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L. Dale Van Vleck

University of Nebraska - Lincoln, dvan-vleck1@unl.edu

C. L. Hart

Cornell University, Ithaca, New York

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HERITABILITY ESTIMATES WHEN DAMS AND DAUGHTERS ARE IN THE SAME AND DIFFERENT HERDS

L. D. VAN VLECK AND C. L. HART
Cornell University, Ithaca, New York

ABSTRACT

The regression of daughter on dam deviations of Holstein first-lactation milk production from herd-mate averages was computed for 38,440 pairs of records made in the same herd and for 10,256 pairs of records where the daughter was in one herd and the dam in another. The corresponding heritability estimates were .42 and .40, respectively, which suggest an environmental covariance of .01 between records of daughters and dams in the same herd. Other analyses were conducted for dams with two daughters with records where 1) both had records in the same herd as the dam, 2) only one had a record in the same herd as the dam, 3) the daughters were full sibs, in the same herd as the dam, 4) the daughters were full sibs, only one in the herd of the dam. These analyses also indicated no evidence for much environmental covariance between daughter and dam records in the same herd. The environmental covariance between records of maternal half-sisters in the same herd is apparently small, but the environmental covariance between records of full sibs in the same herd may be important—.06 to .12 of total variance. Genetic maternal variance was not excluded as a source of likeness between the records of maternal relatives.

Bradford and Van Vleck (1) reported a difference between heritability estimates from daughter-dam regression and from intraclass correlation of artificially sired (A.I.) paternal half sibs of .44 and .25, respectively, for first-lactation milk records of Holstein cows expressed as deviations from herd-mate averages. A later study by Van Vleck and Bradford (3) reported the same pattern for the five major dairy breeds. There are several possible reasons for obtaining such differences. Three of the most obvious are 1) the existence of an environmental covariance between daughter and dam records made in the same herd although necessarily two or three or more years apart in time for first-lactation records, 2) the possibility of genetic maternal effects which would increase the likeness between daughters and dams but not among paternal half-sibs, and 3) a relatively large additive-by-additive genetic variance. Van Vleck and Bradford (4), however, in an analysis of daughter-dam and grand-daughter-granddam regressions found no evidence for additive-by-additive genetic variance. The present study was conducted primarily to determine the importance of environmental covariance between daughter and dam records by comparing the daughter-dam regression for pairs where both were in the same herd with that for pairs in different herds.

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MATERIALS AND METHODS

First-lactation records ($2 \times$, 305-day, M.E.) of Holstein cows coded as registered were taken from the files of the New York Dairy Records Center. First records were defined as beginning before 35 months of age. The approximately 130,000 first records were begun during the period 1950 through 1963. The records were sorted into two orders: one by cow number and one by dam number. These two files were then matched to find daughter-dam pairs, irrespective of the herd where the records were made. The records were expressed as deviations from herd-mate averages for analysis. The herd-mate average is computed from the regression of the true herd-mate average on the actual mature equivalent average. Records of all cows freshening in the same year-season except those of paternal half-sibs are included in the herd-mate average. The regression coefficient is $n/(n+1)$ where n is the number of herd-mates. The breed-year-season average is used for both means in the regression equation. This procedure has been described in detail by Heidhues, Van Vleck, and Henderson (2).

Several analyses were made. The regression of daughter on dam deviations was computed for records of all daughter and dam pairs in the same herd. A similar analysis was made for all pairs of records where the daughter and dam were in different herds for the first lacta-

tion. Four other analyses were made for records of 1) two daughters by different sires and their dam in the same herd (maternal half-sibs in the same herd); 2) two daughters by different sires, one in the herd of their dam and the other in a different herd than the dam (maternal half-sibs in different herds); 3) two daughters by the same sire and their dam in the same herd (full sibs in the same herd); and 4) two daughters by the same sire, one in the same herd as their dam and the other in a different herd than their dam (full sibs in different herds). The record of a twin or duplicate records of the same cow were eliminated. Examination of the data had revealed numerous duplicate records arising because of transfers from one herd to another during the first lactation.

The numbers of records, and means and variances of the records for the various analyses are given in Table 1.

The following equations were used to evaluate the probable importance of additive genetic variance, additive maternal genetic variance, environmental covariance, dominance variance, and additive-by-additive genetic variance. The notation is primarily that of Willham (5), with the addition of environmental covariances and additive-by-additive variance.

$$2b_{da} = A_o^2 + 2\frac{1}{2} A_o A_m + A_m^2 + \frac{1}{2} A_{oo}^2 + 2C_{da}^2$$

$$2r_{fs} = A_o^2 + 2 A_o A_m + 2 A_m^2 + \frac{1}{2} A_{oo}^2 + \frac{1}{2} D_o^2 + 2C_{fs}^2$$

$$4r_{ms} = A_o^2 + 2 A_o A_m + 4 A_m^2 + \frac{1}{4} A_{oo}^2 + 4C_{ms}^2$$

where b_{da} is the daughter-dam regression, r_{fs} is the full sib correlation, r_{ms} is the maternal half-sib correlation, A_o^2 is additive genetic variance, A_m^2 is additive maternal genetic variance, $A_o A_m$ is the covariance between maternal additive genetic and additive genetic effects, A_{oo}^2 is additive-by-additive genetic variance, D_o^2 is dominance genetic variance, and C^2 is environmental covariance (dd between daughter and dam, fs between full sibs, and ms between maternal half-sibs in the same herd). When the pair of records are from animals in different herds the C^2 term drops out.

Unfortunately, there are more unknowns than equations; therefore, solutions could not be obtained for each of the above components.

RESULTS AND DISCUSSION

The estimated regressions and correlations are given in Table 2 in the form of heritability estimates, i.e., the regression or correlation coefficients times the inverse of the additive relationship between the pair of relatives.

TABLE 1
Means (lb) and variances (10 lb²) of records for the various analyses

Analysis	No. of sets	Means				Variances (deviations)				
		Daughter	Pair One	Pair Two	Herd-mate	Dam	Herd-mate	Pair One	Pair Two	Dam
Daughter and dam										
Same herd	37,440	13,182 ^a	13,427	13,039	12,779	13,039	58,187 ^a	43,703
Different herds	10,256	12,874 ^b	12,996	13,032	12,912	13,032	58,492 ^b	46,187
Maternal sibs										
Same herd	6,605	13,023 ^a	13,184	13,208	12,724	13,208	53,415 ^a	40,137
Different herds	1,691	13,378 ^a	13,552	13,480	13,107	13,480	53,034 ^a	43,466
Full sibs										
Same herd	1,509	13,127 ^a	13,176	13,094	12,716	13,094	52,249 ^a	33,709
Different herds	176	13,146 ^a	13,429	13,051	13,063	13,051	73,579 ^a	38,791

^a Daughter and dam in same herd.

^b Daughter and dam in different herds.

TABLE 2
Heritability estimates from daughter-dam regression and sib correlation

Analysis	Daughter dam regression		Sib correlation
	Pair One With Same Dam	Pair Two	
Daughter and dam			
Same herd	.42 ^b (.012) ^a
Different herd	.40 ^c (.022)
Maternal sibs			
Same herd	.38 ^b (.028)	.45 ^b (.029)	.41 ^b
Different herd	.47 ^b (.053)	.54 ^c (.058)	.40 ^c
Full sibs			
Same herd	.49 ^b (.058)	.26 ^b (.062)	.52 ^b
Different herd	.40 ^b (.207)	.07 ^c (.181)	.27 ^c

^a Standard error of estimate.

^b Pair of cows having records in the same herd.

^c Pair of cows having records in different herds.

The first two estimates provide an estimate of the environmental covariance between daughter and dam deviations. Thus, C_{dd}^2 is estimated to be .01 of the total variance. Therefore, .40 estimates $A_o^2 + 2\frac{1}{2}A_oA_m + A_m^2 + \frac{1}{2}A_{oo}^2$.

The analysis of maternal half-sibs in different herds provides another, although related, estimate of the environmental covariance between daughter and dam records in the same herd, $C_{dd}^2 = -.03$. This is in agreement with the estimate in the previous paragraph, that the environmental covariance is small between daughter and dam records.

The environmental covariance between maternal half-sibs in the same herd can be estimated by comparing the maternal half-sib correlations from Lines 3 and 4 of Table 2. This comparison yields $C_{ms}^2 = .00$.

Similarly, the environmental covariance between full sibs, estimated from Lines 5 and 6, is $C_{fs}^2 = .12$. However, both these correlations are estimated from limited data, especially the correlation on Line 6. If, in fact, the true full sib correlation between a pair in different herds is .40, then $C_{fs}^2 = .06$ for full sibs in the same herd. Comparing the full sib correlation with the average daughter-dam regression for the analysis of full sibs in the same herd gives an estimate of $C_{fs}^2 = .07$, if only additive genetic variance contributes to the genetic likeness between daughter-dam and full sib pairs. The data do not allow the testing of this assumption.

Note that the estimates .38 and .45 on Line 4 of Table 2 estimate the same thing. The same is true for estimates .49 and .26 on Line 6.

Note also that the estimates of daughter-dam regression in the same herd contain a portion due to genotype-by-environment interaction. This cannot be separated from the portion due to environmental covariance between daughters

and dams in the same herd. The sib correlations in the same herds also contain a portion due to genotype-environment interaction, but again this cannot be separated from the environmental covariance. The environmental covariance appears small for daughters and dams and maternal sibs in the same herds. Thus, there is no evidence for the possibility of genotype-environment interactions.

The average doubled daughter-dam regression is about .40 and four times the maternal half-sib correlation is also about .40 for pairs in different herds. In the previous study (4), four times the granddaughter-granddam regression was about .40; and four times the intrasib correlation was about .25. Some idea of the importance of additive genetic maternal and additive-by-additive genetic variance can, perhaps, be obtained from equating these estimates to their expectations.

$$\text{Daughter-granddam: } A_o^2 + 2\frac{1}{2}A_oA_m + A_m^2 + \frac{1}{4}A_{oo}^2 = .40$$

$$\text{Daughter-dam: } A_o^2 + 2\frac{1}{2}A_oA_m + A_m^2 + \frac{1}{2}A_{oo}^2 = .40$$

$$\text{Maternal sibs: } A_o^2 + 4A_oA_m + 4A_m^2 + \frac{1}{4}A_{oo}^2 = .40$$

$$\text{Paternal sibs: } A_o^2 + \frac{1}{4}A_{oo}^2 = .25$$

Additive-by-additive genetic variance is apparently near zero. Therefore, $A_o^2 = .25$, $A_oA_m = .075$, and $A_m^2 = -.0375$. However, this is an inadmissible set of estimates since, according to theory, A_m^2 cannot be negative.

After setting $A_{oo}^2 = 0$, the middle two equations show that $A_m^2 = -\frac{1}{2}A_oA_m$. The only way A_m^2 can be positive is if A_oA_m is negative.

The inconsistency found when solving all four equations apparently is between the paternal-sib equation and the other equations. If some

reliance could be placed on the full-sib value found in this study, then the inconsistency may be further delineated. First, assume $D_o^2 = 0$, and use the two extreme estimates of .52 and .27 for the full-sib correlation. The solutions to the equations (daughter-dam, full sib, and maternal sib) are $A_o^2 = .64$, $A_o A_m = -.12$, $A_m^2 = .06$; and $A_o^2 = .14$, $A_o A_m = .13$, $A_m^2 = -.065$. The first set of solutions is admissible but not very likely. The second is inadmissible. Both sets are inconsistent with the paternal half-sib correlation.

If, $\frac{1}{4}D_o^2 + 2C_{fs}^2 = .12$, then the solutions based on the .52 estimate of the full-sib correlation, are $A_o^2 = .40$, $A_o A_m = A_m^2 = 0$. This would appear to be a likely solution, but is inconsistent with the paternal-sib correlation.

CONCLUSIONS

The results, even for relatively large numbers of sets of relatives, are inconclusive. The following points, however, can be put forward: 1) There is little evidence for much environmental covariance between daughter and dam first-lactation deviations. 2) The environmental covariance between maternal half-sibs in the same herd is small. 3) The environmental covariance between deviations of full sibs in the same herd probably is between .06 and .12 of the total variance. 4) The estimates from

daughter-dam regression, full-sib correlation, and maternal half-sib correlation appear to be consistent with each other only if additive genetic variance is the only reason for genetic likeness between relatives. However, this conclusion is not in agreement with the much lower estimate obtained from paternal half-sib correlation in previous studies. The inconsistency seems unlikely to be explained by genetic maternal variance.

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