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ORIGINAL ARTICLE

Genetic analysis of residual feed intakes and other performance test traits of Japanese Black cattle from revised protocol

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ABSTRACT

The performance test protocol for Japanese Black cattle was revised in April 2002. This resulted in restriction of access to concentrate (based on body weight) and modification of the concentrate's ingredients. Genetic parameters of growth and feed utilization traits of the performance test were estimated using 1304 records using the revised protocol. Residual feed intakes (RFIs) as alternative indicators for feed utilization efficiency were included. (Co)variance components were estimated by EM-REML. Heritabilities for growth traits were between 0.26 and 0.47. Heritabilities for feed intakes and conversions ranged from 0.25 to 0.37 and from 0.03 to 0.29, respectively. Genetic variances and heritabilities were lower for the revised protocol. Highly positive genetic correlations of daily gain (DG) with feed intakes indicated selection on DG is expected to increase feed intake. Selection on feed conversion may lead to higher DG. The heritability estimates for RFIs ranged from 0.10 to 0.33 and were generally higher than corresponding estimates for feed conversion ratios. RFI of TDN showed positive genetic correlations with all feed intakes. The reduction of feed intakes could be expected through selection on the RFI without changing body size. RFIs were considered to be alternative indicators to improve feed utilization efficiency under the new performance test.

Key words: *genetic parameter, growth trait, Japanese Black cattle, performance test, residual feed intake.*

INTRODUCTION

Improvement of livestock feed utilization is important for efficient production of animal protein. Enhancing feed utilization through genetic improvement is a key task for livestock production managers, as feeding represents a major determinant of production cost. Improvement of feed utilization also raises the self-sufficiency rate of feeding, which has recently decreased to 27% in the production of beef cattle in Japan.

Feed utilization efficiency of Japanese Black cattle has been measured and evaluated since 1968 by feed conversion ratio (= feed intake/weight gain) of bull calves at performance test. On 1 April 2002, two revisions became effective for the test protocol. One of them involved the access to concentrate. Previous protocol allowed bulls to access concentrate for 1 h twice a day. This resulted in many excessively fat bulls, which raised concerns about nutritional disorders and fat necrosis. The amount of concentrate is now based on the body weight of tested bulls. The other revision involved a change to the concentrate's ingredients. The concentrate now contains more protein and fewer calories. Such restricted feeding may cause linearity

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between weight gain and feed intake, and is expected to reduce variation in the feed conversion ratio. This raises a question: is the feed conversion ratio during a performance test an appropriate measure for genetic improvement of feed utilization?

Residual feed intake (RFI) has been proposed as an alternative indicator of feed utilization efficiency (Koch *et al.* 1963). RFI is intended to indicate how efficiently the consumed feed is utilized for meat or milk production. Generally, RFI is expressed as the difference between actual feed intake and expected feed requirement for maintenance and production. It can be interpreted that animals with low RFI are superior for feed utilization efficiency. RFI differs from feed conversion ratio, which is represented as a simple ratio of feed intake and weight gain, because it accounts for the net energy requirement of maintenance plus production. Thus it is expected that RFI can be used to measure the feed utilization efficiency of each animal, even under restricted feeding conditions.

Several research groups have estimated the genetic parameters of RFIs in beef cattle (e.g. Herd & Bishop 2000; Arthur *et al.* 2001a,b), but only Hoque and Oikawa (2004) have done so for Japanese Black cattle, using a population of Okayama prefecture. The main purposes of performance testing are to investigate the growth and feed utilization abilities of candidate bulls. Thus it is important to examine the effect of revised testing protocol in Japanese Black cattle.

In the present study, genetic parameters for growth and feed utilization traits of Japanese Black cattle under the revised protocol were estimated and compared with the parameters from the previous performance test. Furthermore, parameters of RFI were estimated and the effectiveness of RFI as an indicator of feed utilization efficiency was discussed.

MATERIALS AND METHODS

Performance tests of bull calves were conducted at the test stations approved by the Wagyu Registry Association, and the feeding regime and management were based on the test protocol defined by the association (Wagyu Registry Association 2000). In the previous protocol, the bulls were allowed *ad libitum* access to concentrate for 1 h twice a day. The current protocol restricts the availability of concentrate from 1.0% to 1.3% of body weight (kg) per day. Moreover, concentrate has been modified to contain more protein and fewer calories. DCP was raised from 10.5% to 12.5% and TDN was lowered from 73.0% to 70.5%. Details of the tests were described in Shojo *et al.* (2005).

Analyzes of 1304 bulls tested at 29 stations from April 2002 to March 2006 were carried out. Growth traits analyzed were withers height, chest girth, chest depth, body weight at the end of the test and daily gain (DG) during the test period. Feed utilization traits analyzed included feed intakes and conversion ratios of concentrate, roughage, DCP and TDN.

Additionally, RFI of concentrate, roughage, DCP and TDN obtained from the bulls were analyzed. Each RFI was derived by:

$$\text{RFI} = \text{actual feed intake} - \text{expected feed requirement.}$$

Expected feed requirement was obtained from multiple regression analysis based on the following regression equation:

$$\text{expected feed requirement} = b_1 \times \text{metabolic weight} + b_2 \times \text{weight gain} + b_3 \times \text{intake of the other feed} + \text{Regression intercept,}$$

where b_1, b_2 and b_3 are partial regression coefficients of metabolic weight, weight gain and intake of the other feed, respectively. Metabolic weight and weight gain are

$$\text{metabolic weight} = \left(\frac{\text{body weight at the beginning} + \text{body weight at the end}}{2} \right)^{0.75}$$

and

$$\text{weight gain} = \text{body weight at the end} - \text{bodyweight at the beginning,}$$

respectively. These variables were included in order to obtain the required feed intake for body maintenance and production. When RFI of concentrate is estimated, roughage intake is substituted for the intake of the other feed. Conversely, the concentrate intake is substituted for RFI of roughage to adjust the quantity of energy brought by the other feed. This term was not included in the analysis for RFIs of DCP and TDN because they were not affected by such factors. Coefficients and intercepts of four feed obtained by multiple regression analyzes are presented in Table 1.

The traits were analyzed by multiple-trait animal models (Henderson & Quaas 1976). Fixed effects of test station (29 levels), year effect at the beginning of the test (4 levels) and month effect at the beginning of the test (12 levels) were included in the model. Linear and quadratic partial regressions of the observations on age in days at the beginning of the test and on body condition score, and linear partial regression on inbreeding coefficient (%) were also included in the model as covariates. Means and ranges of the analyzed traits and covariates included in the models are presented in Table 2. Pedigree of the candidate bulls was traced back to the ancestors born in 1960. As a result, 8988 animals without observations were added and 10 292 animals were evaluated for analyzes.

Variance and covariance components were estimated by a series of two-trait analyzes via animal

Table 1 Partial regression coefficients and intercepts of multiple regressions to calculate residual feed intake at performance test of Japanese Black bulls

Residual feed intake	Metabolic weight	Weight gain	Intake of the other feed†	Intercept
Concentrate	5.87	1.19	−0.42	38.46
Roughage	6.74	1.46	−0.74	98.70
DCP	0.92	0.18	–	−15.27
TDN	5.08	1.13	–	15.70

†Intake of roughage or concentrate for residual feed intake of concentrate or roughage, respectively.

Table 2 Basic statistics, heritability (h^2), genetic (σ_a^2) and phenotypic (σ_p^2) variances of growth and feed utilization traits at performance test of Japanese Black bulls

Trait	Mean	SD	Min	Max	σ_a^2	σ_p^2	h^2†
Covariate							
Age at the beginning, day	233	16.71	200	259	–	–	–
Inbreeding coefficient,%	9.23	6.80	0.26	44.35	–	–	–
Body condition score	5.70	0.67	4	8	–	–	–
Growth trait							
Withers height, cm	122.7	3.6	111.0	132.4	3.31	9.30	0.36
Chest girth, cm	167.0	7.2	146.0	190.0	9.31	25.93	0.36
Chest depth, cm	60.3	2.7	50.5	68.0	1.83	3.87	0.47
Body weight, kg	379.7	45.1	262.0	526.0	411.69	1042.36	0.39
DG, kg gain/day	1.13	0.18	0.60	1.77	0.005	0.021	0.26
Feed intake							
Concentrate, kg	430	77	179	746	867.41	2603.53	0.33
Roughage, kg	470	93	225	912	1465.19	3969.88	0.37
DCP, kg	77	14	41	133	17.16	67.53	0.25
TDN, kg	540	68	293	975	718.18	2682.39	0.27
Feed conversion ratio							
Concentrate, kg/kg gain	3.44	0.66	1.68	7.01	0.0361	0.2489	0.14
Roughage, kg/kg gain	3.77	0.80	1.64	7.79	0.0949	0.3301	0.29
DCP, kg/kg gain	0.61	0.11	0.35	1.04	0.0002	0.0063	0.03
TDN, kg/kg gain	4.32	0.59	2.80	6.97	0.0372	0.2579	0.14
Residual feed intake							
Concentrate, kg	0.00	53.70	−201.66	189.19	416.31	1442.96	0.29
Roughage, kg	0.00	71.16	−212.02	328.51	903.27	2738.88	0.33
DCP, kg	0.00	10.83	−36.73	35.69	5.08	44.02	0.12
TDN, kg	0.00	45.39	−166.08	346.23	139.79	1466.26	0.10

†Standard errors of heritabilities of respective analyzes were within the range of 0.03–0.10 and standard deviations of heritabilities estimated from 18 pairwise analyzes ranged from 0.00 to 0.02. $n = 1304$.

models. A total of 171 two-trait analyzes were carried because we had 19 traits. So variance and heritability estimates for each trait are expressed as the average of 18 estimates. All variance and covariance components were iteratively obtained by REML (Patterson & Thompson 1971; Henderson 1984) using the EM algorithm (Dempster *et al.* 1977). The *n*-th iterative solutions, which satisfied both $\|\hat{\mathbf{G}}^{n+1}-\hat{\mathbf{G}}^{n}\|/\|\hat{\mathbf{G}}^{n}\| \le 10^{-6}$ and $\|\hat{\mathbf{R}}^{n+1}-\hat{\mathbf{R}}^{n}\|/\|\hat{\mathbf{R}}^{n}\| < 10^{-6}$, were regarded as convergent (co)variance components. In the expression, $\| \ \|$ denotes the norm of matrix, and $\hat{\mathbf{G}}^{n}$ and $\hat{\mathbf{R}}^{n}$ are matrices of estimated genetic (co)variance and residual (co)variance at *n*-th iteration, respectively. Standard errors of heritability estimates were calculated by pseudo variance approach and of genetic correlations were approximated by the method of Reeve (1955).

RESULTS AND DISCUSSION

Hereafter we refer the current revised performance test as the new test and the previous one as the old test. The basic statistics and genetic parameters from the old test were found in Shojo *et al.* (2005). Means and SDs of growth traits between the old test (Shojo *et al.* 2005) and the new test (Table 2) were not largely different. Mean of concentrate intake of the new test was 131 kg lower than that of the old test. On the other hand, mean of roughage intake was 104 kg higher than that of the old test. Therefore the means of intake and conversion in concentrate became similar with the means in roughage. It explains that the energy required was supplied by the consumption of more roughage during the new test. Total feed (= concentrate + roughage) intake during the test was decreased from 927 kg to 900 kg, but no change was observed in DCP intake. This shows the effect of feeding cattle a high-protein concentrate.

For all of the measured traits, the estimates of genetic and phenotypic variances were lower in the new test (Table 2) than in the old test (Shojo *et al.* 2005). Heritability estimates of a trait obtained from bivariate analyzes were quite similar (Table 2) and they were also found to be lower in the new test. This means that genetic variance was reduced more than phenotypic variance. Heritability estimates for feed intakes were moderate, ranging from 0.25 to 0.37 in the new test (they ranged from 0.33 to 0.74 in the old test). This may reflect the application of restricted feeding protocol of concentrate started in 2002. Heritabilities for feed conversion ratios were estimated to be quite low. The estimates corresponded to 41% in concentrate, 45% in roughage, 14% in DCP, and 67% in TDN of those estimated from the old test. Growth traits also showed decreased heritabilities, but their phenotypic variances were not so different between the two tests. It is estimable that the revised feeding protocol is one of the causes for lower genetic parameters. These heritability estimates would decrease the accuracy (correlation between predicted and true breeding values) of genetic evaluation and then may reduce the efficiency of genetic improvement in feed utilization traits.

Negative genetic correlations were reported between feed conversion ratios and growth traits in the old test except for the roughage conversion ratio (Shojo *et al.* 2005). In the new test, however, feed conversion ratios had genetic correlations of weak positive or nearly zero with withers height, chest girth and chest depth (Table 3). They showed negative genetic correlations with body weight and DG. Selection based on feed conversion ratio is expected to increase DG and body weight but no significant changes are expected for the other growth traits. These relationships are difficult to interpret. Some of them might be due to restricted feeding. Such intentional feeding system might disturb natural genetic relationships as expected between feed conversion ratio and growth traits. Genetic relationships between feed conversion and intake were not consistent between the old and the new tests. Selection based on TDN or DCP conversion ratios from the new test are expected to reduce feed intakes of both concentrate and roughage through favorable positive genetic relationships (Table 3).

The means of four RFIs were zero (Table 2) indicating the property of the regression analyzes that means of prediction errors from multiple regression equation should become zero. Metabolic weight and weight gain used for calculating RFIs had means of 75.1 kg and 128.3 kg, respectively (data not shown in the table). Heritability estimates of four RFIs ranged from 0.10 to 0.33. The estimates were higher than those of feed conversion ratios for concentrate, roughage and DCP, while RFI of TDN was slightly lower. Hoque and Oikawa (2004) analyzed RFIs of Japanese Black cattle obtained from performance test data in Okayama prefecture between 1971 and 2002. They reported three RFI heritabilities of 0.13, 0.24 and 0.25 calculated as simple regression, ordinary multiple regressions and multiple genetic regressions, respectively. In other breeds, a heritability estimate of 0.16 was reported for the steers of Hereford (Herd & Bishop 2000), 0.39 for

Table 3 Estimated genetic correlations (±SE) of daily gain, feed conversion ratio and residual feed intake with growth trait and feed intake at performance test of Japanese Black bulls

Trait	Daily gain	Feed conversion ratio				Residual feed intake			
		Concentrate	Roughage	DCP	TDN	Concentrate	Roughage	DCP	TDN
Growth trait									
Withers height	0.42 ± 0.17	0.11 ± 0.25	0.06 ± 0.20	0.04 ± 0.44	0.20 ± 0.24	–0.08 ± 0.20	–0.08 ± 0.20	–0.61 ± 0.18	0.05 ± 0.29
Chest girth	0.61 ± 0.14	0.02 ± 0.26	0.08 ± 0.20	–0.10 ± 0.46	0.11 ± 0.25	0.06 ± 0.20	0.08 ± 0.19	–0.21 ± 0.27	0.11 ± 0.28
Chest depth	0.37 ± 0.16	0.00 ± 0.23	0.02 ± 0.19	0.10 ± 0.39	0.10 ± 0.23	–0.13 ± 0.18	–0.11 ± 0.18	–0.22 ± 0.24	0.05 ± 0.26
Body weight	0.86 ± 0.06	–0.11 ± 0.25	–0.03 ± 0.20	–0.33 ± 0.46	–0.06 ± 0.25	–0.09 ± 0.20	–0.03 ± 0.19	–0.46 ± 0.23	–0.02 ± 0.28
Daily gain	–	–0.39 ± 0.24	–0.47 ± 0.18	–0.74 ± 0.23	–0.53 ± 0.21	–0.14 ± 0.22	–0.17 ± 0.21	0.14 ± 0.28	–0.14 ± 0.32
Metabolic weight	0.80 ± 0.08	–0.09 ± 0.25	0.07 ± 0.19	–0.66 ± 0.33	0.03 ± 0.25	–0.06 ± 0.20	0.04 ± 0.19	–0.58 ± 0.19	0.01 ± 0.28
Weight gain	1.00 ± 0.00	–0.39 ± 0.24	–0.47 ± 0.18	–0.75 ± 0.22	–0.53 ± 0.21	–0.21 ± 0.22	–0.29 ± 0.20	0.14 ± 0.28	–0.17 ± 0.32
Feed intake									
Concentrate	0.51 ± 0.16	0.49 ± 0.20	–0.39 ± 0.18	0.57 ± 0.23	0.22 ± 0.24	0.56 ± 0.14	–0.05 ± 0.20	0.28 ± 0.26	0.37 ± 0.25
Roughage	0.13 ± 0.20	–0.12 ± 0.24	0.76 ± 0.08	0.09 ± 0.42	0.29 ± 0.23	0.05 ± 0.20	0.74 ± 0.09	–0.41 ± 0.23	0.33 ± 0.26
DCP	0.96 ± 0.02	–0.34 ± 0.27	–0.47 ± 0.17	–0.46 ± 0.44	–0.48 ± 0.23	0.25 ± 0.22	–0.02 ± 0.21	0.16 ± 0.34	0.16 ± 0.32
TDN	0.80 ± 0.09	0.14 ± 0.27	0.04 ± 0.22	0.31 ± 0.37	0.12 ± 0.28	0.26 ± 0.21	0.21 ± 0.20	–0.18 ± 0.31	0.41 ± 0.28

bulls and heifers of Angus (Arthur *et al.* 2001a) and 0.39 and 0.43 for bulls of Charolais at the ages of 15 months and 19 months, respectively (Arthur *et al.* 2001b). Heritability estimates for RFIs of concentrate and roughage in our study were within the literature values. Additionally, estimated genetic variances of 416.31 kg^2 for RFI of concentrate and 903.27 kg^2 for RFI of roughage indicate the existence of sufficient genetic variations for improving RFIs of Japanese Black cattle.

Genetic correlations of RFIs with growth traits were generally negative or close to zero ranging from –0.61 to 0.14 (Table 3). They indicate that the selection of bulls with smaller RFIs leads to increased body size.

Genetic correlations between feed intake and RFI were 0.56 in concentrate and 0.74 in roughage. In contrast, a genetic correlation between RFI of concentrate and roughage intake was nearly zero (0.05). The estimate between RFI of roughage and concentrate intake was also nearly zero (–0.05). These results suggest that the feed intakes can be reduced if respective RFIs are used for selection. Moreover the intake of one feed may be treated as an independent trait when RFI of the other feed is used as a selection criterion. RFI of TDN positively correlated with concentrate and roughage intakes. Improving RFI of TDN may create favorable responses not only on TDN intake but also on concentrate and roughage intake. These genetic correlations of RFI of TDN with feed intakes were higher and more appreciated than corresponding relationships of feed conversion ratios. However, continuous accumulation of performance records should be important, considering the fairly large standard errors of genetic correlations.

Our study showed that the revisions to the testing protocol reduced the genetic variation of growth and feed utilization traits and also changed the genetic correlation estimates. It seemed that DG might not be effective enough as a selection criterion because of unfavorable genetic relationships of DG with feed intakes. Moreover DG is no longer effective due to the fact that heavier bulls tend to receive more concentrate than lighter bulls in terms of energy requirement for maintenance. This is because metabolic weight is not proportionally related with actual body weight. Accumulation of such feeding can result in large difference in weight gain during the test. RFI may be advantageous, as it simultaneously considers both energy requirement for maintenance and energy requirement to achieve the gain. Selection on RFIs, especially RFI of TDN, can make favorable correlated responses in DG and all feed intakes without changing body size. Although RFI of TDN had a slightly lower heritability than feed conversion ratio of TDN, it shows a certain amount of genetic variation and stronger and better genetic relationships with four feed intakes. Considering the system of current beef cattle production, there is no doubt such a measure will soon become one of the most important characters of the breed. Due to the limited performance test data, the standard errors in this study were considered not to be small. Continuous accumulation and analysis of performance data are necessary for monitoring the change of genetic parameters and immediate reaction in Japanese Black cattle.

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