

**GENETIC EVALUATION ACROSS BREEDS AND COUNTRIES:
PROSPECTS AND IMPLICATIONS**

L.L. Benyshek, W.O. Herring and J.K. Bertrand
Animal and Dairy Science Department
The University of Georgia, Athens GA 30602

SUMMARY

Procedures including data structure and models for computing genetic evaluations across breeds and international borders are reviewed. Problems of animal identification across international borders will have to be solved by the organizations controlling the data if International Cattle Evaluation is to become a reality. The incorporation of crossbred data into current National Cattle Evaluation programs, along with the sharing of data by breed organizations with each other, will have to occur before large scale across breed mixed model analyses can be conducted.

INTRODUCTION

Within breed and across herd beef cattle genetic evaluation procedures based on mixed model best linear unbiased prediction techniques are generally established and accepted by the registered purebred and commercial cattle industry of the United States. The animal model (or in some cases the equivalent reduced animal model) has become the model of choice for National Cattle Evaluation (NCE) programs throughout the world, with some small variation in effects included in and parameters used with the model. Hough et al. (1985) and Benyshek et al. (1988) indicate that genetic change for yearling weight can occur, using intense selection based on NCE results, at more than twice the rate compared to selection based on information generated from within herd testing programs.

As breeders have increased post natal growth through selection, there have been correlated responses to that selection in other characteristics. At present, the most difficult correlated response to deal with has been birth weight, which has a direct effect on calving ease. The increased birth weight problem is amplified in crossbreeding programs because of heterosis and the fact that additive genetic values are not comparable across breeds. The commercial cattle industry of the U.S. has embraced the NCE technology and is now demanding comparisons across breeds through NCE, even though considerable breed comparison results are available from experimental data such as the U.S. Meat Animal Research Center Germ Plasm Evaluation Project.

Major importation of beef cattle germ plasm from Europe began in the late 1960's; however, germ plasm had been crossing the border between the U.S., Canada and Mexico for many years prior to that time. Most international trade in germ plasm was accomplished without good genetic information or with information having less accuracy than NCE programs can now provide. It is logical to develop international genetic evaluation programs which can be part of any international trading agreement for germ plasm. Countries which can

agree on an evaluation system which crosses their borders should have some financial advantage in such trading programs.

Obviously, the opportunity for enhanced genetic evaluation programs because of increased data and pedigree diversity is of major concern to breeders. Registered purebred breeders, particularly "elite" breeders, are concerned about pedigree diversity as they intensify selection for traits of economic importance and/or move their selection programs toward "optimums" rather than "maximums" through NCE. International genetic evaluation will ensure a further increase in selection intensity, as was the case when breeders moved from within herd programs to across herd evaluation programs.

INTERNATIONAL BEEF CATTLE EVALUATION

Parnell et al. (1986) discussed the efficiency and place of multi-herd beef cattle evaluation and many of the issues raised in that paper would also apply to across country analyses of field data. In the dairy industry, international evaluation of sires has received considerable research attention when compared to beef evaluation. Actual joint analyses, pooling of data from two countries, have been conducted by Banos et al. (1992). Conversion techniques, not requiring joint analyses, for comparing sires evaluated in different countries have been developed by Schaeffer (1985), Goddard (1985) and Wilmink et al. (1986). Banos et al. (1992) compared the various conversion techniques with results from joint mixed model analyses and found the linear model combined method superior to other procedures if a joint analyses of data from two or more countries was not feasible. Powell and Sieber (1992) also compared the techniques of Goddard (1985) and Wilmink et al. (1986) along with a least squares method and found the least squares method to be slightly superior. Conversion techniques have been adapted for beef sire evaluations by Cunningham and Friedrich (1992) and Lin et al. (1992).

Data Structure and Across Countries Identification

As with NCE programs, across country programs need a data structure which provides for connectedness of animals across contemporary groups. If the within breed and country analysis is well connected, it becomes a matter of the number of sires used in the two or more countries providing data and/or the number of genetic relationship ties between animals in those countries. Several authors have discussed connectedness in reference to linear models: Foulley et al. (1990), Tosh and Wilton (1990), Fernando et al. (1983), Petersen (1978) and Weeks and Williams (1964). Foulley et al. (1992) discussed a criterion for measuring degree of connectedness between factors in genetic evaluation linear models. This criterion is defined as the Kullback-Leibler distance between the joint distribution of the maximum likelihood estimators of contrasts among the levels of two factors respectively and the product of their marginal distributions. Kennedy and Trus (1993) discussed and compared four measures of genetic connectedness between management units under an animal model.

Johnston (1992) computed a genetic evaluation for the Hereford and Polled Hereford breeds in the U.S. and Canada. Three data sets,

U.S. Hereford (n = 1,167,3850), U.S. Polled Hereford (n = 503,081) and Canadian Hereford (n = 306,333), representing 109,113 sires and 918,666 dams were merged for the analysis of weaning weight. Analyses of individual populations showed similar additive genetic direct and maternal genetic variances across the populations. A similar negative covariance between additive genetic and maternal genetic effects was found across populations. Thus, genetic parameters were found to be similar across the breeds. Permanent environmental variance was found to be slightly higher for the U.S. Hereford population than the other two populations which were very similar to each other. The merged analysis required the identification of animals used across populations, no trivial matter since precise records of transfer across populations were not available. Editing procedures used name, tattoo and birth date as the basis for identification. Performance on some animals was recorded in more than one population, resulting in another editing concern. Dual and tri-registered sires (n = 3,405) (termed "international sires" in the analysis) accounted for only three percent of the total number of sires; however, they were the sires of 20.2 percent of the animals providing records for the analysis. As paternal and maternal grandsires, these international bulls were represented in 53.6 and 18.5 percent of the records, respectively. Thus it was assumed that at least a reasonable degree of connectedness existed in the merged data. The model used to analyze the merged data was as follows:

$$y = Xb + Z_1u + Z_2m + Z_3pe + e ,$$

where y was the observation vector of adjusted 205 day weaning weight; X is an incidence matrix relating the fixed contemporary group effect to the observation vector; b is the vector of contemporary group effects; Z_1 , Z_2 , and Z_3 , are incidence matrices relating the random weaning direct, weaning maternal and dam's permanent environment effects respectively, to the vector of random effects u , m and pe ; and e is a vector of random residual errors. The results suggest a single combined genetic evaluation for the North American Hereford and Polled Hereford populations is feasible. The single analysis would eliminate the current industry problem of some sires having more than one predicted genetic value.

Genotype By Environment Interaction

Several genotype by environment (GxE) interactions could, and probably do, affect (to some unknown degree in most cases) the across herd genetic evaluations presently being conducted in several countries throughout the world. It seems logical to expect that the expansion of multi-herd genetic evaluation programs across countries will amplify the problem in some cases. However, international analyses will probably not encounter more genotype by environment interaction problems than those in large countries such as the U.S. or Australia where rather diverse environments exist within country.

A number of studies have examined and found significant sire by environment interactions in field records, using an analysis of

variance including interaction components in the model, Parnell et al. (1986). Sire by herd or sire by contemporary group interactions are of concern in both national and international analyses. The studies demonstrating this interaction have used sire models which could not account for the number of effects accounted for in animal models. Bertrand et al. (1987) showed that accounting for dam effects reduced the sire by contemporary group interaction by 20 percent for birth weight and 38 percent for weaning weight; however, the interaction still caused reranking of some sires.

Experimental data has given some insight into the importance of GxE interaction effects in beef cattle. Studies involving diverse climates have shown significant GxE interactions; Frisch (1981) and Pahnish et al. (1983, 1985). Genotype by environment interactions for growth involving different nutritional levels have not been easily demonstrated; Soto-Murillo et al. (1993), Bishop (1993), Bailey et al. (1990), Baker et al. (1991), Hough and Benyshek (1988).

Cow productivity and reproductive efficiency traits may be more affected by GxE interactions than direct growth characteristics as shown by Morris et al. (1993).

Heterogeneous Variances

The effect of heterogeneous variances on multi-herd genetic evaluation, using mixed linear statistical models has gained considerable research attention recently in dairy; however little information has been published in beef cattle. Within-herd difference in variance components for economic dairy traits have been shown by Brotherstone and Hill (1986), Short et al. (1990), Smothers et al. (1991), Winkelman and Schaeffer (1988). In beef cattle Garrick et al. (1989) showed genetic variances to be different across sex and percent Simmental subclasses. Methods of estimation and accounting for the effects of within-herd heterogeneous variances in dairy records have been discussed by Weigel et al. (1993), Weigel and Gianola (1992) and Gianola et al. (1992). Quaas et al. (1989) discussed models to account for heterogeneous variances in beef cattle field data.

Across country heterogeneous variances probably exist for some breeds; however, the work by Johnston (1992) with Hereford populations in North America showed similar additive direct and maternal genetic variances for weaning weight.

ACROSS BREED EVALUATIONS

Crossbreeding has become the breeding system of choice for U.S. beef producers. To maximize the benefits from crossbreeding it is necessary to have breed comparisons on a variety of economically important characteristics. A number of studies have been conducted to characterize breeds and determine levels of heterosis such as those by Wyatt and Franke (1986), Cundiff et al. (1986) and Amer et al. (1992). National cattle evaluation programs result in changes in breeds over time, Benyshek et al. (1988); thus experiments to compare breeds conducted in the past may or may not be relevant to current producers. As commercial producers realize that optimum production systems may be more profitable than maximum production systems, the

need has developed for current accurate information comparing breeds and even more specifically comparing individual sires from those breeds through across breed genetic values.

The commercial industry in the U.S. is concerned with implementing a "value based" marketing system which will also require more precise genetic information on more traits, which can only be obtained on a large scale through field data and across breed evaluation. Value based marketing will require genetic values for carcass traits. However, the effect on other characteristics, such as reproduction, due to correlated responses to selection for carcass merit will have to be monitored to ensure efficient and profitable production. In addition, some breeders are looking to other breeding schemes, such as composites, to reach targeted production goals or to develop specified or branded products. Across breed genetic values appear to offer the best genetic means for producers to attain current production goals in the U.S. as discussed by Notter (1989, a, b).

Elzo and Famula (1985) and Elzo and Bradford (1985) discussed multibreed sire evaluation within countries and across countries using a sire-maternal grandsire model. These papers provide models which account for additive and nonadditive, intra- and inter-locus, direct and maternal genetic effects using data from crossbreeding programs. The authors contend that extension of the models to across country analyses would: a) lead to more precise sire evaluation for exotic, hybrid and native sires in a native country, b) provide the opportunity to obtain early evaluations for sires of possible interest in a native country, and c) obtain enhanced evaluations of sires used across countries.

Multibreed, multiple-trait mixed model analyses require the inverse of a multiple-trait heterogeneous covariance matrix of direct and maternal additive genetic effects, G^{-1} . Elzo (1989) has shown a recursive procedure to compute G^{-1} for inbred and noninbred multibreed populations.

Arnold et al. (1992) extended the sire-maternal grandsire models of Elzo and Famula (1985) to the animal model used in most NCE programs in the U.S. This work provides the reduced animal model formulations for mixed model procedures to simultaneously evaluate animals of diverse genetic composition, using heterogeneous genetic and environmental (co)variances. These models allow simultaneous analysis of data from multiple purebred populations as well as from any resulting crossbred progeny. Arnold et al. (1992) begins with the following multiple-breed model, which is expanded from a single-breed animal model to include nonadditive genetic effects:

$$y = Xb + Zu + Wh + e$$

where X , Z and W are incidence matrices relating fixed contemporary group effects b , additive genetic values u and nonadditive genetic values h to the y observation vector, respectively. Using the logic of Quaas and Pollak (1981) and Famula et al. (1983) u may be expressed as the total additive genetic value:

$$u = Qg + a$$

where Q is a matrix relating fractions of fixed breed group effects to the animal, with these fractional contributions proportional to the breed composition of the animal; g is a vector of fixed additive breed group effects; and a is a vector of random additive genetic effects. It is thought that g is a fixed additive genetic effect that is intrinsic to the purebred animals of a particular breed in comparison to the other breeds in the evaluation, although one of the authors has recently questioned whether g really is a fixed breed effect, (Arnold, personal communication). The nonadditive genetic (heterosis) effect h can be partitioned into fixed and random components:

$$h = Sd + T\gamma$$

where S is the incidence matrix relating the vector of fixed heterosis effects d to parents of the individual making the record and T is an incidence matrix relating the vector of random heterosis effects γ to the vector of observations. Substitution of u and h into the above model provides the multiple-breed model:

$$y = Xb + ZQg + Za + WSd + WT\gamma + e$$

where y is the vector of observations and X , ZQ , Z , WS and WT are incidence matrices relating effect vectors b , g , a , d and γ to the observation vector y , respectively.

Wilton (1994) presented a multibreed mixed model analysis of the Ontario Beef Cattle Improvement Association data. This analysis may be the first attempt at using mixed model techniques on field data from several breeds, including crossbred data.

Notter and Cundiff (1991) and Nuñez-Dominguez et al. (1993) discussed a method to use within-breed genetic predictions to adjust breed evaluations (Meat Animal Research Center data) for sire sampling and genetic trend. The breed comparisons developed in this work have been used to construct breed comparison tables for computing across breed genetic values for beef animals as described by Notter (1989,a,b). These "breed tables" have been met with limited acceptance by the industry, even though at the present time they provide the only means to compute across breed genetic values.

It would appear that incorporation of mixed model technology into the prediction procedures will be required to give across breed genetic evaluations the same credibility as NCE programs. There are computational problems to be solved and breed associations control breed data which means each association will have to decide if participation is warranted in such a program.

Data Structure For Across Breed Genetic Evaluation

Regardless of analysis technique, the computation of across breed genetic values requires a data structure which will allow the comparison of breeds within contemporary group. For this type of analysis, not only must some sires be used across contemporary groups, but breeds must also be represented across contemporary groups. Initially this connectedness will have to be provided by

data from experimental purebred herds in which more than one breed is represented or data from crossbreeding studies. Throughout the U.S. and Canada a considerable amount of data is available (eg. U.S. Meat Animal Research Center Germ Plasm Evaluation Project). Field records from breeders, purebred and commercial, involving more than one breed also exist, but because of a lack of centralized record processing it will be difficult, although not impossible, to utilize this data in the U.S. Many registered purebred breeders are producing more than one breed; however, registration of animals is within breed.

PROSPECTS AND IMPLICATIONS

The prospect for across breed and international genetic evaluation of beef cattle is extremely good. Theoretical considerations have progressed to the point that applications research is moving steadily forward in the U.S. and Canada, and technology transfer to the industry has started in the U.S. It would appear that this technology will be well in place for the industry before the year 2000. The implications are straightforward from a quantitative geneticists' point of view. This technology will enhance selection intensity, thus leading to increased genetic change and a more efficient industry with greater profitability for producers and economical beef products for consumers.

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