Heritability and Repeatability Estimates for Reproductive Traits of Japanese Black Cows

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ABSTRACT: Reproductive data collected from more than 20,000 Japanese Black cows of Hyogo and Shimane Prefectures were analyzed. Averages of age at first calving, gestation length, days open and calving interval were 25.1 mo, 289 d, 112 d and 401 d, respectively. Variance components were obtained by REML procedure and the heritability estimate of age at first calving was 0.22. In gestation length the heritability estimate was 0.40 and no permanent environmental effect was estimated. Estimated variance components of calving interval were similar to those of days open and the heritability and repeatability of calving interval were 0.05 and 0.09, respectively. Random farm effects accounted for approximately 10% of phenotypic variations in all traits. Genetic and farm correlations between age at first calving and calving interval were 0.27 and 0.39, respectively. It was found that temporary environment was an important source of variation for calving intervals of Japanese Black. (Asian-Aust. J. Anim. Sci. 2002. Vol. 15, No. 12: 1680-1685)

Key Words: Reproductive Trait, Japanese Black Cattle, REML, Heritability, Repeatability

INTRODUCTION

Genetic evaluation of carcass traits using animal model for Japanese Black has been undertaken since 1991 by Wagyu Registry Association. Currently 890,000 breeding animals are evaluated with 680,000 carcass records. It is now an essential tool for breeding Japanese Black and the increasing genetic trends in marbling score indicate the success of breeding plans.

While carcass characteristics remain as primary breeding objectives for Japanese Black, a demand for incorporating reproductive performances in breeding plan is increasing because of their effects in herd productive efficiency. For a measure of fertility, calving date is often used because it is considered to be less biased in seasonal mating schemes (MacGregor and Casey, 1999). However, in countries where year-round artificial insemination (AI) is taken place for the majority, calving interval (CI) seems to be an appropriate measure of fertility. Although many studies have reported REML estimates of genetic parameters for reproductive performances in dairy breeds (e.g., McGuirk et al., 1999; Weigel and Rekaya, 2000; Pryce et al., 2001), not many have dealt with beef breeds.

A few parameter estimates using reproductive records from Japanese Black cattle are reported (Oyama et al., 1996; Uchida, 2001) because of systematic data collection. However enough information is not yet available to build

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solid breeding strategies on reproductive traits of the breed. The objective of the present study is to estimate genetic parameters of reproductive traits.

MATERIALS AND METHODS

Data preparation

All historical pedigree data and reproductive records were obtained from Wagyu Registry Association. Every year approximately 480,000 calves of Japanese Black are produced from 600,000 breeding cows in Japan. For each birth the parents of the calf. dates of insemination and birth, owner of cow, etc. are kept as reproductive records. Out of the whole database, 65,276 reproductive records from 17,303 Hyogo cows and 59,553 records from 15,612 Shimane cows registered after October 1990 were chosen for analysis because of changes in body condition scoring system. The records covered animals born from 1990 to 2001.

Firstly the cows, which have been used as ET donors or recipients, were excluded because egg collection disturbs their estrous cycles. Then age at first calving (AFC), gestation length (GL), days open (DO) and CI were calculated. In Japan AI produces more than 90% of progenies, and producers sometimes postpone AI to sell calves at appropriate ages. It mostly occurs in the area where the calf market is held only once or a few times per year. Consequently such cows must show longer DO. Meyer et al. (1990) emphasized that ignoring open cows may foreclose the most variable information on genetic difference because they are likely to be genetically worst. However the cows with longer DO in AI breeding system due to their poor reproductive ability cannot be distinguished from the cows with longer DO due to

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intentional decision by producers. In the present study DO was required to be greater than 20 d but less than 365 d. This data edit might remove some genetically worst cows from analyses. The GL records shorter than 241 d, of twins, abortion and stillbirth were also eliminated. The CI of a cow was the sum of DO and following GL. The CI of a cow was eliminated if any of individual records of DO or following GL was not a valid record. If a cow had valid GL at first calving and if her AFC was within 3 SDs. then her AFC was treated as a valid record. The farm owning only one cow was excluded from the analyses of AFC. DO and CI to achieve robust analyses and to avoid confounding between random farm and permanent environmental effects in the repeatability models.

Analytical procedure

Single-trait EM-REML procedure (Dempster et al., 1977) was used to estimate variance components. For the analyses a Fortran computer program was developed using FSPAK (Perez-Enciso et al., 1994) and an algorithm of Meuwissen and Luo (1992) for computing inbreeding coefficient. Although the traits analyzed in the present study were not normally distributed, no transformation was carried out due to little effect on estimates (Meyer et al., 1990; Ponzoni and Gifford, 1994).

Reproductive traits were described by following mixed linear model:

$$y=Xb+(Tf)+Za+(Wc)+e$$

where y=vector of observations, b. f. a. c and e=unknown vectors of fixed effects (year of calving, month of calving, sex of calf and body condition score) and covariates (age at calving, inbreeding coefficients of cow and calf), random farm effects (fitted for AFC, DO and CI), additive genetic effects, permanent environmental effects (fitted for GL, DO and CI) and temporary environmental effects, respectively, and X. T. Z and W=known incidence matrices relating y to each unknown vector. The random vectors were assumed to follow

$$E\begin{bmatrix} f \\ a \\ c \\ e \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} \text{ and } V \begin{bmatrix} f \\ a \\ c \\ e \end{bmatrix} = \begin{bmatrix} I\sigma_f^2 & 0 & 0 & 0 \\ 0 & A\sigma_a^2 & 0 & 0 \\ 0 & 0 & I\sigma_c^2 & 0 \\ 0 & 0 & 0 & I\sigma_c^2 \end{bmatrix}$$

where I and A = identity and additive relationship matrices, respectively. The σ_f^2 , σ_o^2 , σ_o^2 and σ_e^2 = variances of farm effect, additive genetic effect, permanent environmental effect and temporary environmental effect, respectively.

Regardless of the base year for genetic evaluation, all available pedigree data were utilized for calculation of inbreeding coefficients used for covariates. Ancestors could be traced until 1918.

It is reported that bull calves tend to extend GL than heifer calves (McGuirk et al., 1999) and DO may also be affected by sex of calf at previous parturition due to physiological reasons such as recovery of uterus after delivery. Thus two levels of calf sex (bull or heifer) were included for AFC. GL and DO. On the other hand, four levels of sex (bull & bull, bull & heifer, heifer & bull or heifer & heifer) were considered for CI because CI was the sum of DO and GL, and sexes of calves affecting DO and GL were considered different. For example heifer & bull indicates the cow calves a heifer and then conceives a bull. The former calf is considered to affect DO and latter calf affects GL.

Body condition of Japanese Black is scored only once at the registration and it is usually a few months before the first parturition. The score might be genetically determined in some degree. However the farms in the model seemed not to fully explain the treatment for individual cow. In this study the score was included in the model for AFC as a fixed effect to account for nutritional treatment of each cow. Body condition was scored by experienced type classifiers using 1 (emaciated and carrying virtually no fat) to 9 (excessively fat) scale and the heifers scored 1 or 9 cannot be registered. Hence they actually distribute between 2 and 8, and heifers with Score 2 or 8 were treated as Score 3 or 7, respectively, because of limited numbers.

Genetic base year was placed in 1965 and the number of evaluated animals varied from 45,874 to 58,354. Iterations were carried out until average change rate of all variance components in the model became less than 10⁻⁶. Heritability and repeatability estimates were computed as

$$\sigma_a^2/\sigma_p^2$$
 and $(\sigma_a^2 + \sigma_c^2)/\sigma_p^2$.

respectively, where σ_p^2 = phenotypic variance (the sum of all variances). Average information matrices (Johnson and Thompson, 1995) were calculated by a simple expression proposed by Ashida and Iwaisaki (1999) to obtain sampling (co)variances of the REML estimates.

The 16,534 cows, which have both AFC and CI and have not moved to another farm, were selected for bivariate analysis from data sets of the two traits. The analytical model was the same for univariate analyses and the additive genetic, farm and temporary environmental covariances between AFC and CI were assumed. Genetic parameters were estimated by REMLF90 (Misztal, 2001). The cows and their 22,468 ancestors were evaluated.

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RESULTS AND DISCUSSION

Average numbers of records per cow were 4.0 in GL and 3.4 in DO and CI. In GL, the number of records per cow distributed from 1 to 11 and 46.4% of 28,935 cows had less and equal to three records. Summary of analyzed reproductive traits is shown in Table 1. Because GL has small variation and CI is the sum of DO and GL, similar variations were observed in DO and CI. To obtain one calf per year, DO has to be improved more than a month.

Best linear unbiased estimators (BLUEs) for month of calving showed large differences (Table 2). The AFC and CI in spring to summer months tended to be shorter than in fall to winter. The summer parturitions were associated with shorter GL and DO. Although the tendency that bull calf prolonged GL. DO and CI was observed, the differences between BLUEs were trivial. McGuirk et al. (1999) also reported shorter GL in summer and longer GL in bull calf. However MacGregor and Casey (1999) showed no significant effect of previous sex of calf in CI. The BLUEs for body condition score indicated moderate cows (Score 4 to 6) were associated with earlier AFC. In age at calving, no consistent regression coefficients were observed in between DO and CI. The reason for this remains unclear.

Table 3 shows the estimated proportion to phenotypic variance attributed to each random effect. Heritability of AFC was estimated to be 0.22. In the literature a substantial variation in heritabilities for AFC is found. For example, 0.04 for Japanese Black in Hiroshima (Oyama et al., 1996), 0.075 for Boran (Haile-Mariam and Kassa-Mersha, 1994), 0.109 for Japanese Black (Uchida, 2001), 0.22 for Angus (Frazier et al., 1999) and 0.38 for Holstein-Friesian (Ojango and Pollott, 2001) were reported. These reports and our estimates indicate that a large difference in genetic variation between breeds and also between lines within a breed exits for AFC. Economically AFC is important because it determines when an animal begins its productive life and hence could influence the lifetime productivity of an animal (Ojango and Pollott, 2001). Genetic variations are essential to enhance improvement and it is found that AFC of Hyogo and Shimane is heritable.

Heritability estimate of 0.40 was obtained for GL and

Table 1. Summary statistics of reproductive traits

Item	Trait ¹			
Item	AFC (mo)	GL(d)	DO(d)	CI (d)
Mean	25.1	289.2	111.7	401.3
SD	3.0	5.0	65.2	65.3
CV (%)	11.8	1.7	58.4	16.3
No. of observations	24,595	117,044	72,740	72,740
No. of cows with observations	24,595	28,935	21,278	21,278

¹ AFC: Age at first calving, GL: Gestation length, DO: Days open, CI: Calving interval.

was similar to 0.298 (MacNeil et al., 1984), 0.36 to 0.45 (Azzam and Nielsen, 1987) for various (mainly beef) breeds and 0.45 for Holstein-Friesian (McGuirk et al., 1999). Because the genes acting in an additive fashion strongly control GL, a caution is needed for the genetic change in the trait. Although such change in GL is expected to be small due to its limited overall variation and it is unrealistic for GL itself to become a breeding objective, an attention should be paid for the correlated response in GL through selection for other traits.

Because GL indicated small variation, CI and DO showed similar estimates as expected. Heritabilities of both DO and CI were estimated to be 0.05. Literature values are also low and they are estimated to be 0.01 for Holstein (Pryce et al., 2001), 0.01 to 0.03 (Frazier et al., 1999), 0.036

Table 2. Best linear unbiased estimators of effects included in the models

Source	Trait ¹				
Source	AFC (mo)	GL(d)	DO(d)	CI(d)	
Fixed Effect					
Month of calving					
January	0.27	1.33	2.10	5.41	
February	-0.17	1.49	0.49	-3.19	
March	-0.35	0.33	-0.26	-5.50	
April	-0.41	0.05	2.95	-7.97	
May	-0.39	-0.37	1.00	-10.50	
June	-0.27	-0.51	-1.40	-8.22	
July	-0.14	-0.67	-1.60	-4.27	
August	0.10	-0.74	-2.35	0.17	
September	0.21	-0.84	-2.80	2.78	
October	0.24	-0.63	-1.86	8.60	
November	0.55	-0.04	0.37	12.39	
December	0.36	0.59	3.35	10.29	
Sex of calf					
Bull	0.00	0.31	0.70	-	
Heifer	0.00	-0.31	-0.70	-	
Bull & bull	-	-	-	0.60	
Bull & heifer	-	-	-	0.88	
Heifer & bull	-	-	-	0.09	
Heifer & heifer	-	-	-	-1.57	
Body condition score					
3	0.37	-	-	-	
4	-0.01	-	-	-	
5	-0.33	-	-	-	
6	-0.44	-	-	-	
7	0.41	-	-	-	
Regression coefficient ²					
Age at calving (L, yr)	-	0.27	0.51	3.76	
Age at calving (Q, yr)	-	-0.04	0.24	-0.59	
Inbreeding coefficient of	0.01	0.00	0.17	0.22	
cow (L, %)					
Inbreeding coefficient of	0.01	-0.04	-	-0.01	
calf (L, %)					
¹ AFC: Age at first calving, 0	GL: Gestatio	n length.	DO: Days	open, CI:	

AFC: Age at first calving, GL: Gestation length, DO: Days open, Cl: Calving interval.

²L: Linear regression coefficient, Q: Quadratic regression coefficient.

Table 3. Estimates of phenotypic variance, proportion to phenotypic variance explained by each random effect and repeatability

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Item -	Trait ¹				
	AFC	GL	DO	CI	
$\sigma_p^{2/2}$	8.87	27.2	4,284	4,198	
Heritability	0.215	0.403	0.047	0.047	
	±0.026	±0.011	±0.009	±0.009	
Repeatability		0.403	0.087	0.092	
	-	±0.004	±0.005	±0.005	
Proportion to σ_p^2					
Farm	0.095	-	0.095	0.084	
Permanent environment	-	0.000	0.040	0.045	
Temporary environment	0.690	0.597	0.818	0.824	

^TAFC: Age at first calving, GL: Gestation length, DO: Days open, CI: Calving interval.

for cows having at least 50% Holstein genes (Veerkamp et al., 2001), 0.043 (Haile-Mariam and Kassa-Mersha, 1994), 0.047 (Ojango and Pollott, 2001). 0.05 (Oyama et al., 1996) and 0.052 (Uchida, 2001). In the present study, more than 80% of total variations in DO and CI are due to uncontrollable microenvironmental effects. improvement of such traits may be conducted by indirect selection through other correlated trait. However it heavily relies on the accuracy of genetic correlation, which is complex to estimate and is usually labile when selection applies. Even though the heritability estimate may be low. genetic variation certainly exists. It was found that predicted breeding values of CI distributed from -20.0 to 27.6 d and the variation should be used for selection.

In the AI breeding system the farm can be a major source of variation for female reproductive abilities because the time of AI and the condition of individual cow depend on the decisions and management practice of producers. As expected, large farm variances (approximately 10% of total variation) are estimated in all traits (Table 3). Weigel and Rekaya (2000) reported even larger proportion of herdmonth or herd-season variations in days from calving to first insemination for Holstein. It is clear that the female reproductive traits are heavily influenced by farm managing practice, such as feed control or heat detection skill. Although the farm code is included in calving records, they do not always correspond with the actual management practice. For example, the owner and manager of a cow can be different and the code indicates only the owner. A system of recording the code actually reflects the management practice may be necessary to account for such an effect.

No permanent environmental variation was observed in GL and hence the repeatability estimates were equal to the

heritabilities. It indicates that all the environmental effects in GL are temporary. In DO and CI the permanent environmental variances were similar to additive genetic variances. In the literature the repeatabilities of CI are estimated to be 0.06 (Ojango and Pollott. 2001), 0.071 (Haile-Mariam and Kassa-Mersha. 1994) and 0.26 (Pryce et al., 2001). Meyer et al. (1990) reported 0.102 to 0.216 of repeatabilities for days to calving of Hereford. Angus and Zebu cross in Australia. Our estimates lie within the range but close to the lower side of these literature estimates. Permanent environmental effect on each cow is considered to be formed when she is in growing stage. Our low estimates may be due to relatively intensive and uniform cow-calf operation in Japan compared with other countries where cattle are usually kept in extensive grazing condition.

Genetic correlation between AFC and CI showed the cow delivered the first calf earlier tended to have shorter CI (Table 4). Genetic correlation between AFC and CI are estimated to be -0.60 and -0.93 (Frazier et al., 1999), -0.054 (Haile-Mariam and Kassa-Mersha, 1994), 0.05 (Oyama et al., 1996) and 0.89 (Ojango and Pollott, 2001). Mialon et al. (2001) also estimated 0.43 of genetic correlation between age at first positive progesterone test and interval from calving to first positive progesterone test for Charolais. These inconsistent estimates in both signs and magnitude suggest that genetic relationships can be largely varied between breeds and hence they should be estimated for each breed and strain to discuss correlated response.

Improvement in reproductive performance results in increased number of calves born and increased production efficiency of the herds. This is of course the primary objective. Furthermore and maybe more importantly, a ment on genetic diversity and effective population size is expected for Japanese Black. The effective population size of Japanese Black has been sharply decreasing and currently the breed has the size of only 17.2 (Nomura et al., 2001). This is mainly due to intensive use of a few AI sires. which are prominent only in marbling. MacNeil et al. (1989) showed the detrimental effects of inbreeding to reproduction and maternal performance in Hereford females. The average inbreeding coefficient of their females was 26.5% whereas it was 12.2% for cows with records during past two years in our AFC data. Thompson et al. (2000) also showed the association of the levels of inbreeding above 10% with older ages at calving using Holstein. From the

Table 4. Estimates of heritability (diagonals), genetic (upper) and farm (lower) correlations from hivariate analysis

iam (lower) correlations from orvariate analysis					
Trait ¹	AFC	CI			
AFC	0.171	0.269			
CI	0.387	0.038			

AFC: Age at first calving, CI: Calving interval.

mixed models in our combined data, small but unfavorable

 $[\]frac{1}{2} \frac{\sigma^2}{\sigma^2}$ = Phenotypic variance.

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partial regression coefficients of 0.012 mo (0.37 d) and 0.22 d increase in AFC and CI, respectively, were estimated for 1% increase in inbreeding coefficient of cow (Table 2). Rapid increase in inbreeding clearly associates with smaller effective size and results in not only declines in reproductive performances but the enhanced incidence of detrimental alleles including genetic diseases.

In a long term the inbreeding level cannot be reduced as long as Japanese Black is kept as a pure breed. Therefore the strategy to achieve slower increase in inbreeding will be required. Selection for multiple objectives can avoid intensive use of a few specific sires and is a strategy to be considered. Such selection will slowly reject those detrimental genes from population and the reproductive performances seem to be suitable characters for diversification of breeding objective.

Genetic parameters of female reproductive traits for Japanese Black were generally similar to the estimates for other breeds. Heritabilities of DO and CI were estimated to be low whereas AFC and GL were found to be more heritable. It was also found that earlier AFC was associated with shorter CI. Low heritability and large farm effect estimated in CI indicate the difficulty of genetic improvement. Thus both predicted breeding values and farm management should be considered to improve CI of Japanese Black.

IMPLICATIONS

Reproductive performances are important breeding objectives because they directly affect the herd productive efficiency. In this study it became clear that some of the reproductive traits of Japanese Black were largely under environmental control. Even though the relative importance of genetic source may be low, genetic variations certainly exist and they should be used for selection schemes.

REFERENCES

- Ashida, I. and H. Iwaisaki. 1999. An expression for average information matrix for a mixed linear multi-component of variance model and REML iteration equations. Anim. Sci. J. 70:282-289.
- Azzam, S. M. and M. K. Nielsen. 1987. Genetic parameters for gestation length, birth date and first breeding date in beef cattle. J. Anim. Sci. 64:348-356.
- Dempster, A. P., N. M. Laird and D. B. Rubin. 1977. Maximum likelihood from incomplete data via the EM algorithm. J. Roval Stat. Soc. B39:1-38.
- Frazier, E. L., L. R. Sprott, J. O. Sanders, P. F. Dahm, J. R. Crouch and J. W. Turner. 1999. Sire marbling score expected progeny difference and weaning weight maternal expected progeny difference associations with age at calving and calving interval

- in Angus beef cattle, J. Anim. Sci. 77:1322-1328.
- Haile-Mariam, M. and H. Kassa-Mersha. 1994. Genetic and environmental effects on age at first calving and calving interval of naturally bred Boran (zebu) cows in Ethiopia. Anim. Prod. 58:329-334.
- Johnson, D. L. and R. Thompson. 1995. Restricted maximum likelihood estimation of variance components for univariate animal models using sparse matrix techniques and average information. J. Dairy Sci. 78:449-456.
- MacGregor, R. G. and N. H. Casey. 1999. Evaluation of calving interval and calving date as measures of reproductive performance in a beef herd. Livest, Prod. Sci. 57:181-191.
- MacNeil, M. D., L. V. Cundiff, C. A. Dinkel and R. M. Koch. 1984. Genetic correlations among sex-limited traits in beef cattle. J. Anim. Sci. 58:1171-1180.
- MacNeil, M. D., D. D. Dearborn, L. V. Cundiff, C. A. Dinkel and K. E. Gregory. 1989. Effects of inbreeding and heterosis in Hereford females on fertility, calf survival and preweaning growth. J. Anim. Sci. 67:895-901.
- McGuirk, B. J., I. Going and A. R. Gilmour. 1999. The genetic evaluation of UK Holstein Friesian sires for calving ease and related traits. Anim. Sci. 68:413-422.
- Meuwissen, T. H. E. and Z. Luo. 1992. Computing inbreeding coefficients in large populations. Genet. Sel. Evol. 24:305-313.
- Meyer, K., K. Hammond, P. F. Parnell, M. J. Mackinnon and S. Sivarajasingam. 1990. Estimates of heritability and repeatability for reproductive traits in Australian beef cattle. Livest. Prod. Sci. 25:15-30.
- Mialon, M. M., G. Renand, D. Krauss and F. Ménissier. 2001. Genetic relationship between cyclic ovarian activity in heifers and cows and beef traits in males. Genet. Sel. Evol. 33:273-287.
- Misztal, I. 2001. REMLF90 Manual. ftp://nce.ads.uga.edu/pub/ignacy/blupf90/. Accessed June 11, 2001.
- Nomura, T., T. Honda and F. Mukai. 2001. Inbreeding and effective population size of Japanese Black cattle. J. Anim. Sci. 79:366-370.
- Ojango, J. M. K. and G. E. Pollott. 2001. Genetics of milk yield and fertility traits in Holstein-Friesian cattle on large-scale Kenyan farms. J. Anim. Sci. 79:1742-1750.
- Oyama, K., F. Mukai and T. Yoshimura. 1996. Genetic relationships among traits recorded at registry judgment, reproductive traits of breeding females and carcass traits of fattening animals in Japanese Black cattle. Anim. Sci. Technol. (Jpn.) 67:511-518.
- Perez-Enciso, M., I. Misztal and M. A. Elzo. 1994. FSPAK: An interface for public domain sparse matrix subroutines. Proc. 5th World Cong. Genet. Appl. Livest. Prod. 22:87-88.
- Ponzoni, R. W. and D. R. Gifford. 1994. Reproductive and some peri-natal variables in a mixed breed beef cattle herd. J. Anim. Breed. Genet. 111:52-64.
- Pryce, J. E., M. P. Coffey and G. Simm. 2001. The relationship between body condition score and reproductive performance. J. Dairy Sci. 84:1508-1515.
- Thompson, J. R., R. W. Everett and N. L. Hammerschmidt. 2000. Effects of inbreeding on production and survival in Holsteins. J. Dairy Sci. 83:1856-1864.

Uchida, H. 2001. Perspectives of research and project in breeding of Japanese beef cattle. In: Proceedings of the 98th Congress of Japanese Society of Animal Science. p. 15. (in Japanese)
Veerkamp, R. F., E. P. C. Koenen and G. De Jong. 2001. Genetic correlations among body condition score, yield, and fertility in

first-parity cows estimated by random regression models. J. Dairy Sci. 84:2327-2335.

Weigel, K. A. and R. Rekaya. 2000. Genetic parameters for reproductive traits of Holstein cattle in California and Minnesota. J. Dairy Sci. 83:1072-1080.