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RELATIONSHIP IN A HERD WITH RELATED
PARENTS AND ITS EFFECT ON BIAS
OF HERITABILITY ESTIMATES

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Introduction

Estimation of genetic parameters in cattle population based on records collected from stations and farms for many years. In such population, some offsprings may array at the same level of generation on pedigree as their parent, bulls may not always mate with cows at random, size of herd may be limited and variable, and there will be genetic relationship among breeding cattle.

Intra-class correlation for sib and regression of offspring on parent techniques are widely applied for estimating heritability of economic characters in animal population[6]. However, the techniques can strictly be used only if no genetic relationship exist among parents. Some estimation procedures for population with related and/or inbred parents have been presented in some papers[2,3,4]. FUJISHIMA and FREDEEN[2] presented general formulae for estimating heritability in a population with related parents by analysis of variance techniques. Furthermore, they revealed that to ignore the genetic relationship among parents would lead to biased estimates of heritability.

The purposes of this study are to estimate the genetic relationship among individuals and inbreeding coefficient in a herd, and to investigate the effect of ignoring the relationship on the bias of heritability estimates in the population.

Materials

The herd under consideration was a population of Holstein Friesian breed which have been kept at Niikappu National Livestock Breding Station, Shizunai, Hokkaido. The date which were actually used for this study, were pedigree records of the daughters calved from 1964 through 1972. The

list of sires and the number of dams mated are given in Table 1. The
number of sires and dams are 18 bulls and 232 cows, though some of the
cows were repeatedly mated with different bulls. This herd is an unclosed
herd, since some bulls and cows have been occasionally imported from abroad.
Pedigree records were traced back to the fifth generation, when available.

TABLE 1.   Sires and the number of dams mated with them

Sire (Code number)	Number of dams mated	Sire (Code number)	Number of dams mated	Sire (Code number)	Number of dams mated
103	7	402	62	1801	16
305	16	404	14	1802	4
308	9	701	14	1967	4
309	6	801	33	1971	3
312	5	1109	5	1972	4
341	3	1603	17	1985	10

Total number of sires=18.
Total cumulative number of dams=232.

Methods

Genetic relationship among individuals was defined as the correlation
coefficient between the genotypes of two individuals by WRIGHT[7], which is
generally called WRIGHT's coefficient of relationship, but hereafter is called
genetic correlation. Also, WRIGHT's coefficient of inbreeding is called in-
breeding coefficient.

Calculations of inbreeding coefficient and genetic correlation among par-
ents were carried out on the basis of the method which was proposed by
ABE and NISHIDA[1]. The computer program prepared by NISHIDA[5] was used
for actual calculation, which was modified in part so that it might be more
useful to our data. Genetic correlations and inbreeding coefficients which
were calculated were as follows:

(1) correlation between mates, which is designated as m'_1,
(2) correlation among dams which were mated same sire, which is
     designated as m'_2,
(3) correlation among sires and dams which mated with other sires,
     which is designated as m_1,
(4) correlation among dams which mated with different sires, which
     is designated as m_2,
(5) correlation among sires, which is designated as m_3,
(6) inbreeding coefficient of daughter, which is designated as F,

(7) inbreeding coefficient of sires, which is designated as F_S,

(8) inbreeding coefficient of dam, which is designated as F_D.

The Actual number of combinations for m's value in this population are presented in the second column of Table 3. Since the number of combinations for m'_2, m_1 and m_2 are too enormous to calculate, these correlations were estimated on a random sample of 500 combinations.

The relationship among parents and/or offspring are presented in Fig. 1. In this figure, X and Y are individuals under consideration, S_X and D_X (and also S_Y and D_Y) are sire and dam of X (and of Y), r_{XY} is genetic correlation between two individuals X and Y, a is path coefficients from gamete to zygote (defined as $\sqrt{1/2(1+F)}$), and b (b') is path coefficient from sire (dam) to its gamete (defined as $\sqrt{(1+F_S)/2}$ or $\sqrt{(1+F_D)/2)}$. From path theory, r_{XY} can be expressed as follows:

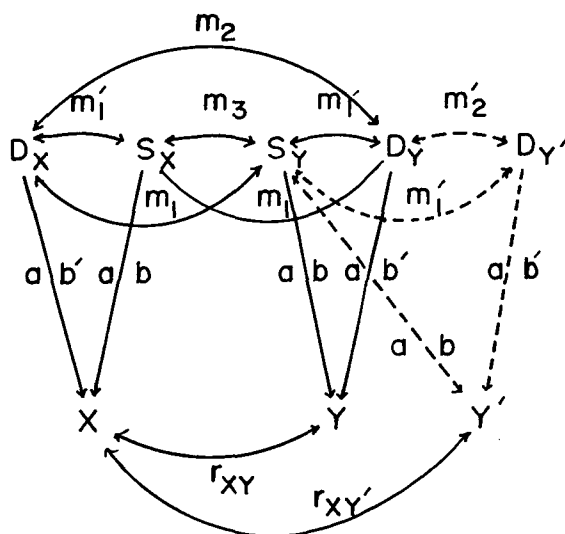$$r_{XY} = 2(ab)(ab')m_1 + (ab')^2 m_2 + (ab)^2 m_3 \qquad (1)$$

Fig. 1.   Relationship between individuals.

When S_X is identical with S_Y and D_X is identical with D_Y, $m_2 = m_3 = 1$ and $m_1 = m'_1$, and r_{XY} in equation (1) becomes genetic correlation between full-sib (and designated as r_1). Similarly, r_{XY} becomes genetic correlation between half-sib (designated as r_2) when S_X is identical with S_Y but D_X is different from D_Y ($m_3 = 1$, $m_1 = m'_1$ and m_2, $m'_2 \neq 1$), and r_{XY} becomes genetic correlation between non-sib when S_X and D_X are different from S_Y and D_Y respectively ($m_1 = m'_1$ and m_2, $m'_2 \neq 1$). These paramaters can be expressed as follows:

$$r_1 = a^2(b'^2 + b^2 + 2m'_1 bb'),$$
$$r_2 = a^2(b^2 + 2m'_1 bb' + m_2 b'^2), \qquad (3)$$
$$r_3 = a^2(2m_1 bb' + m_2 b'^2 + m_3 b^2).$$

Genetic correlation between full-sib, half-sib or non-sib was computed, according to equation (3).

FUJISHIMA and FREDEEN[4] developed general formulae for estimating heritability in a population with inbred and related parents. However the formula which they presented applied to the hierarchical model in which each sire mates with several dams and each dam produces several progenies. In usual dairy cattle populations encountered in practice, the size of full-sib is small, and estimation of heritability bases on analysis of variance with one way classification of sire group only or intrasire regression of daughter on dam. However, the formulae for these techniques can be derived according to same development as they used.

The model for the observation (X_{ij}) on the jth daughter of ith sire may be expressed as follows:

$$X_{ij} = \mu + s_i + e_{ij} \quad (i = 1, \cdots s, \ j = 1, \cdots n_j)$$

were μ is population mean, s_i is the effect of ith sire, e_{ij} is the uncontrolled environmental and genetic deviation attributable to the daughter, s is the number of sire, and n_i is the number of daughters from ith sire. The analysis of variance is as in Table 2. From Table 2, genetic and environmental variance, and heritability may be estimated as follows:

$$\sigma_G^2 = (MS_S - MS_W)/k(\hat{r}_2 - \hat{r}_3),$$
$$\sigma_E^2 = MS_W - (1 - \hat{r}_2) \hat{\sigma}_G^2$$
$$\hat{h}^2 = \frac{\hat{\sigma}_G^2}{\hat{\sigma}_E^2 + \hat{\sigma}_G^2} \qquad (4)$$

TABLE 2. Analysis of variance for half-sib

Source of variation	Degree of freedom	Mean squares	Expected mean squares
Among sire	$s-1$	MS_S	$W + kS$
Within sire	$N-s$	MS_W	W

where $W = (1 - r_2) \sigma_G^2 + \sigma_E^2$,
$\quad S = (r_2 - r_3) \sigma_G^2$
$\quad N = \Sigma n_i$,
$\quad k = (N - \Sigma n_i^2/N)/(s-1)$,
$\quad \sigma_G^2 =$ genetic variance,
$\quad \sigma_E^2 =$ environmental variance.

If the parents do not inbreed nor relate with each other, or if the genetic relationship and inbreeding of parents are ignored, all m's values would be equal to zero and $r_2 = 1/4$ and $r_3 = 0$. In such a condition, the estimate of heritability (designated as $4t$) may be expressed as

$$4t = \frac{4S}{W+S} \tag{5}$$

The relationship of $4t$ with $\hat{h}^2$ or real heritability (h^2) may be expressed as

$$4t = \frac{4\hat{h}^2(\hat{r}_2 - \hat{r}_3)}{1 - \hat{h}^2 \hat{r}_3}, \quad \text{or} = \frac{4h^2(\hat{r}_2 - \hat{r}_3)}{1 - h^2 \hat{r}_3} \tag{6}$$

In the estimation of heritability from intra-sire regression of daughter on dam, the model for the observation (X_{ijk}) on the kth daughter of jth dam (its observation is DX_{ij}) within ith sire family may be expressed as follows:

$$X_{ijk} - \bar{X}_{i..} = \beta(DX_{ij} - \overline{DX}_{i.}) + e_{ijk}$$

where $\bar{X}_{i..}$ is average of ith sire group, $\overline{DX}_{i.}$ is the average of dam mated with ith sire, e_{ijk} is the uncontrolled environmental and genetic deviation attributable to the duaghter, and β is the intra-sire regression of daughter on dam. β may be estimated as follows:

$$b = \hat{\beta} = \frac{\Sigma(X_{ijk} - \bar{X}_{i..})(DX_{ij} - \overline{DX}_{i.})}{\Sigma(DX_{ij} - \overline{DX}_{i.})^2}$$

Heritability estimate can be calculated as follows:

$$\hat{h}^2 = \frac{2b}{1 - (1 - 2b)\,\hat{m}_2'} \tag{7}$$

If parents are not ralated or ignoring the genetic relationship among parents (then $m_2' = 0$),

$$\hat{h}^2 = 2b \tag{8}$$

The relationship of $2b$ with $\hat{h}^2$ or h^2 may be expressed as follows:

$$2b = \frac{\hat{h}^2(1 - \hat{m}_2')}{1 - \hat{h}^2 \hat{m}_2'}, \quad \text{or} = \frac{h^2(1 - \hat{m}_2')}{1 - h^2 \hat{m}_2'} \tag{9}$$

Results and Discussion

Average genetic correlations among parents $(m$'s values) are presented in Table 3. The average estimates of m_1', m_2', m_1, m_2 and m_3 were 0.08, 0.10, 0.12, 0.08 and 0.37 respectively. Comparing m_1' with m_1, it is found

TABLE 3.   Average genetic correlations among parents
and inbreeding coefficient

Parameter	Actual total number of combinations	The number of sampled combinations	Estimates Average	Range
m'_1	232	232	0.08	0.00~0.59
m'_2	3138	500	0.10	0.00~0.59
m_1	3944	500	0.12	0.00~0.71
m_2	23658	500	0.08	0.00~0.59
m_3	153	153	0.37	0.00~0.55
F_S			0.01	0.00~0.10
F_D			0.04	0.00~0.31
F			0.04	0.00~0.31

that the relationship between cows and bulls that actually mated ($m'_1=0.08$) was less than the relationship between cows and bulls that did not mate ($m_1=0.12$). If matings had been practiced at random in this station, both m'_1 and m_1 value would be equal to 0.12, that was the weighted mean of m'_1 and m_1. This fact shows that in general, the mating system practiced in this station was unrelated mating rather than random mating though some pairs of full-sib or half-sib mated. m'_2 value is larger than m_2, and this shows that sib cows tended to mate with the same bull. If taking unrelated mating into consideration as described above, this tendency in mating would be due to avoidance of inbreeding rather than to development of family lines. The relationship among sires is very high ($m_3=0.37$) in comparison with other m's values. This shows clearly that the sons from the specified sires have been saved as breeding bulls in this station.

Average inbreeding coefficients of sires, dams and daughters are 0.01, 0.04 and 0.04 respectively, as presented in Table 3. Sires were inbred less than dams and daughters. The main cause of this discrepancy might be that the highly inbred bulls have been avoided to save for breeding, and that good breeding bulls have been occasionally imported from abroad.

Genetic correlations among full-sib, half-sib and non-sib in the daughter population which were calculated according to equation (3) are presented in Table 4. Average estimates of r_1, r_2 and r_3 are 0.53, 0.30 and 0.12 respectively. In the population that parents are not inbred nor related with each other, the corresponding value of r_1, r_2 and r_3 are 0.50, 0.25 and 0.00 respectively. The rate of increase in genetic correlation was larger among non-sib than among full-sib or half-sib.

The results obtained for the relationship among parents or daughters, apparently indicate that the parents related with each other in this herd and

TABLE 4.   Average genetic correlations among
full-sib, half-sib and non-sib

Parameter	Average vaues of estimates
r_1	0.53
r_2	0.30
r_3	0.12

the mating system was unrelated mating rather than random mating.

In order to investigate the bias in heritability estimates which were calculated according to equation (6) or (9), are given in Table 5, when heritabilities are 0.2, 0.4, 0.6 or 0.8. In this table, the bias in each of the heritability estimates are expressed as the ratio of estimates ($4t$ or $2b$) to heritability (h^2); that are, $4t/h^2$ or $2b/h^2$. As shown in this table, ignoring the genetic relationships among parents leads the heritability estimates from intra-sire correlation ($4t$) to underestimation by 24 to 18 percent, and the heritability estimates from intra-sire regression of daughter on dam ($2b$) to underestimation also, but the biases are only 8 to 2 percent, in this population. It also shows the discrepancy between $4t$ and $2b$.

TABLE 5.   Bias of heritability estimates due
to ignoring the genetic correlation
among parents in this population

h^2	$4t$	$4t/h^2$	$2b$	$2b/h^2$
0.2	0.15	0.76	0.18	0.92
0.4	0.31	0.78	0.38	0.94
0.6	0.48	0.80	0.58	0.96
0.8	0.65	0.82	0.78	0.98

Summary

In this study, the genetic correlation among parents and inbreeding coefficient which are necessary for estimating genetic parameters in the herd encountered in practice were estimated, and its effect on the bias of heritability estimate was investigated. The population considered was a herd of Holstein Friesian breed which had been kept in Niikappu National Livistock Breeding Station.

Result obtained for genetic correlation among parents show that in this herd most of parents were more or less inbred and related with each other, and that the mating system which had been practiced in this station was

unrelated mating rather than random mating. If ignoring the genetic rela-
tionship among parents for estimating the heritability of this population, the
estimate obtained from intra-sire correlation techniques would lead to down-
ward bias but the estimates obtained from intra-sire regression of daughter
on dam would lead to minor downward bias.

Acknowledgement

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