for lowering *RFI* should be preferred over selection for lowering *FCR* for getting better correlated responses in carcass traits.

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