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Abstract

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Keywords

Mixed Model Methods, Best Linear Unbiased Prediction, Accuracy, Computer Simulation, Performance Testing

Disciplines

Agriculture | Animal Sciences

Comments

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USE OF AN ANIMAL MODEL IN SITUATIONS OF LIMITED SUBCLASS NUMBERS AND HIGH DEGREES OF RELATIONSHIPS¹

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ABSTRACT

Breeding value estimation procedures for two traits with moderate and high heritability were evaluated by using a single-trait animal model and computer-simulated data designs. Of interest were the effects of differing numbers of animals and degrees of relationships among animals within and across contemporary groups (tests). Test effects were assumed fixed and animal effects were assumed random. Family size, number of families per contemporary group, and degree of genetic relationships within and across contemporary groups were varied to determine interrelationships among the factors. Results were compared on the basis of accuracy by using both the correlation of true and estimated breeding values and the prediction error variance obtained from the inverse of the coefficient matrix of the mixed-model equations. Small contemporary groups in conjunction with evaluation of closely related families caused average accuracy to decrease relative to that obtained with the same number of unrelated animals because genetically related animals were less accurately evaluated relative to one another. Connecting contemporary groups with a genetic relationship matrix formed a large set of interdependent equations and improved the average accuracy of predicted breeding values. The slight decrease in accuracy for genetically related animals was more than offset by the increase in accuracy of evaluation for their unrelated test mates because the proportion of fixed effects to random effects was smaller. Care must be exercised in designing evaluation schemes involving small populations, and the decision of which fixed effects to include in the model is critical.

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Introduction

Since publication of Henderson's seminal paper (1973), mixed-model methodology has been applied extensively to genetic evaluations of dairy and beef cattle. Much of the research in this area has concentrated on refinement of

algorithms to handle large, complex data sets that consist of animals with differing numbers and degrees of genetic relationships (hereinafter referred to as direct genetic ties). Many studies involved traits that were lowly heritable and often sex-limited; in both situations, information on relatives is very important.

In general, inclusion of the additive genetic relationship matrix (A) increases accuracy of genetic evaluations (Kennedy and Moxley, 1975; Pollak et al., 1977; Jensen, 1980; Carlson et al., 1984). Very little work, however, has been conducted to ascertain the behavior of mixed-model equations in conditions of small populations, moderate to highly heritable traits, and closely related animals. In this paper, the influence of differing degrees of

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genetic relationships, number of fixed effects, contemporary group size, and total data set size on the accuracy of breeding value estimations is examined.

Materials and Methods

Animal Model with Relationships

An animal model was chosen, as opposed to a sire model, under the assumptions that animals being tested were potential herd sires and that performance records of individuals were available for moderate to highly heritable traits. In addition, by including the additive genetic relationship matrix, sires with no performance records of their own could be evaluated, and records of sires could contribute to the evaluation of their progeny. All reports to date have been favorable regarding the benefits of including genetic relationships in breeding value estimation procedures. Henderson (1975c,d) demonstrated how inclusion of sire relationships improved accuracy of evaluation and Pollak and Quaas (1981) examined the possibility of eliminating genetic groups by using the complete relationship matrix to account for genetic differences among herds and for genetic trend. Designed genetic ties such as reference AI sires in beef cattle have proved useful, though recent work suggests that naturally occurring ties may now be sufficient (Wilson, 1982; Mabry et al., 1987).

The animal model used in this study assumed that animals of a single breed were evaluated and that the only appropriate fixed effect was due to confounded effects of location and season (test effect). The only random variable in the model was breeding value. Heritabilities (h^2) of two traits under consideration were assumed to be .40 and .50 for the moderate and highly heritable traits, respectively, and each trait was evaluated with a single-trait model. Results will be presented for $h^2 = .40$ because patterns were similar for both h^2 .

For an animal model that includes both animals with records and genetically related animals with no records,

$$y = X\beta + Zu + e, \quad [1]$$

where y is an $n \times 1$ vector (augmented to $t \times 1$ with the addition of a $t - n$ null vector when evaluating animals without records) of observations on the trait of interest; X is an $n \times p$ incidence matrix; Z is a $t \times t$ matrix equal to

an $n \times n$ identity matrix relating observations to the animals that made them and augmented by null rows and vectors for animals that are to be evaluated but have no records; β is a $p \times 1$ vector of unknown fixed effects; u is a $t \times 1$ vector of random breeding values, which can be partitioned into u_1 , an $n \times 1$ vector representing animals having records, and u_2 , a $(t - n) \times 1$ vector for related animals with no records; and e is an $n \times 1$ vector of random errors. Thus,

$$E \begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \end{bmatrix}, \text{ and}$$

$$V \begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} V & A\sigma_G^2 & I_n\sigma_e^2 \\ A\sigma_G^2 & A\sigma_G^2 & 0 \\ I_n\sigma_e^2 & 0 & I_n\sigma_e^2 \end{bmatrix},$$

where $V = A\sigma_G^2 + I_n\sigma_e^2$, A = additive genetic relationship matrix, σ_G^2 = additive genetic variance, and σ_e^2 = residual variance.

If the ratio of the residual variance to the additive genetic variance (σ_e^2/σ_G^2) is known, Henderson's (1973) mixed-model equations may be written as

$$\begin{bmatrix} X'X & X'Z & 0 \\ Z'X & Z'Z & 0 \\ 0 & 0 & 0 \end{bmatrix} + A^{-1}k \begin{bmatrix} \beta \\ \hat{u}_1 \\ \hat{u}_2 \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \\ 0 \end{bmatrix}, \quad [2]$$

where $k = \sigma_e^2/\sigma_G^2 = (1 - h^2)/h^2$; h^2 = heritability of the trait being evaluated and 0 represents rows and columns of zeros required to include evaluation of animals with no records that are related to animals with records.

Test effects were absorbed into the random animal effects, and A^{-1} was built directly by using Henderson's (1975b) method. This resulted in the system of equations:

$$\left[\begin{array}{cc} Z'MZ & 0 \\ 0 & 0 \end{array} \right] + A^{-1}k \left[\begin{array}{c} \hat{u}_1 \\ \hat{u}_2 \end{array} \right] = \left[\begin{array}{c} Z'My \\ 0 \end{array} \right], \quad [3]$$

where $M = I_n - X(X'X)^{-1}X'$.

Measure of Variability

Henderson (1973) showed that mixed-model solutions have minimum prediction error variance (PEV) that is measured by the variance of prediction error, $\text{Var}(\mathbf{u} - \hat{\mathbf{u}})$. This measurement is useful because it is easy to calculate if the inverse of the mixed-model coefficient matrix can be obtained directly, and it is related to accuracy, which is defined as the correlation between the estimated and true breeding values (Henderson, 1973; Berger, 1983). Therefore, accuracy and PEV were the criteria by which the designs in this study were compared.

Modeling Procedures

The computer programs required for generation of coefficient matrices and the resulting PEV were written in FORTRAN 66. Composite literature values (Wood, 1986) for standard deviations of gain (.12) and backfat (.10) of swine (traits with moderate to high h^2) were used to generate error variances, which were calculated as standard normal deviates. The variance ratios (k) were obtained from the h^2 . After the animal equations with fixed effect absorbed were built, constants needed to adjust the equations for information from the relationship matrix were added to the appropriate elements of the coefficient matrix. That matrix was inverted by using the LINVIF routine in IMSL (1984), and PEV were calculated from the diagonal elements of the inverse. After all $\text{Var}(\mathbf{u} - \hat{\mathbf{u}})$ had been accumulated for each class, the average was calculated.

Because a direct inverse of the coefficient matrix was desired, size and numbers of contemporary groups and total number of animals were kept small. Designs examining relationships included animals with no genetic ties, full-sib ties and half-sib ties. Family size (number of sibs) varied from one for unrelated animals to three for full sibs. Numbers of families were constrained by total number of

animals in the contemporary groups, but 16 families was the average test group; 5 families and 25 families represented the two extremes. The number of unrelated animals was based on the total number of animals in the multiple-member families.

Direct genetic ties across contemporary groups are of interest because comparison of all animals in different test groups is then possible. In this study, half-sibs (sire ties) were used to tie contemporary groups together. A direct genetic tie was defined as a relationship between animals in different families through a common relative. Number of ties was based on the number of sets of animals so tied. Also of interest was the question of how additional ties of the same kind would affect accuracy. Therefore, number of ties also was varied.

Results and Discussion

Changes in Accuracy Due to Estimation of Fixed Effects

With best linear unbiased predictors (BLUP), as well as least squares, some of the available information must be used to estimate β to adjust for fixed effects, resulting in a decrease in accuracy. The impact can be seen in the set of mixed-model equations obtained after absorption of a single fixed effect, which for the animal model [3], is

$$\left[I_n - J_n(1/n) + I_n k \right] [\hat{\mathbf{u}}] = [\mathbf{y} - J_n(1/n)\mathbf{y}], \quad [4]$$

where J_n is an $n \times n$ matrix of ones and $Z = I_n$. If n and k (σ_e^2/σ_G^2) are equal, the diagonal elements of the coefficient matrix in [4] will be smaller than those in selection index equations, and the off-diagonal elements will change to nonzero numbers, resulting in larger diagonal elements in the inverse and a larger PEV (Van Raden, 1984). If β is ignored, however, a biased estimate of \mathbf{u} will result (Henderson, 1973).

Thus, it is important to understand exactly how the inclusion of β will influence the PEV. If one looks at the estimator of one fixed effect

$$\hat{\beta} = L'y, \quad [5]$$

where $L' = (X'V^{-1}X)^{-1}X'V^{-1}$, $V^{-1} = (ZAZ'\sigma_G^2 + I_n\sigma_e^2)^{-1}$ and $A = I_n$, the elements of the row vector L' will be proportional to the amount of information (from genetic relation-

ships) available on the observations belonging to the particular fixed effect. Note that

$$\begin{aligned}\text{Var}(\hat{\beta}) &= (\mathbf{X}'[\mathbf{I}_n - \mathbf{Z}(\mathbf{Z}'\mathbf{Z} + \mathbf{I}_n\mathbf{k})^{-1}\mathbf{Z}']\mathbf{X})^{-1} \\ &= (\mathbf{X}'\mathbf{X})^{-1}(\sigma_e^2 + \sigma_G^2).\end{aligned}\quad [6]$$

This effect due to $\hat{\beta}$ is found in solutions to $\hat{\mathbf{u}}$, where

$$\begin{aligned}\hat{\mathbf{u}} &= (\mathbf{Z}'\mathbf{Z} + \mathbf{I}_n\mathbf{k})^{-1}[\mathbf{Z}'\mathbf{y} - \mathbf{Z}'\mathbf{X}\hat{\beta}] \\ &= (\mathbf{Z}'\mathbf{M}\mathbf{Z} + \mathbf{I}_n\mathbf{k})^{-1}\mathbf{Z}'\mathbf{M}\mathbf{y}\end{aligned}\quad [7]$$

and the PEV, where

$$\text{Var}(\mathbf{u} - \hat{\mathbf{u}}) = [(\mathbf{Z}'\mathbf{M}\mathbf{Z} + \mathbf{I}_n\mathbf{k})^{-1}] \sigma_e^2 \quad [8],$$

because [5] is included as $\mathbf{Z}'\mathbf{X}\hat{\beta} + (\mathbf{Z}'\mathbf{Z} + \mathbf{I}_n\mathbf{k})\hat{\mathbf{u}} = \mathbf{Z}'\mathbf{y}$ in both cases. This information becomes critical when the number of fixed effects is large relative to the amount of data available, as in this study.

Numbers of Animals

Unrelated Animals. As shown in the previous section, increasing the total number of animals within fixed effects is advantageous.

Inasmuch as $\lim_{n \rightarrow \infty} 1/n = 0$ for [4], the more

animals in a subclass, the more accurate is the evaluation. At the limit, the fixed effect is known without error and can be substituted for the estimator obtained under BLUP, giving selection index values (Henderson, 1973). Table 1 contains results from a comparison of unrelated individuals. By redistributing 80 animals from 10 individuals in each of eight tests to 40 individuals in each of two tests, accuracy was increased by 4.3% for $h^2 = .40$. The percentage increase was small because h^2 was relatively high. Increasing the total number of animals by adding more contemporary groups did not affect accuracy when animals in different groups were unrelated.

Wilton et al. (1975) constructed similar tables for sire evaluations within and across groups. They also showed that increasing the total number of animals per group improved accuracy. In an evaluation of subgroup size relative to number of progeny, Ojala et al. (1985) found that three daughters per subclass were sufficient for sire evaluation, assuming that sires were unrelated. Fewer than three progeny per subclass resulted in unacceptable

TABLE 1. COMPARISON OF AVERAGE ACCURACY OF EVALUATION FOR DIFFERENT DISTRIBUTIONS OF INDIVIDUAL ANIMALS

Distribution	Average accuracy of evaluation ^a
	$h^2 = .40$
10 animals in each of two tests (n = 20)	.599
10 animals in each of five tests (n = 50)	.599
10 animals in each of eight tests (n = 80)	.599
40 animals in each of two tests (n = 80)	.625

$$^a r_{\mathbf{u}\hat{\mathbf{u}}} = \sqrt{1 - [\mathbf{V}(\mathbf{u} - \hat{\mathbf{u}})]/\sigma_G^2}.$$

loss of information and higher PEV. Total progeny numbers per sire, across subgroups, ranged from 20 to 320. Taking a different approach, Chuahan (1985) compensated for small subclass numbers by treating portions of the effect due to herd-period-season as random. This decreased the effective number of daughters necessary to achieve a given level of accuracy, as Henderson (1975a) predicted, because it was not necessary to use information to fit a fixed effect.

Families. When family structure was considered, the effect of increasing numbers of animals became more complicated because numbers had to be distributed between more and/or larger families. Full-sibs have, on the average, half of their genes in common, whereas half-sibs share only a quarter of their genes, and unrelated animals have no genes in common by descent. Therefore, the accuracy of breeding value estimates made from records on full-sibs should be higher than corresponding values estimated for half-sibs, which would, in turn, be expected to be more accurate than estimates on unrelated individuals.

In situations involving small numbers per subclass, however, the presence of nonzero off-diagonal elements may have a detrimental effect on accuracy of evaluation. The reason can be found by inspection of the equation for obtaining the inverse of a positive definite submatrix (\mathbf{P}):

$$\mathbf{P} = \begin{bmatrix} P_{11} & P_{12} \\ P_{21} & P_{22} \end{bmatrix}, \quad \mathbf{P}^{-1} = \begin{bmatrix} p_{11} & p_{12} \\ p_{21} & p_{22} \end{bmatrix},$$

$$\text{and } P^{11} = [P_{11} - P_{12}P^{22}P_{21}]^{-1}. \quad [9]$$

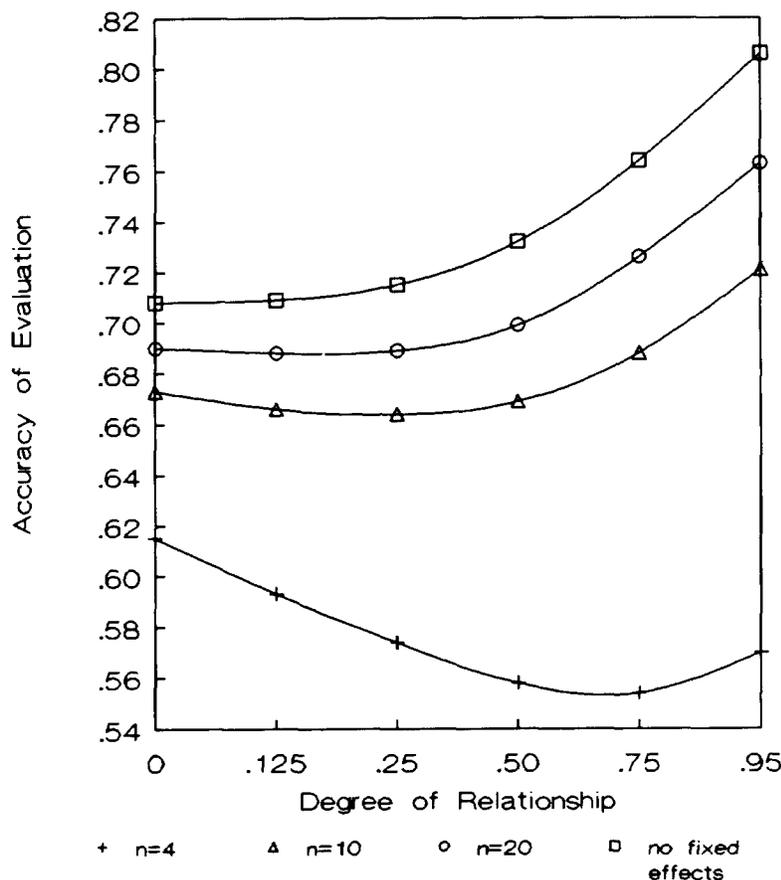


Figure 1. Influence of degree of relationship on accuracy of evaluation of a trait with $h^2 = .50$, for differing numbers of animals in a single contemporary group with one fixed effect, and for a situation in which no fixed effects are included in the model.

If P_{11} is a scalar, then the quantity $(P_{12}P_{22}^{-1}P_{21})$ is dependent on the number of observations and on the magnitude of the off-diagonal elements relative to the diagonals of P_{22} . This is similar to the weighting process used to determine β and is data-dependent. Typically, the coefficient matrix for an animal model is relatively sparse, with few off-diagonal elements relative to the magnitude of the diagonal elements. In such a situation, inclusion of relative information as off-diagonal elements changes the inverse little. But, when the matrix loses diagonal dominance, as with small numbers and close genetic ties, the inverse is different and may lead to larger PEV.

A design matrix consisting of a single contemporary group with one or no fixed effects, differing numbers of animals ($n = 4, 10, 20$) and degrees of relationships (i.e., proportion of genes in common) was used to

explore the effects on accuracy of evaluation. The results using $h^2 = .50$ are presented in Figure 1 because they more clearly defined the pattern of results. As shown, there is a quadratic effect on accuracy when a fixed effect is fitted. At one end of the relationship continuum, for unrelated animals, the coefficient matrix is "diagonally dominant," and accuracy is primarily a function of h^2 and numbers of animals. As the degree of relationship approaches one, the coefficient matrix becomes blocks of diagonal and off-diagonal elements that are close to being equal, resulting in "block" dominance and an increase in accuracy relative to the situation in the middle of the continuum.

The minimum point for accuracy is a function of the number of fixed effects (they influence the diagonal elements of the matrix), degree of relationship and number of animals.

TABLE 2. AVERAGE PREDICTION ERROR VARIANCES FOR ANIMALS IN TESTS TIED BY HALF-SIBS

No. per family	Total ^a no.	No. of sires	No. ^b of ties	Avg prediction error variance ($h^2 = .40$) ^c
2	92	46	0	.00338
		44	1	.00337
		42	2	.00336
		40	3	.00336
		38	4	.00335
		36	5	.00334
3	138	46	0	.00323
		44	1	.00322
		42	2	.00321
		40	3	.00320

^aThree tests with 5, 16, and 25 pens, respectively, giving a total of 92 (two animals per family) and 138 (three animals per family) individuals.

^bHalf-sib ties were generated by placing progeny sired by the same sire into all three tests. The number of sires so used determined the number of ties.

^cA value of .07589 was used for the genetic standard deviation.

A similar result for actual beef cattle data has been reported by Slinger and Lewis (1986). Evaluation of traits with high h^2 (.50) will result in larger PEV under these conditions than evaluation of traits with moderate h^2 (.40). Kennedy and Schaeffer (1989) extended the analogy to identical twins or clones, treating animals as repeated measures of the same genotype because A is singular under such circumstances.

Ties Across Tests

Half-Sib Ties. To determine whether the pattern in Figure 1 continued when subsets of data were tied through genetic relationships, a series of data set designs was evaluated. Half-sib ties were used to connect contemporary groups by modeling full-sib families within different groups that had the same sire across groups. Number of ties varied from zero to five for two full-sibs per family and from zero to three for three full-sibs per family, to provide an indication of how these factors interacted. Table 2 contains average PEV of animals being tested. As number of ties increased, the average PEV gradually declined, and the animals in contemporary groups with three members per family were more accurately evaluated than those in groups consisting of families with two full-sibs.

If the accuracies of prediction are carried out to enough (five) digits for individual animals, however, it may be seen that the equations behave similarly to those for smaller data sets (Table 3). The results are data-

dependent, but, in general, for a fixed number of observations, as number of half-sib ties and number of families per test increased, animals with direct ties had decreasing accuracies of prediction. For example, the accuracy of prediction for two half-sib families with three members each (one direct tie) in a contemporary group consisting of 16 families (.67733) is larger than that of comparable half-sib families tied by three sires across groups (.67699). Although not large in magnitude, these differences serve to illustrate that the pattern of change in accuracy is similar to that previously discussed.

The increase in accuracy of evaluation of untied animals in the same group, however, more than compensated for the very small decrease in the accuracy for closely related individuals. The end result was the observed increase in average accuracy (Table 2). For small numbers of animals per contemporary group, the connections with larger groups through half-sib ties more than offset the nonzero off-diagonals, resulting in a greater accuracy throughout (Table 3).

As number of half-sib ties increased, the rate of change in accuracy of prediction for directly and indirectly tied animals in small tests decreased even as overall accuracy increased. Conversely, the rate of change accelerated in the negative direction for the directly tied animals in the larger tests, whereas the positive rate of change decreased for the indirectly tied animals (Table 4). On the basis of these observations and similar patterns in other designs, it seems that the

TABLE 3. COMPARISON OF ACCURACY OF EVALUATION OF FULL-SIB ANIMALS WITH DIFFERING NUMBERS OF HALF-SIB TIES ACROSS TESTS

No. ^a of ties	No. of pens	Accuracy ^b ($h^2 = .40$)			
		Direct		Indirect	
		Two full sibs per family		Three full sibs per family	
0	5	—	.60208	—	.62298
0	16	—	.64348	—	.66369
0	25	—	.65001	—	.67012
1	5	.62290	.60267	.64384	.62391
1	16	.65795	.64353	.67733	.66377
1	25	.66358	.65003	.68278	.67015
2	5	.62309	.60319	.64423	.62474
2	16	.65779	.64357	.67717	.66383
2	25	.66345	.65004	.68263	.67018
3	5	.62323	.60365	.64454	.62545
3	16	.65763	.64360	.67699	.66387
3	25	.66332	.65005	.68248	.67019
4	5	.62330	.60404	—	—
4	16	.65745	.64361	—	—
4	25	.66318	.65006	—	—
5	5	.62333	—	—	—
5	16	.65726	.64361	—	—
5	25	.66303	.65005	—	—

^aDirect = animals having the same sire; Indirect = test mates of animals with direct ties.

^bHalf-sib ties were generated by placing progeny sired by the same sire into all three tests. The number of sires so used determined the number of ties.

effect of number of ties on accuracy of prediction is also of a quadratic nature and varies in magnitude relative to the strength of the ties.

Accuracy of Sire Evaluations. One advantage of using the animal model is that related animals with no records of their own can also be evaluated simultaneously. A measure of accuracy of evaluation for those animals also is obtained. Sire average PEV obtained by evaluating progeny with differing numbers and degrees of ties as well as differing numbers of observations are summarized in Table 5.

Because the portion of the relationship matrix directly concerned with sires was relatively sparse (they were assumed to be unrelated), the average PEV decreased as more information about greater numbers of progeny was simulated.

Implications

In general, accuracy of evaluation of moderately to highly heritable traits can be improved by using a single-trait mixed model with relationships. Exceptions include populations

TABLE 4. PERCENTAGE CHANGE IN ACCURACY RELATIVE TO UNITED TESTS FOR FULL-SIB FAMILIES TIED ACROSS TESTS BY SIRES (HALF-SIB TIES)^a

No. of ties ^b	No. of pens					
	5		16		25	
	DIR	IND	DIR	IND	DIR	IND
1	3.3424	.0979	2.1993	.0078	2.0450	.0031
2	3.3719	.1840	2.1755	.0140	2.0258	.0046
3	3.3936	.2601	2.1517	.0186	2.0066	.0062
4	3.4045	.3245	2.1249	.0202	1.9859	.0077
5	3.4901	—	2.0966	.0202	1.9637	.0061

^a $h^2 = .40$.

^bDIR = directly tied animals; IND = test mates of directly tied animals.

TABLE 5. AVERAGE PREDICTION ERROR VARIANCES OF EVALUATIONS FOR SIRES OF FULL-SIB FAMILIES TIED ACROSS TESTS BY HALF-SIB TIES

No. of full-sibs per family	Total no. of animals ^a	No. of sires	No. of ties ^b	Average ^c PEV
2	92	46	0	.00486
		44	1	.00484
		42	2	.00481
		40	3	.00477
		38	4	.00474
		36	5	.00470
3	138	46	0	.00461
		44	1	.00457
		42	2	.00454
		40	3	.00450

^aThree tests with 5, 16, and 25 pens, respectively, giving a total of 92 (two animals per family) and 138 (three animals per family) individuals.

^bHalf-sib ties were generated by placing progeny sired by the same sire into all three tests. The number of sires so used determined the number of ties.

^cPEV = prediction error variance; $h^2 = .40$.

of closely related animals and a large number of fixed effects relative to total numbers of animals. Pedigrees linking families within a subclass are useful when the diagonal elements of the equations are large relative to the off-diagonals. Even closely related animals in small groups will be evaluated with increased accuracy if small subsets are tied with larger ones. Thus, these results have implications for applications of mixed-model methodology to small, unbalanced data sets.

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