Variance Component Estimates with Dominance Models for Milk Production in Holsteins of Japan Using Method R

Takayoshi Kawahara*, Yusaku Gotoh, Satoshi Yamaguchi[1] and Mitsuyoshi Suzuki[2]

Holstein Cattle Association of Japan, Hokkaido Branch, Sapporo 010-8555, Japan

ABSTRACT : Fractions of herd-year-season, sire by herd interaction, additive genetic and dominance genetic variances were estimated for milk production traits in Holsteins of Japan using Method R. Inbreeding depressions for milk production traits were also estimated. Estimated fractions of herd-year-season variances ranged from 0.056 to 0.074 for yield traits and from 0.033 to 0.035 for content traits. Estimated fractions of additive genetic variances to phenotypic variances (heritabilities across a herd in the narrow sense) were 0.306, 0.287, 0.273, 0.255, 0.723, 0.697 and 0.663 for milk, fat, SNF and protein yields, and fat, SNF and protein contents, respectively. Estimated fractions of dominance genetic variances ranged from 0.019 to 0.022 for yield traits and from 0.014 to 0.018 for content traits. Fractions of variances for sire by herd interaction were estimated to range from 0.020 to 0.025 for yield traits and 0.011 to 0.012 for content traits. Estimates of inbreeding depression for milk, fat, SNF and protein yields were -36.16 kg, -1.42 kg, -3.24 kg and -1.15 kg per 1% inbreeding for milk, fat, SNF and protein yields, respectively. Estimates of depression per 1% inbreeding for content traits were positive at 0.39×10^{-3}%, 0.31×10^{-3}% and 0.82×10^{-3}% for fat, SNF and protein contents, respectively. (*Asian-Aust. J. Anim. Sci. 2006. Vol 19, No. 6 : 769-774*)

INTRODUCTION

In order to be able to estimate simultaneously random breeding values of animals and fixed environmental effects, Henderson (1973) presented the BLUP procedures. The BLUP method is now used in many countries for national genetic evaluations because, computationally, it is relatively easy to use. Herd management effects have been treated as fixed ever since Henderson (1973) introduced the BLUP method. However, herd management effects have characteristics of both random and fixed effects (Van Vleck, 1987). If herd management effects are treated as random, then a model for genetic evaluation must include effects to consider changes over time of herd management environments and sire by herd interaction to avoid potential biases in estimated breeding value (Schaeffer et al., 2001).

The sire by herd interaction occurs when the differences among daughter groups are not the same in different environments. Small REML estimates of the variance of sire by herd interaction were reported, ranging from 1% to 4% of phenotypic variance for milk production traits (Meyer, 1987; Dimov et al., 1995). The animal model including sire by herd interaction has been used in U.S. national proofs for milk production traits (VanRaden and

Wiggans, 1991). However, the variance of sire by herd interaction for milk production traits is not reported in Holsteins in Japan.

On the other hand, genetic variance for milk production can be partitioned into additive and nonadditive variations. Dominance genetic variance that results from interactions of genes at the same locus as parents is one component that has to be included in nonadditive genetic variance. Furthermore, Kawahara et al. (2002) showed that the average of inbreeding coefficient has increased rapidly in recent years and the depression on inbreeding for milk production traits is easily recognizable in the Holstein population of Japan. Both dominance genetic effects and inbreeding depressions from combinations of parents, as well as additive genetic effects for milk production traits will be applicable to the selection by mating programs (Misztal and Lawlor, 1999). In addition, VanRaden et al. (1992) and Van Tassell et al. (2000) reported that inclusion of dominance genetic effects in genetic evaluation models could avoid overestimation of the additive genetic variance and increase the accuracy of estimates of additive genetic effects (breeding values).

Lately, the estimation of genetic parameters with such complicated models has become feasible, thanks to the development of new statistical techniques and computational procedures in recent years. Method R can be used for estimating the genetic parameters from large data sets and complicated mixed models (Reverter et al., 1994). However, if the numerator relationship matrix in a mixed model is created by using incomplete pedigrees, then

* Corresponding Author: Takayoshi Kawahara. Tel: +81-11-726-3111, Fax: +81-11-726-3135, E-mail: tkawa@holstein.jp
[1] Hokkaido Dairy Cattle Milk Recording and Testing Association, Sapporo 060-0004, Japan.
[2] Obihiro University of Agriculture and Veterinary Medicine, Obihiro 080-8555, Japan.

Table 1. Number of records, levels of herd-calving periods, herd-year-season, sire×herd interaction, calving year-month within region, cows with records, total animals included in additive relationship matrix and parent classes in dominance relationship matrix for milk and fat, protein and solid non fat (SNF)

	Milk and fat	SNF	Protein
Records	32,501,000	3,248,972	2,990,253
Herd-calving periods	23,881	23,871	23,357
Herd-year-season	867,890	867,556	789,455
Sire-herd	553,812	553,503	511,222
Calving year-month within region	2,830	2,814	2,766
Calving age within parity	80	80	80
Cows with records	1,235,950	1,235,401	1,150,665
Total animals	1,724,634	1,724,292	1,662,789
Genetic groups	31	31	31
Dominance classes	3,726,313	3,724,642	3,476,360

Method R may not be resistant to biases caused by assortative mating (Misztal, 1997; Hofer, 1998). Additionally, an accurate estimate of dominance genetic variance requires a large data set (Misztal, 1997).

The objectives of this study are to estimate fractions of herd management (herd-year-season), sire by herd interaction, additive genetic and dominance genetic variances using Method R, and to estimate depressions on inbreeding for milk production traits in Holsteins of Japan.

MATERIALS AND METHODS

Data sets of milk production and pedigree for Holsteins in Japan were provided by the Hokkaido Dairy Cattle Milk Recording and Testing Association and the Holstein Cattle Association of Japan, Hokkaido branch. Records on milk, fat, solid non-fat (SNF) and protein yields, and fat, SNF and protein contents consisted of 305-d (≤240-d) records, with twice daily milking of Holstein cows calving between January 1985 and October 2001. Lactation records including a range of 1st to 5th lactations (18 to 119 in calving months) were used. Consequently, the data used for analysis included 1,235,950 cows with 3,250,100 records on milk and fat yields and fat content, 1,235,401 cows with 3,248,972 records on SNF yield and content, and 1,150,665 cows with 2,990,253 records on protein yield and content (Table 1). The means and standard deviations of milk, fat, SNF and protein yields, and fat, SNF and protein contents were 7,899±1,804 kg, 301±71 kg, 689±155 kg, 253±56 kg, 3.83±0.42%, 8.74±0.30% and 3.18±0.21%, respectively. Those records were adjusted to account for the heterogeneous variance within herd-year using procedures developed by Weigel and Gianola (1993). The means and standard deviations for the records after they were adjusted were 7,899±2,064 kg, 301±83 kg, 689±180 kg, 253±66 kg, 3.83±0.46%, 8.74±0.32% and 3.18±0.22%, respectively.

The mixed model used for this analysis was

$$y = X\beta + Mm + Qs + Za + ZWf + Zc + e$$

Where y is a vector of records for milk production traits; β is a vector including fixed effects for herd and calving periods (1985-1989, 1990-1994 and 1995-2001), calving year-month within each region (14 classes), calving ages within each parity (1st, 2nd and 3rd≤), and a fixed regression on inbreeding coefficients of individual cows which will be reflect inbreeding depression; m is a vector of random herd-year-season effect (season subclasses within herd-year were classified from 1 to 12 flexible-length groups so that the number of records within each subclass was 2 or more); s is a vector of random sire by herd interactions; a is a vector of random additive genetic effects (breeding values); f is a vector of random parental dominance effects; c is a vector of random repeated records effects within cows; and e is a vector of random residual effects. The number of records, animals and levels for each effect are included in Table 1. X, M, Q, Z and W were known incidence matrices relating to respective effects.

The expectations and variances that were assumed are as follows.

$$E\begin{bmatrix} y \\ m \\ s \\ a \\ f \\ c \\ e \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix},$$

$$\text{Var}\begin{bmatrix} m \\ s \\ a \\ f \\ c \\ e \end{bmatrix} = \begin{bmatrix} I_m\sigma_m^2 & 0 & 0 & 0 & 0 & 0 \\ 0 & I_s\sigma_s^2 & 0 & 0 & 0 & 0 \\ 0 & 0 & A\sigma_a^2 & 0 & 0 & 0 \\ 0 & 0 & 0 & F\sigma_f^2 & 0 & 0 \\ 0 & 0 & 0 & 0 & I_c\sigma_c^2 & 0 \\ 0 & 0 & 0 & 0 & 0 & I_e\sigma_e^2 \end{bmatrix}$$

Where σ_m^2 is a variance of herd-year-season effect; σ_s^2 is a variance for sire by herd interactions; σ_a^2 is an additive genetic variance; σ_f^2 is a dominance genetic variance

Table 2. Means (M) and standard deviations (SD) for estimates of fraction of variance for each effect of herd-year-season (hys^2), additive (a^2) and dominance genetics (d^2), sire×herd (sh^2), permanent environment (p^2) and residual (e^2) on variance across herd, and inbreeding depression for milk production traits

	Milk (kg)	Fat (kg)	SNF (kg)	Protein (kg)	Fat (%)	SNF (%)	Protein (%)
	M±SD	M±SD	M±SD	M±SD	M±SD	M±SD	M±SD
hys^2	0.056±0.000	0.061±0.000	0.064±0.001	0.074±0.002	0.033±0.001	0.033±0.000	0.035±0.000
a^2	0.306±0.002	0.287±0.003	0.273±0.003	0.255±0.001	0.723±0.003	0.697±0.001	0.663±0.002
d^2	0.022±0.003	0.019±0.003	0.021±0.002	0.022±0.002	0.014±0.001	0.014±0.002	0.018±0.002
sh^2	0.020±0.001	0.020±0.001	0.023±0.001	0.025±0.001	0.012±0.001	0.012±0.001	0.011±0.001
p^2	0.144±0.003	0.151±0.004	0.155±0.002	0.164±0.004	0.086±0.003	0.064±0.002	0.063±0.002
e^2	0.452±0.001	0.462±0.001	0.465±0.002	0.461±0.001	0.133±0.001	0.181±0.001	0.210±0.001
d^2/a^2	0.073±0.010	0.068±0.010	0.075±0.008	0.085±0.007	0.019±0.002	0.020±0.003	0.027±0.004
inb	-36.16	-1.42	-3.24	-1.15	0.39×10^{-3}	0.31×10^{-3}	0.82×10^{-3}

among parental animals; σ_c^2 is a variance for random repeated records within cows; and σ_e^2 is a residual variance. σ_f^2 is one quarter of the total dominance genetic variance (σ_d^2), and three quarters of σ_d^2 is included in σ_c^2. Therefore, $\hat{\sigma}_d^2$ is estimated from $4 \times \hat{\sigma}_f^2$ and the estimate of the permanent environmental variance ($\hat{\sigma}_p^2$) is $\hat{\sigma}_c^2 - 3\hat{\sigma}_f^2$. A is an additive numerator relationship matrix, F is a dominance relationship matrix among parent classes, and I is an identity matrix. F^{-1} was created using the algorithm defined in Hoeschele and VanRaden (1991). Three generations (until grandparents) were considered when creating dominance parents. Animals born before 1950 were assumed as the base population and, therefore, unrelated. Inbreeding coefficients were calculated by the procedure described by VanRaden (1992). All cows with records were born after 1981. The average inbreeding coefficients for cows that were born between 1981 and 1999 increased from 0.8% to 4.0%. When estimating variance components, inbreeding coefficients were considered in A to account for the reduced variance of Mendelian sampling that results from inbreeding (VanRaden, 1992), but not in F.

Fractions of variance components (Method R estimates) were estimated with the JAADOM program developed by Misztal (1997). This program was used for obtaining solutions from mixed models by iteration on data (Schaeffer and Kennedy, 1986) and second-order Jacobi iteration, and estimating parameters using Method R (Reverter et al., 1994). Method R requires an R value, which is the linear regression for the random effect of solutions predicted from full data on solutions predicted from partial data. The convergence criterion of the R value was set to 1±0.0002 in this study. In addition, the Method R algorithm was applied 10 times for each trait with different partial data sampled randomly by using 1 and prime factors (3, 107, 223, 337, 457, 593, 719, 957 or 997) as seeds, and each partial data set contained approximately 50% of the whole data sampled randomly. Moreover, the cows used for this analysis were restricted to only animals with known parents so that Method R estimates were not affected by biases caused by

assortative mating.

Heritability, in the narrow sense, for each trait was estimated as a fraction of additive genetic variance from the total variance. Also, heritability in the broad sense was estimated as the sum of fractions of additive and dominance genetic variances. Repeatability was estimated as the sum total of fractions of additive genetic, dominance genetic, permanent environmental and sire by herd variances.

RESULTS AND DISCUSSION

Table 2 shows the means and standard deviations of estimated fractions of herd-year-season, additive genetic, dominance genetic, sire by herd interaction, permanent environmental and residual variances for milk production traits. Estimated fractions of herd-year-season variances ranged from 0.056 to 0.074 for yield traits and from 0.033 to 0.035 for content traits. Estimated fractions of additive genetic variances (heritabilities across the herd in the narrow sense) were 0.306, 0.287, 0.273, 0.255, 0.723, 0.697 and 0.663 for milk, fat, SNF and protein yields, and fat, SNF and protein contents, respectively.

Estimated fractions of dominance genetic variances ranged from 0.019 to 0.022 for yield traits and 0.014 to 0.018 for content traits. Dominance genetic variances for production traits have been estimated by many authors in North America. These fractions of dominance genetic variances for milk, fat and protein yields were estimated as ranging from 0.013 to 0.06, 0.016 to 0.24 and 0.016 to 0.053, respectively (Tempelman and Burnside, 1990; VanRaden et al., 1992; Miglior et al., 1995; Van Tassell et al., 2000). Fractions of dominance genetic variances for yield and content traits estimated in this study were higher than those estimated by Miglior et al. (1995). However, these estimates in this study for yield traits were smaller than estimates by Tempelman and Burnside (1990), VanRaden et al. (1992) and Van Tassell et al. (2000).

Fractions of sire by herd interaction variances were estimated to range from 0.020 to 0.025 for yields and from 0.011 to 0.012 for contents. In the case of using first

Table 3. Means (M) and standard deviations (SD) for estimates of across- and within-herd heritabilities in the narrow (h_{ns}^2) and the broad (h_{bs}^2) senses, and across- and within-herd repeatabilities (r) for milk production traits

	Milk (kg)	Fat (kg)	SNF (kg)	Protein (kg)	Fat (%)	SNF (%)	Protein (%)
	M±SD	M±SD	M±SD	M±SD	M±SD	M±SD	M±SD
Across herd							
h_{ns}^2	0.306±0.002	0.287±0.003	0.273±0.003	0.255±0.003	0.723±0.003	0.697±0.002	0.663±0.002
h_{bs}^2	0.328±0.003	0.307±0.004	0.294±0.002	0.276±0.005	0.737±0.003	0.711±0.003	0.682±0.002
r	0.492±0.001	0.478±0.001	0.471±0.002	0.465±0.001	0.834±0.001	0.786±0.001	0.755±0.001
Within herd							
h_{ns}^2	0.324±0.002	0.306±0.003	0.292±0.003	0.275±0.003	0.748±0.003	0.721±0.002	0.688±0.002
h_{bs}^2	0.347±0.003	0.327±0.004	0.314±0.003	0.299±0.005	0.762±0.003	0.735±0.003	0.706±0.002
r	0.521±0.001	0.509±0.001	0.503±0.002	0.502±0.001	0.863±0.001	0.813±0.001	0.783±0.001

lactation records in the population of British Friesian-Holsteins, Meyer (1987) reported that fractions of sire by herd interaction variances were estimated to be higher for yield traits (ranging from 0.021 to 0.043) than content traits (ranging from 0.017 to 0.029). These tendencies, as estimated, for sire by herd interaction variances to be higher for yield traits is in keeping with the results of our study. Also, Dimov et al. (1995) indicated that estimated fractions of variances for sire by herd interaction were very small; between 0.015 and 0.019 using the first lactation model and between 0.019 and 0.021 using the repeatability model for milk and fat yields in U.S. Holsteins, respectively. Further, in the Holstein population of Japan, Wada et al. (1991) found that the effect of sire by herd interaction was estimated to be significant (p<0.01) for milk yield, however, it's square of mean was very small. It was suggested that fractions of sire by herd interaction variances obtained from this study were relatively small, and similar to estimate by Meyer (1987) and Dimov et al. (1995).

Estimates of inbreeding depression for milk, fat, SNF and protein yields were -36.16 kg/%, -1.42 kg/%, -3.24 kg/% and -1.15 kg/%, respectively. Estimates of depression per 1% inbreeding for content traits were positive at 0.39×10^{-3}%, 0.31×10^{-3}% and 0.82×10^{-3}% for fat, SNF and protein contents, respectively. Estimated inbreeding depressions for yield traits were larger than those estimated by Kawahara et al. (2002), whose data was also based on Holsteins of Japan, at -24.8 kg/%, -0.9 kg/%, -2.1 kg/% and -0.7 kg/% for milk, fat, SNF and protein yields, respectively. Also, these estimates of inbreeding depressions by our study were slightly larger than estimates by Short and Lawlor (1992), Miglior et al. (1995), Wiggans et al. (1995) and Van Tassell et al. (2000), whose data was based on North American Holsteins. Increased inbreeding reduces the phenotypic performance (inbreeding depression) and the genetic variation due to Mendelian sampling among the progeny of a particular set of parents. Inbreeding affects estimates of the accuracy of genetic evaluations (Boichard and Lee, 1992). The genetic evaluation accounting for inbreeding depression is also expected to increase estimates

of genetic trends as inbreeding increases (Wiggans et al., 1995). Kawahara et al. (2002) reported that means of inbreeding coefficients in Holsteins of Japan were 4.01% and 5.11% for cows and bulls born during 2000 respectively and have increased rapidly in recent years. However, the affects of inbreeding depression for production traits have been ignored for the national genetic evaluation of Holsteins in Japan (National Livestock Breeding Center, 2003). If genetic evaluations were adjusted to include the inbreeding depression, it is predicted that genetic trends for production traits would increase even further as inbreeding coefficients increase.

Table 3 presents estimates of across- and within-herd heritabilities in the narrow and the broad senses, and across- and within-herd repeatabilities for milk production. Estimates of within-herd heritabilities in the narrow and the broad senses were larger than estimates of across-herd heritabilities in the narrow and the broad senses. Estimates of within-herd heritabilities in the narrow sense were 0.324, 0.306, 0.292, 0.275, 0.748, 0.721 and 0.688 for milk, fat, SNF and protein yields, and fat, SNF and protein contents, respectively. Estimates of within-herd heritabilities in the broad sense for those traits ranged from 0.299 to 0.762 and were slightly larger than estimates of those in the narrow sense. Previous studies for within-herd heritabilities in the narrow sense for production traits in Holsteins of Japan have been provided by various authors (Suzuki and Van Vleck, 1994; Suzuki et al., 1997; Pereira et al., 2001). These estimates of within-herd heritabilities in the narrow sense using the repeatability animal model ranged from 0.29 to 0.33, 0.28 to 0.31 and 0.26 to 0.29 for milk, fat and protein yields, respectively. Within-herd heritabilities in the narrow sense were estimated by our study to be slightly higher than estimates using REML by Suzuki and Van Vleck (1994) and Suzuki et al. (1997), and slightly lower than estimates using Method R by Pereira et al. (2001).

In the present study, estimates of within-herd repeatabilities ranged from 0.502 to 0.521 for yield traits and 0.783 to 0.863 for content traits. On the other hand, estimates of within-herd repeatabilities reported by Suzuki

and Van Vleck (1994), Suzuki et al. (1997) and Pereira et al. (2001) ranged from 0.53 to 0.54, 0.47 to 0.52 and 0.46 to 0.52 for milk, fat and protein yields, respectively. It was suggested that estimates of repeatabilities by our study were within the ranges of the aforementioned literature's estimates.

The development of reproduction techniques in dairy cattle, such as artificial insemination, embryo transfer, embryo splitting, *in vitro* embryo production and multiple ovulation and embryo transfer (MOET), is increasing the incidence of family groups of three-quarter sibs, half sibs, full sibs and clones. A population constructed of families of close relatives may observe remarkably inbreeding depression as inbreeding increases. Furthermore, such large populations of close relatives produce and share similar additive genetic effects and non-additive genetic effects (VanRaden et al., 1992). Therefore, animal models that ignore inbreeding depressions or nonadditive genetic effects have a high possibility of underestimating or overestimating for additive genetic effects. However, dominance genetic variances for production traits estimated by this study were very small. This result suggests that the possibility of overestimating additive effects in the Holstein population of Japan may be low, supposing that dominance genetic effects are ignored in the animal model. Nevertheless, as it is predicted that the incidence of families of three-quarter sibs and full-sibs will increase in proportion as the use of technologies, such as MOET, increases, animal models including nonadditive genetic effects such as dominance genetic effects may be useful in order to increase the accuracy of estimation of additive genetic effects in the Holstein population of Japan.

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