

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Faculty Papers and Publications in Animal
Science

Animal Science Department

August 1991

Estimated Breeding Values for Meat Characteristics of Crossbred Cattle with an Animal Model¹

L. Dale Van Vleck

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

A. F. Hakim

Anim. Prod Res. Inst., Ain Shams Univ., Cairo, Egypt

Larry V. Cundiff

University of Nebraska-Lincoln, lcundiff2@unl.edu

R. M. Koch

University of Nebraska-Lincoln, rkoch1@unl.edu

J. D. Crouse

USDA-ARS, Roman L. Hruska Meat Animal Research Center

See next page for additional authors

Follow this and additional works at: <https://digitalcommons.unl.edu/animalscifacpub>



Part of the [Animal Sciences Commons](#)

Van Vleck, L. Dale; Hakim, A. F.; Cundiff, Larry V.; Koch, R. M.; Crouse, J. D.; and Boldman, K. G., "Estimated Breeding Values for Meat Characteristics of Crossbred Cattle with an Animal Model¹" (1991). *Faculty Papers and Publications in Animal Science*. 246.

<https://digitalcommons.unl.edu/animalscifacpub/246>

This Article is brought to you for free and open access by the Animal Science Department at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Faculty Papers and Publications in Animal Science by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Authors

L. Dale Van Vleck, A. F. Hakim, Larry V. Cundiff, R. M. Koch, J. D. Crouse, and K. G. Boldman

Estimated Breeding Values for Meat Characteristics of Crossbred Cattle with an Animal Model^{1,2}

L. D. Van Vleck^{*,†}, A. F. Hakim³, L. V. Cundiff^{*}, R. M. Koch[†],
J. D. Crouse^{*}, and K. G. Boldman^{*,†}

^{*}ARS, Roman L. Hruska Meat Animal Research Center,
U.S. Department of Agriculture, Clay Center, NE 68933 and

[†]Department of Animal Science,
University of Nebraska, Lincoln 68583-0908

ABSTRACT: Longissimus muscle area, shear force measure, and sensory panel scores for flavor, juiciness, and tenderness, and marbling score were obtained from 682 steer carcasses, resulting from crosses among five *Bos taurus* and *Bos indicus* breeds. The single-trait model used included birth year and as covariates breed fractions, weaning age, and days on feed. The numerator relationship matrix was for 1,350 animals (682 steers, 74 pure breed and 52 F₁-cross sires and 542 dams). The coefficient matrix was inverted to examine standard errors of prediction. Estimated breeding value is the sum of the estimate of

genetic deviation and the weighted (fractions) sum of estimates of breed effects. Heritabilities used in estimating breeding values were .62, .06, .05, .11, .05, and .43 for longissimus muscle area, shear force, flavor, juiciness, tenderness, and marbling score. Sires within a breed or crossbred group tended to rank similarly due to large differences among breed effects (e.g., the six Sahiwal sires ranked in the highest six places for shear force). These results illustrate that for traits with large breed differences, selection of the proper breed should be done before selection within that breed.

Key Words: Beef Cattle, Genetic Evaluation, Breed Differences, Crossbreeding, Meat Characteristics

J. Anim. Sci. 1992. 70:363-371

Introduction

Crossbreeding is a widely used system for production of beef cattle. Palatability characteristics of beef are important to consumers. Crouse et al. (1989) reviewed differences among breeds of *Bos taurus* and *Bos indicus* cattle and their crosses and reported that tenderness decreases with increase in fractions of Brahman and Sahiwal inheritance. This paper examines the genetic evaluation of

sires and dams using an animal model for carcass traits based on measurements on slaughtered crossbred steers. Of particular interest were the importance of breed effects included in estimated breeding values and the standard errors of estimated breeding values that included breed effects.

Materials and Methods

The data available were observations on longissimus muscle area (square centimeters), required shear force (kilograms), marbling score, and sensory panel scores for flavor, juiciness, and tenderness on 395 reciprocal backcross steers and on 287 single-cross steers resulting from original matings of Hereford, Angus, Brahman, Sahiwal, and Pinzgauer bulls with Hereford and Angus cows. The mating design and data collection have been described by Crouse et al. (1989) for the backcross (20 Hereford-Angus, 5 Hereford-Brahman, 4 Hereford-Sahiwal, 5 Hereford-Pinzgauer, 5 Angus-

¹Published as Paper No. 9493, Journal Ser., Nebraska Agric. Res. Div., Univ. of Nebraska, Lincoln 68583-0908.

²Karin Meyer is thanked for supplying codes from her DFREML programs, which were modified to obtain estimated breeding values and the inverse of the coefficient matrix.

³Dept. of Sheep and Goat Res., Anim. Prod. Res. Inst., Ain Shams Univ., Cairo, Egypt.

Received February 8, 1991.

Accepted August 21, 1991.

Table 1. Numbers of animals measured, means^a, and standard deviations^a by year of measurement

Year	No.	Mean						Standard deviation					
		Longis- simus	Shear	Fla- vor	Juici- ness	Tender- ness	Marb- ling	Longis- simus	Shear	Fla- vor	Juici- ness	Tender- ness	Marb- ling
1	144	70	8.4	7.0	7.0	6.7	5.6	5.9	2.15	.46	.64	1.23	1.15
2	143	71	7.8	7.1	7.1	6.6	4.9	5.8	1.84	.41	.59	1.12	.88
3	122	71	5.0	5.3	5.3	5.4	4.6	8.2	2.14	.22	.35	.56	.91
4	74	72	6.0	5.0	5.0	4.9	5.0	8.0	1.86	.26	.32	.58	.79
5	133	70	5.7	4.9	5.1	4.8	4.7	7.9	1.81	.25	.36	.70	.61
6	66	71	5.1	4.7	5.1	5.1	5.1	8.0	1.70	.33	.47	.70	1.16
Weighted	682	71	6.6	5.9	5.9	5.7	5.0	7.1	1.94	.33	.47	.86	.91

^aLongissimus muscle area (cm²); shear force (kg); flavor, juiciness, tenderness (taste panel score; 9 = extremely flavorful, juicy, tender, . . . , 1 = extremely bland, dry, tough); marbling score (1 unit per degree of marbling; 1 = devoid, . . . , 5.0 = small, . . . , 10 = abundant).

Brahman, 6 Angus-Sahiwal, and 7 Angus-Pinzgauer bulls) data (Phase 4) and by Koch et al. (1982b) for the single-cross data (Phase 2), for which panel scores were available. Their results suggested that heterosis was not important for these traits, so heterosis effects were not included in the model. Estimates of heritability and environmental variances to use in the animal model evaluations were obtained initially from an analysis based on an animal model using REML (Hakim et al., 1990) with the same data that included the single-cross data of 13 Hereford bulls with Angus cows; 14 Angus bulls with Hereford cows; and 9 Pinzgauer, 17 Brahman, and 6 Sahiwal bulls with both Hereford and Angus cows; and the 395 backcross data described by Crouse et al. (1989). Further examination of the data revealed that variances and means were different for the Phase 2 (Koch et al., 1982b) and Phase 4 (Crouse et al., 1989) data (Table 1). Phase 2 measurements (yr 1 and 2) were made at Kansas State University and the Phase 4 measurements (yr 3 to 6) were made at the U.S. Meat Animal Research Center. Because the model would account for year-location difference in means, each record was standardized for

differences in variation by dividing by the standard deviation for the year the measurement was made.

The standardized records were then reanalyzed with the multiple-trait REML package of K. Meyer (1985, 1986) as described by Hakim et al. (1990), except that breed effects were modeled by the fraction of inheritance from each breed, as described in the next paragraph, rather than by the breed-cross combination. The estimates of heritability and genetic and phenotypic correlations from the combined Phases 2 and 4 data are given in Table 2 and in general differ little from the analysis before standardization. Single-trait analyses with the same model were also carried out with derivative-free REML (Smith and Graser, 1986; Graser et al., 1987) using the DFREML programs (Meyer, 1988, 1989 and personal communication). Heritability estimates for both analyses were similar except for the even smaller estimates for flavor and tenderness scores with the single-trait analysis compared with the multiple-trait analysis. The estimates of heritabilities and environmental variances from these single-trait analyses were then used to estimate breeding

Table 2. Estimates of heritability (diagonal) and genetic (below diagonal) and phenotypic (above diagonal) correlations with a multiple-trait animal model with REML^{a,b,c}

Trait	Trait					
	Longissimus	Shear	Flavor	Juiciness	Tenderness	Marbling
Longissimus	.60	-.05	.05	.07	.00	.00
Shear	-.14	.09	-.26	-.26	-.70	-.18
Flavor	.16	-.82	.03	.16	.34	.12
Juiciness	-.01	-.95	.78	.14	.50	.18
Tenderness	-.04	-.96	.89	.95	.10	.19
Marbling	-.40	-.53	.79	.60	.74	.45

^aREMLPK programs of Karin Meyer with modified quadratics.

^bApproximate standard errors: heritability, .05 - .13; genetic correlation, .12 - .94; phenotypic correlation, .02 - .04.

^cRecords standardized by dividing by standard deviation for year of measurement.

values. Thus, the procedure as used here is equivalent to joint estimation of variance components and of breeding values for single traits (i.e., variance component estimation is carried to convergence and then the same mixed-model equations are used to estimate breeding values [e.g., Gianola et al., 1986]). The exception was that a minimum heritability of .05 was used in estimating breeding values under the assumption supported by the multiple-trait analyses that heritability may be larger than the sample estimate suggested. For practical purposes, heritability of .05 is not greatly different from zero. The heritabilities and residual environmental variances used for the single-trait animal model evaluations are shown in Table 3. Flavor, juiciness, tenderness, and marbling measurements are scored from 1 to 9 or 10 and thus are ordered categorical traits. Threshold analyses may yield larger estimates of heritability for an underlying normal scale, but the number of categories suggests no great increase in heritability. For these analyses, the categorical scores were treated as continuous variables.

The statistical model included linear covariates for weaning age and days on feed (assumed homogeneous over breeds), effects associated with the 6 yr of birth, additive genetic values for the 682 steers with records, and five covariates with coefficients corresponding to fractions of inheritance from the breeds involved in the cross (Touchberry, 1970; Koger et al., 1975; Dillard et al., 1980; Robison et al., 1981). The regression coefficients for breeds are estimates of breed effects. Parents of the steers were incorporated by augmenting the equations for additive genetic values of parents (without records) as described by Henderson (1977). The parent equations are tied to the steer equations through the inverse of the numerator relationship matrix (Henderson, 1976). This procedure is equivalent to assigning parents of the foundation sires and dams to groups according to their breeds (Westell, 1984; Westell et al., 1984, 1988; Elzo and Famula, 1985; Quaas, 1988).

The EBV for a steer is a function of the breed contributions and the solution for its additive genetic value as a deviation from the breed contributions for the steer. For example, if steer X results from a Pinzgauer bull mated to a Pinzgauer \times Angus cow, then

$$EBV(X) = .75 \hat{P} + .25 \hat{A} + \hat{g}_x$$

where \hat{P} is the regression coefficient for Pinzgauer breed effect, \hat{A} is the regression coefficient for Angus breed effect, and \hat{g}_x is the solution for the additive genetic value of steer X as a deviation from the function of breed effects specific to that steer.

Estimated breeding values for parents, which cannot have observations because the records are available only on slaughtered animals, are calculated as the function of breed effects weighted by fractions of genes inherited from the various breeds plus the parent's solution for additive genetic value as a deviation from the breed group effect from the mixed-model equations.

This application of an animal model is different from most applications in that none of the animals, sires and dams, for which EBV are wanted have records. Solutions for the steers are from records of steers and relationships through the sires and dams. Predicted breeding values of sires and dams are functions of solutions for breed effects and solutions for the steers. Of particular interest were ranges in EBV both across and within breeds and ranges of the standard errors of prediction (SEP), which determine whether sufficiently large differences exist for effective selection. The SEP are calculated from elements of the inverse of the coefficient matrix of the mixed-model equations. The order of the matrix for inversion was 1,363, which included equations for two covariates, six year effects, five breed effects, 682 steers, and 668 parents.

Let the inverse elements of interest with the breeding values of animals X and Y be denoted as follows:

$$C = \begin{bmatrix} C^{11} & C^{12} & C^{13} & C^{14} & C^{15} & C^{1x} & C^{1y} \\ C^{12} & C^{22} & C^{23} & C^{24} & C^{25} & C^{2x} & C^{2y} \\ C^{13} & C^{23} & C^{33} & C^{34} & C^{35} & C^{3x} & C^{3y} \\ C^{14} & C^{24} & C^{34} & C^{44} & C^{45} & C^{4x} & C^{4y} \\ C^{15} & C^{25} & C^{35} & C^{45} & C^{55} & C^{5x} & C^{5y} \\ C^{1x} & C^{2x} & C^{3x} & C^{4x} & C^{5x} & C^{xx} & C^{xy} \\ C^{1y} & C^{2y} & C^{3y} & C^{4y} & C^{5y} & C^{xy} & C^{yy} \end{bmatrix}$$

where the numerals indicate the five breed effects. The estimated breeding value for animal X is

$$EBV(X) = \hat{u}_x = \sum_i f_{xi} \hat{b}_i + \hat{g}_x$$

where \hat{b}_i is the solution for the i^{th} breed effect, \hat{g}_x is the solution for the additive genetic value of animal X as a deviation from its breed group effects, and f_{xi} is the fraction of inheritance of animal X from breed i .

Then prediction error variance (PEV) for predicted breeding value is:

Table 3. Estimates of parameters for a single-trait^a animal model with derivative-free REML^b that were used in estimating breeding values

Parameter	Trait					
	Longissimus	Shear	Flavor	Juiciness	Tenderness	Marbling
h^2	.62	.06	.05 ^c	.11	.05 ^d	.43
σ_e^2	.32	.69	.97	.80	.67	.44

^aTraits standardized by dividing by standard deviation for year of measurement.

^bDFREML programs of Karin Meyer.

^cEstimate from DFREML was .00 but .05 was used in EBV calculations.

^dEstimate from DFREML was .03 but .05 was used in EBV calculations.

$$PEV_4 = V(u_x - \hat{u}_x) = \left[\sum_i f_{xi}^2 c^{ii} + \sum_{i \neq j} f_{xi} f_{xj} c^{ij} + 2 \sum_i f_{xi} c^{ix} + c^{xx} \right] \sigma_e^2$$

where σ_e^2 is the environmental variance for the trait. The subscript on PEV stands for the number of terms in the equation. The first term involves sampling variances of estimators of breed effects, the second term involves sampling covariances among estimators of breed effects, the third term involves sampling covariances between estimators of breed effects and the prediction error for additive genetic value as a difference from breed effects, $(g_x - \hat{g}_x)$, and the fourth term corresponds to variance of prediction error for $(g_x - \hat{g}_x)$. As an example of the effects of these contributions to PEV, three different expressions to approximate PEV were compared with PEV₄ for marbling score. The first approximation used only the diagonal for g_x and is reported for all traits in Table 5:

$$PEV_1 = c^{xx} \sigma_e^2$$

The next approximation used breed and animal diagonals:

$$PEV_2 = \left(\sum_i f_{xi}^2 c^{ii} + c^{xx} \right) \sigma_e^2$$

The third approximation was calculated from the small block of the inverse associated with breed effects and includes the sampling covariances among estimators of the breed effects:

$$PEV_3 = \left(\sum_i f_{xi}^2 c^{ii} + \sum_{i \neq j} f_{xi} f_{xj} c^{ij} + c^{xx} \right) \sigma_e^2$$

The purpose of obtaining approximations of PEV₄ was to examine the effect of sampling variances and covariances involving estimates of the breed effects on PEV and standard error of prediction, $SEP = (PEV)^{.5}$.

Results and Discussion

Breed effects may have a large influence on EBV in an analysis among breeds. Although this data set is relatively small, the breed regression coefficients found illustrate the importance of the breed effects. The regression coefficients are equivalent to solutions for breed effects and are shown in Table 4. The constraint imposed to obtain solutions to the singular set of mixed-model equations was to set the regression coefficient for the Angus breed effect equal to zero. Thus, the solutions shown are relative to Angus effects; as expected, the estimates of breed effects from the animal model analyses are similar to those reported from fixed effect analyses of the same data (Koch et al., 1982b; Crouse et al., 1989). The important point is that for most of these six traits, differences in the breed effects are quite large. The breed effects would be expected to have a major impact on ranking of bulls for EBV across breeds for these traits. The results shown here should, however, be considered primarily as illustrative because the samples of bulls are small for each breed and selection within breed because the sires we used may have changed the breeds (Notter and Cundiff, 1991).

Range of Estimated Breeding Values. Visual examination of EBV for both sires and dams revealed a continuum from high to low. Table 5 shows the ranges for breed solutions, across-breed EBV, and estimated genetic deviations (within-breed EBV) for sires and dams.

For shear force and tenderness scores, the range in estimates of breed effects was about three phenotypic standard deviations (SD) and a little more than two SD for longissimus muscle area and marbling score. The ranges in across-breed EBV for sires, including crossbred sires, is obviously greater than the range for the imbedded function of breed solutions. The range in EBV of sires across breeds was from 3.5 to 4.5 phenotypic SD for longissimus muscle area, tenderness, marbling score, and shear force. The ranges for flavor score were smallest of all traits for breed effects,

Table 4. Solutions and (standard errors of differences of breed solutions from Angus solutions) for breed effects^a

Breed	Trait					
	Longissimus	Shear	Flavor	Juiciness	Tenderness	Marbling
Hereford	-.41(.16)	.22(.14)	-.01(.17)	-.10(.16)	-.39(.14)	-.68(.15)
Angus	0	0	0	0	0	0
Brahman	-.12(.25)	1.65(.20)	-.68(.24)	-1.31(.23)	-1.82(.20)	-2.22(.23)
Sahiwal	-.97(.30)	2.63(.21)	-.80(.25)	-1.48(.25)	-2.82(.21)	-2.02(.27)
Pinzgauer	1.10(.26)	.58(.19)	-.12(.24)	-.38(.22)	-.50(.20)	-1.37(.23)

^aRecords standardized by standard deviation for year of measurement (Table 1).

sire EBV and dam EBV. The narrow ranges reflect small differences among the breeds for flavor score and small genetic differences within breeds, which is a reflection of the heritability used in the analysis (.05) and the genetic variability in the data set (estimate for h^2 of .00). A similar situation is apparent for tenderness score, for which there is small heritability within breeds but a large difference among breeds. Similarly, most of the differences in juiciness score are among breeds.

Ranges in EBV for dams were generally smaller

than for sires; otherwise, they followed the same pattern as for sire EBV. The reduced range for dams existed because there were no single-breed dams of the Pinzgauer, Brahman, and Sahiwal breeds for which one or another of the breed effects was at one of the extremes for the six traits. This result again emphasizes the importance of the breed effects on EBV among breeds.

The middle of Table 5 shows the ranges of within-breed EBV for the purebred sires. The number of sires sampled is small, so definite

Table 5. Ranges in breed solutions, estimates of sire and dam breeding values, and deviations from breed solutions and maximum and minimum standard errors of predictions of breeding values

Item	Trait ^a					
	Longissimus	Shear	Flavor	Juiciness	Tenderness	Marbling
Phenotypic SD	.92	.86	1.01	.95	.84	.88
	Ranges					
Breed solutions	2.07	2.63	.80	1.48	2.82	2.22
Sire EBV	3.33	2.88	.99	1.96	3.01	3.46
Dam EBV	3.02	1.59	.55	1.04	1.71	2.63
Deviations of sires from						
breed effects	3.03	.31	.31	.52	.25	2.25
Hereford (13) ^b	2.06	.16	.24	.41	.17	1.43
Angus (14)	1.76	.24	.17	.40	.20	1.24
Brahman (27)	1.85	.23	.11	.28	.17	1.47
Sahiwal (6)	1.43	.31	.13	.42	.17	.52
Pinzgauer (14)	2.58	.24	.21	.36	.17	1.00
Deviations of dams from						
breed effects	2.62	.21	.17	.36	.16	1.53
	SE of predictions ^c					
Largest for sires	.66	.21	.22	.31	.19	.55
Smallest for sires	.36	.18	.20	.25	.17	.32
Largest for dams	.67	.21	.22	.31	.19	.55
Smallest for dams	.54	.20	.22	.30	.18	.47
Genetic SD	.72	.21	.23	.31	.19	.58

^aRecords standardized by dividing by standard deviation for year of measurement (Table 1). Heritabilities of .05 assumed for flavor and tenderness (Table 3).

^bNumber of sires.

^cCalculated from diagonal elements of inverse of coefficient matrix corresponding to the animal alone, which would also correspond to SEP within breed.

conclusions are not possible. Nevertheless, for the traits with large heritability estimates, longissimus muscle area especially, and also marbling score, the ranges within breed are quite large compared to the range in breed solutions. Thus, for such traits within-breed variation is important in selection of sires. The ranges in within-breed EBV for flavor seemed lower for the *Bos indicus* than for the *Bos taurus* breeds. The range in within-breed EBV for juiciness was lower for Brahman than for the other breeds. The range in EBV for marbling score of the six Sahiwal bulls was much lower than for other breeds.

Examination of the breed composition of the highest and lowest ranking 10 bulls and their EBV for the six traits is informative. For longissimus muscle area, nine Pinzgauer bulls occupied the top 10 ranks; the eighth-place bull was a Pinzgauer \times Hereford cross. The low 10 bulls were Hereford, Sahiwal, Angus, and their crosses. For shear force (the high scores are those requiring more force) all six Sahiwal bulls were at the top of the list, followed by four Brahman bulls. All 10 of the bulls with the lowest EBV for shear force were Angus. For flavor score, the six Sahiwal and four of the Brahman bulls were the lowest 10 bulls. The highest EBV were for six Angus, two Hereford, and two Angus \times Hereford bulls. If heritability of zero had been used, all bulls would have had the same evaluation except for the breed effects. For juiciness score, Angus bulls occupied nine of the top 10 of the EBV list, and seven Brahman and three Sahiwal bulls were in the bottom 10 of the list. Rankings for tenderness score mirrored those for shear force. Angus bulls occupied all 10 of the high ranks and the six Sahiwal bulls occupied the bottom six ranks; Brahman bulls made up the other four in the bottom 10. A smaller heritability would have reduced the within-breed range but would not have affected the contribution of breed effects to the evaluations. Top and bottom rankings on EBV for marbling score also were generally breed-specific; the low 10 ranks were Brahman bulls and nine Angus bulls and one Hereford-Angus cross were in the high 10. For these breeds and traits, which encompassed a wide range of heritability estimates, the breed contributions to EBV largely determined relative ranking of the best and poorest bulls, with individual differences determining rank within breed.

Standard Errors of Predicted Breeding Values. The bottom half of Table 5 demonstrates that the range in EBV is considerably larger than the SEP for individual EBV for both sires and dams. Breed effects, as already noted, contributed importantly to the range in EBV for some traits, but, as will be seen later, the sampling variances of estimates of breed effects may not contribute much to SEP.

The largest and smallest SEP as compared to the genetic standard deviations are shown in the bottom half of Table 5 for sires and dams. These SEP were computed from diagonal elements only of the inverse of the coefficient matrix. In contrast to $V(g_i - \hat{g}_i)$, which, according to properties of mixed-model equations (e.g., Henderson, 1963, 1973, 1975), is equal to $(1 - r_{gg}^2)\sigma_g^2$, $V(\text{EBV})$ is larger by contributions of elements of the inverse matrix associated with estimates of breed effects. Thus, especially for traits with small heritability, some of the SEP may be greater than σ_g . With large data sets, the sampling variances of the fixed breed effects, however, would be small.

The maximum SEP in Table 5 can be used to show that even approximate accuracy values (r_{gg}) cannot be obtained when sampling variances of estimates of breed effects are included in the SEP. The usual way to use Table 5 to obtain r_{gg} would be to reason that $\text{SEP}/\sigma_g = [(1 - r_{gg}^2)\sigma_g^2/\sigma_g^2]^{.5} = (1 - r_{gg}^2)^{.5}$. Thus, if $\text{SEP}/\sigma_g = .55$, then solve for r_{gg} from $.55 = (1 - r_{gg}^2)^{.5}$ with $r_{gg}^2 = .70$. But if $\text{SEP}/\sigma_g = 1.00$, solving for r_{gg}^2 gives 0.00. The same problem may occur when fixed genetic group effects are included in animal models for estimating breeding values. Generally, inverses of the full coefficient matrix are not possible to obtain. The diagonal element of the inverse associated with each animal, that is, $V(g_i - \hat{g}_i)$, however, corresponds to $(1 - r_{gg}^2)\sigma_g^2$ for comparing animals within the same breed or breed cross and generally will be within the statistical limits for r_{gg} .

Four ways of calculating SEP for marbling scores are summarized in Table 6 for sires, dams, and steers with the records. Comparison of the last three columns indicates that use of off-diagonal elements for sampling covariances among estimates of breed effects and between estimated breed effects and estimated genetic prediction error is not necessary, even with a data set as small as this one. Table 6 also shows that using just the diagonal element of the inverse associated with $g_i - \hat{g}_i$ will underestimate PEV, but that the magnitude of the underestimation may not be large enough to be of much concern. Certainly, the off-diagonal elements between $(g_i - \hat{g}_i)$ and breed effects do not seem to be important.

The entries in the first column of Table 6 illustrate the well-known fact that information on an animal itself is more valuable than information on a single or a few relatives. The SEP for steers were all similar because each steer had only one record, its own. Extra accuracy is mostly from half-sib information. Calculated from the diagonal element of the inverse of the coefficient matrix for a steer with $\text{SEP} = .44$ and $\sigma_g = .58$ for marbling

Table 6. Comparison of largest and smallest values from four methods of calculating standard errors of prediction for marbling score^{a,b}

Group	Animal diagonal alone = (1)	(1) + Breed diagonals = (2)	(2) + Breed off-diagonals = (3)	(3) + Animal by breed off-diagonals = (4)
Sires				
Largest	.55	.59	.59	.59
Smallest	.32	.36	.36	.33
Dams				
Largest	.55	.57	.57	.57
Smallest	.47	.48	.48	.48
Steers				
Largest	.44	.48	.48	.46
Minimum	.41	.42	.42	.42

^aRecords standardized by dividing by standard deviation for year of measurement.^bMethod 4 is exact; genetic standard deviation is .58.

score, the corresponding $r_{gg} = .65$ corresponds closely to $r_{gg} = (h^2)^{.5} = .66$ for a single record calculated from selection index principles. For a sire or a dam with $SEP = .55$, based on the diagonal element, the corresponding $r_{gg} = .32$, which is expected for a sire or dam having only one progeny with a record.

Examination of the inverse elements of the coefficient matrix corresponding to breed effects for marbling score reveals an obvious problem with calculating PEV for EBV that contain estimates of group or breed effects. In order by Hereford, Angus, Brahman, Sahiwal, and Pinzgauer, the inverse block is as follows:

.0539	0	.0304	.0416	.0349
0	0	0	0	0
.0304	0	.1226	.0675	.0611
.0416	0	.0675	.1663	.0696
.0349	0	.0611	.0696	.1214

This inverse corresponds to the constraint that the estimate for the Angus effect is zero. The constraint does not change rankings according to EBV but may raise the question of what the appropriate PEV is.

The PEV for comparison within breed or breed cross is not affected by the sampling variance of the estimate of the breed effect. The PEV of an EBV, however, would include sampling variances of the breed effects (i.e., the PEV for an Angus bull would not include any component for estimating the Angus effect, whereas the PEV for any other breed would include sampling variance for the

estimate of the breed effect). Although seldom stressed in genetic evaluations, only differences in EBV are estimable when group or breed effects are included. The correct PEV is then for the difference in EBV. For example, suppose a $P \times A$ cross sire, x , is compared to a $B \times H$ cross sire, y . The EBV are as follows:

$$\begin{aligned}\hat{u}_x &= .5\hat{b}_A + .5\hat{b}_P + \hat{g}_x \\ \hat{u}_y &= .5\hat{b}_H + .5\hat{b}_B + \hat{g}_y\end{aligned}$$

The PEV for $u_x - u_y$ is

$$\begin{aligned}&PEV[(u_x - u_y) - (\hat{u}_x - \hat{u}_y)] \\ &= \\ &V\{[.5\hat{b}_A + .5\hat{b}_P + (g_x - \hat{g}_x)] \\ &\quad - [.5\hat{b}_H + .5\hat{b}_B + (g_y - \hat{g}_y)]\}.\end{aligned}$$

Let C be the matrix of inverse elements shown in the Methods section, then:

$$PEV[(u_x - u_y) - (\hat{u}_x - \hat{u}_y)] = (-.5 \ .5 \ -.5 \ 0 \ .5 \ 1 \ -1) C (-.5 \ .5 \ -.5 \ 0 \ .5 \ 1 \ -1)'$$

A matrix of PEV of differences calculated in this way for each pair of animals would be correct but would be unwieldy and unlikely to be used. Within-breed PEV for each animal might be sufficient. That could be improved slightly and relatively easily, if desired and if the inverse elements can be obtained, by publishing the sampling variance-covariance matrix of estimates of breed effects and incorporating those into PEV of differences as just illustrated with covariances between breed effects and \hat{g}_x and \hat{g}_y ignored.

This discussion has ignored several potential problems with predicting breeding values from records of crossbred animals. Heterosis effects based on expected heterozygosity can be added to the model as fixed effects, which would improve,

but not be included in, the predictions of breeding values. Phenotypic prediction of response from a particular cross would need to include the heterosis effects. The model becomes more unwieldy if, for example, one-fourth of the Hereford \times Angus heterosis effect for .25 (HA) is not one-half of the heterosis effect for .50 (HA). Including the breed or breed-cross combination as fixed effect in the model for genetic evaluation would allow prediction of the genetic deviations free of heterosis and breed additive effects, although with possibly increased sampling variance. Estimated breeding values among breeds would, however, require adding estimates of differences in breed additive effects. Prediction of progeny performance would require estimates of various combinations of heterosis effects.

The model used here adjusted for slaughter age by a common regression for all breeds and breed groups. The suitability of an age-adjusted end point and of a common regression may need to be examined.

Less tractable problems occur if the breed or breed-cross affects genetic and environmental variances (e.g., Koch et al., 1982a; Elzo, 1990) and if there is genotype \times environment interaction. Joint estimation of environmental variances by breed combinations might be possible but joint estimation is likely to be difficult if not impossible for genetic variances by breed combination, depending on the amount and kind of available records. The importance of these factors for comparing EBV across breeds needs to be determined.

Implications

Breed effects were important in ranking for breeding value for most of the carcass and meat traits. This result, if true with larger sets of data, may reduce the need for breeding values across breeds. Separate evaluations by breed followed by selection within breed would seem to be effective. The analysis described uses records from crossbred animals. For carcass traits, the carcass characteristics of the crossbred animals are the most direct measures of estimated breeding values of parents. Consideration of breed effects in genetic evaluation would allow monitoring of changes in differences among breeds. Such information would aid in making decisions for crossbreeding.

Literature Cited

- Crouse, J. D., L. V. Cundiff, R. M. Koch, M. Koohmaraie, and S. C. Seideman. 1989. Comparisons of *Bos indicus* and *Bos taurus* inheritance for carcass beef characteristics and meat palatability. *J. Anim. Sci.* 67:2661.
- Dillard, E. U., O. Rodriguez, and O. W. Robison. 1980. Estimation of additive and non-additive direct and maternal genetic effects from crossbreeding beef cattle. *J. Anim. Sci.* 50:853.
- Elzo, M. A. 1990. Recursive procedures to compute the inverse of the multiple trait additive genetic covariance matrix in inbred and noninbred multibreed populations. *J. Anim. Sci.* 68:1215.
- Elzo, M. A., and T. R. Famula. 1985. Multibreed sire evaluation procedures within a country. *J. Anim. Sci.* 60:942.
- Gianola, D., J. L. Foulley, and R. L. Fernando. 1986. Prediction of breeding values when variances are not known. *Genet. Sel. Evol.* 18:485.
- Graser, H.-U., S. P. Smith, and B. Tier. 1987. A derivative-free approach for estimating variance components in animal models by restricted maximum likelihood. *J. Anim. Sci.* 64:1362.
- Hakim, A. F., L. D. Van Vleck, L. V. Cundiff, R. M. Koch, J. D. Crouse, and K. G. Boldman. 1990. Estimates of genetic and phenotypic covariances among carcass and sensory characteristics of crossbred cattle with a multiple trait animal model. *J. Anim. Sci.* 68(Suppl. 1):238(Abstr.).
- Henderson, C. R. 1963. Selection index and expected genetic advance. In: *Proc. Statistical Genet. and Plant Breeding*. NAS-NRC Publication 982. pp 141-163. Washington, DC.
- Henderson, C. R. 1973. Sire evaluation and genetic trends. In: *Proc. Animal Breeding Genetics Symp. in Honor of Dr. Jay L. Lush*. pp 10-41. ASAS and ADSA, Champaign, IL.
- Henderson, C. R. 1975. Best linear unbiased estimation and prediction under a selection model. *Biometrics* 31:423.
- Henderson, C. R. 1976. A simple method for computing the inverse of a numerator relationship matrix used in prediction of breeding values. *Biometrics* 32:89.
- Henderson, C. R. 1977. Best linear unbiased prediction of breeding values not in the model for records. *J. Dairy Sci.* 60:783.
- Koch, R. M., L. V. Cundiff, and K. E. Gregory. 1982a. Heritabilities and genetic, environmental and phenotypic correlations of carcass traits in a population of diverse biological types and their implications in selection programs. *J. Anim. Sci.* 55:1319.
- Koch, R. M., M. E. Dikeman, and J. D. Crouse. 1982b. Characterization of biological types of cattle (cycle III). III. Carcass composition, quality and palatability. *J. Anim. Sci.* 54:35.
- Koger, M., F. M. Peacock, W. G. Kirk, and J. R. Crockett. 1975. Heterosis effects on weaning performance of Brahman-Shorthorn calves. *J. Anim. Sci.* 40:826.
- Meyer, K. 1985. Maximum likelihood estimation of variance components for a multivariate mixed model with equal design matrices. *Biometrics* 41:153.
- Meyer, K. 1986. Restricted maximum likelihood to estimate genetic parameters—in practice. *Proc. 3rd World Cong. Genet. Applied Livest. Prod.*, Lincoln, NE. XII:454.
- Meyer, K. 1988. DFREML, a set of programs to estimate variance components under an individual animal model. *J. Dairy Sci.* 71(Suppl. 2):33.
- Meyer, K. 1989. Restricted maximum likelihood to estimate variance components for animal models with several random effects using a derivative-free algorithm. *Genet. Sel. Evol.* 21:317.
- Notter, D. R., and L. V. Cundiff. 1991. Across-breed expected progeny differences: Use of within-breed expected progeny differences to adjust breed evaluations for sire sampling and genetic trend. *J. Anim. Sci.* 69:4763.
- Quaas, R. L. 1988. Additive genetic model with groups and relationships. *J. Dairy Sci.* 71:1338.
- Robison, O. W., B. T. McDaniel, and E. J. Rincon. 1981. Estimation of direct and maternal additive and heterosis effects from crossbreeding experiments in animals. *J. Anim. Sci.* 52:44.
- Smith, S. P., and H.-U. Graser. 1986. Estimating variance compo-

- nents in a class of mixed models by restricted maximum likelihood. *J. Dairy Sci.* 69:1156.
- Touchberry, R. W. 1970. A comparison of the general merits of purebred and crossbred dairy cattle resulting from twenty years (four generations) of crossbreeding. *Proc. 19th Annu. Natl. Breeders Roundtable*. p 18. Kansas City, MO.
- Westell, R. A. 1984. Simultaneous evaluation of sires and cows for a large population. Ph.D. thesis. Cornell Univ., Ithaca, NY.
- Westell, R. A., R. L. Quaas, and L. D. Van Vleck. 1984. Genetic groups in an animal model. *J. Anim. Sci.* 59(Suppl. 1): 175(Abstr.).
- Westell, R. A., R. L. Quaas, and L. D. Van Vleck. 1988. Genetic groups in an animal model. *J. Dairy Sci.* 71:1310.