PERSPECTIVES FOR MULTIBREED GENETIC EVALUATION OF CATTLE IN BRAZIL[*]

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SUMMARY

Availability of large numbers of records from purebred and crossbred animals in cattle organizations, and increased demand from producers to have genetic predictions for both purebred and crossbred animals has renewed interest in the implementation of multibreed genetic evaluation procedures. Multibreed genetic evaluation procedures are currently used for the genetic evaluation of purebred and crossbred animals in most US breed associations. Brazil with its enormous cattle population (167 million), composed largely of Zebu and Zebu crossbreds (80%), and many well-organized large size cattle operations (many with 10,000 cattle or more) is likely to have a substantial number of datasets amenable to be analyzed using multibreed genetic evaluation procedures. Currently, however, only intrabreed genetic evaluation procedures are used in Brazil regardless of the breed composition of cattle populations. Intrabreed procedures ignore interbreed nonadditive genetic effects, and assume that genetic parameters are the same in all breed groups. Multibreed genetic evaluation procedures account for both aspects, thus they should be preferred to intrabreed procedures to genetically evaluate populations composed of purebred and crossbred animals. Multibreed genetic evaluation procedures yield more accurate additive genetic predictions, permit direct comparison of animals of different breed composition, and allow additive and nonadditive genetic improvement in multibreed populations. However, they are more complex computationally, require larger number of genetic parameters, and have problems of confounding and multicollinearity. Here, multibreed populations are characterized, genetic evaluation models, procedures, and implementation issues are discussed, and general comments relative to the Brazilian multibreed situation are made when relevant.

KEY WORDS: Cattle, crossbreeding, genetic evaluation, multibreed, prediction

INTRODUCTION

Genetic evaluation of large unbalanced cattle populations has matured substantially in the last 20 years. Probably most large-scale genetic evaluations of beef and dairy cattle

populations around the world use some form of linear and(or) nonlinear intrabreed prediction methodology computed with an in-house program or with a program such as MTDFREML (Boldman et al, 1995) and ASREML (Gilmour et al., 2000). As its name indicates, intrabreed methodologies assume that all animals in the population belong to a single breed. However, arguably most cattle populations have been and continue to be produced by crossbreeding, either by upgrading to one of the parental breeds, or by producing a composite with fractions of several breeds. In either case, and particularly if populations are kept open (i.e., crossbred animals are constantly being produced from parental populations), substantial numbers of crossbred animals will be produced. Crossbred animals serve as links among purebred parental populations, thus generating a single multibreed population composed of purebred and crossbred animals. Two aspects complicate the genetic analysis of multibreed populations. Interbreed nonadditive genetic effects may be important for some traits in some breed combinations, and heterogeneity of variances and covariances may exist among breed groups (purebred and crossbred). Thus, data from multibreed populations must be analyzed using multibreed procedures in order to account for both additive and nonadditive genetic effects, and for heterogeneity of variances and covariances across purebred and crossbred groups. In contrast, if intrabreed procedures are used to analyze multibreed data, they will not explain nonadditive genetic effects, and assume that all traits have the same variances and covariances across all breed groups (purebred and crossbred).

Brazil has a population of 167 million cattle, 79.5% beef (ANUALPEC, 2004), and 80% are either Zebu or Zebu crossbreds (Josahkian, 2000). Consequently, there is a large number of subpopulations of various sizes composed of either *Bos indicus* × *Bos indicus* and *Bos indicus* × *Bos Taurus* breeds that fit the description of a multibreed population. Currently all genetic evaluation procedures used for major genetic evaluations in Brazil are intrabreed, even though many of the populations evaluated are multibreed, or animals (particularly sires) from these populations will be used in crossbreeding situations. Thus, it seems relevant to discuss the feasibility of pursuing research and development efforts on multibreed genetic evaluation procedures. The discussion will cover the following topics: 1) characterizing multibreed populations, 2) large field multibreed populations, 3) basic multibreed genetic evaluation model, 4) applied multibreed genetic evaluation models, 5) multibreed expected progeny differences, 6) implementation factors, and 7) final remarks.

Characterizing Multibreed Populations

Multibreed populations are populations composed of interbreeding purebred and crossbred animals. In multibreed populations sires and dams can be of any breed composition. Based on the mating scheme multibreed populations can be classified as complete and incomplete.

Complete multibreed populations have a complete diallel-type mating scheme, i.e., sire and dam groups are the same and sires are mated to dams of all breed groups. Systems like this are more likely to exist in simple two-breed experimental or field settings. If

more breeds were involved it would be highly unlikely that all subclasses would ever be represented in substantial numbers, and many subclasses may never be created at all.

An example of a complete experimental multibreed population is the Angus-Brahman multibreed herd of the University of Florida. Table 1 shows the numbers of sires mated across breed groups of dams in this herd between 1989 and 2004. This herd was created to study variability of economically important traits in a multibreed context and to help validate multibreed genetic evaluation procedures.

The Chilean Holstein-Other breeds multibreed population is an example of a complete field multibreed population, where Holstein encompasses US and Canadian Holstein, and Other breeds includes Friesian germplasm from various European countries and New Zealand (Elzo et al., 2004). The mating strategy in the Chilean population during the period of this study appeared to have been an incomplete upgrading to Holstein.

Table 1. Number of sires by breed-group-of-sire × breed-group-of-dam combination in the Angus-Brahman multibreed herd of the University of Florida between 1989 and 2004

Breed group of dam	Breed group of sire[1]					
	Angus	¾ A ¼ B	½ A ½ B	¼ A ¾ B	Brahman	Brangus
Angus	35	12	17	20	30	33
¾ A ¼ B	25	16	19	18	32	28
½ A ½ B	33	15	20	20	36	33
¼ A ¾ B	23	13	16	16	30	22
Brahman	23	11	15	18	49	23
Brangus	23	9	18	18	27	36

[1] A = Angus, B = Brahman.

Table 2. Number of sires by breed-group-of-sire × breed-group-of-dam combination in the Chilean Holstein-Other breeds multibreed population between 1990 and 2000

Breed group of dam	Breed group of sire[1]				
	Holstein	¾ H ¼ O	½ H ½ O	¼ H ¾ O	Other breeds
Holstein	182	10	19	2	50
¾ H ¼ O	387	30	49	8	119
½ H ½ O	513	37	87	15	215
¼ H ¾ O	431	36	91	13	212
Other breeds	509	45	108	20	329

[1] H = Holstein; O = Other breeds.

In incomplete multibreed populations sires and(or) dams are not represented in some of the breed groups, and sires may or may not be mated to dams of all breed groups. Probably the vast majority of experimental and field multibreed populations in the world match the definition of an incomplete multibreed population. Most cattle experimental herds have been designed to compare only a small subset of all possible breed group combinations. Similarly, most field designs have been geared to either upgrade to a

specific breed or to produce animals of some predetermined breed composition (e.g., 5/8 breed A and 3/8 breed B). In both situations, incomplete multibreed mating designs will result.

The Sanmartinero-Brahman multibreed herd at La Libertad in Colombia is a good example of an incomplete experimental multibreed herd (Table 3). The Sanmartinero-Brahman herd was originally designed to compare breed groups of cattle.

If the vast majority of sires used in a population undergoing upgrading belong to the introduced breed, then an extremely unbalanced incomplete multibreed population will result. Such was the case of the Thai Holstein-Other breeds multibreed population (Koonawootrittriron et al, 2002) managed by the Dairy Farming Promotion Organization (DPO), where most of the sires used from 1991 to 2000 were Holstein (Table 4). Other breeds included Native *Bos indicus*, Brahman, Red Sindhi, Sahiwal, Jersey, and Red Dane.

Table 3. Number of sires by breed-group-of-sire × breed-group-of-dam combination in the Sanmartinero-Brahman multibreed herd at La Libertad, Colombia, between 1971 and 1996

Breed group of dam	Breed group of sire[1]		
	Sanmartinero	½ S ½ B	Brahman
Sanmartinero	88	0	14
½ S ½ B	14	10	18
¾ S ¼ B	14	0	0
Brahman	41	1	22

Table 4. Number of sires by breed-group-of-sire × breed-group-of-dam combination in the DPO Holstein-Other breeds multibreed population, Thailand, between 1991 and 2000

Breed group of dam	Breed group of sire	
	Holstein	H × Other breeds[1]
(0.8-1.0)H (0.2-0.0)O	89	6
(0.6-0.8)H (0.4-0.2)O	103	6
(0.4-0.6)H (0.6-0.4)O	76	5
(0.2-0.4)H (0.8-0.6)O	17	2
(0.0-0.2)H (1.0-0.8)O	14	1

[1]H = Holstein, O = Other breeds = Native, Brahman, Red Sindhi, Sahiwal, Jersey, Red Dane.

Large Field Multibreed Populations

Much larger field multibreed populations of beef cattle than the ones described above exist in the US and Brazil. In the US, these multibreed populations were generated as a

byproduct of the upgrading process used to create populations of British and Continental (European non-British) cattle, or by using a multiplicity of mating alternatives to generate *Bos Taurus ×Bos indicus* breeds (e.g., Simbrah, Brangus). In Brazil, similar processes of upgrading and use of crossbreeding to create new breeds have contributed to the generation of a variety of multibreed populations of various sizes and breed compositions (e.g., Nelore, Black and Red Angus, Braford, Brangus; Fazendas Paquetá Limitada, 2004). The main difference between the two countries is the substantially larger proportion of *Bos indicus* germplasm in Brazilian multibreed cattle populations.

In the US, data from animals composed of various breeds can be sent to various breed associations. This has generated national breed datasets with substantial amounts of multibreed data. The ownership and data structure of these national datasets allow the consideration of several alternative national multibreed genetic evaluation strategies (Elzo, 1995, 2000).   The simplest, and the most restrictive alternative, would be for breed associations that possess such datasets to conduct intra-association multibreed genetic evaluations. A better alternative would be for some breed associations to jointly conduct multibreed genetic evaluations. Such an agreement was reached between the American Simmental-Simbrah and the Canadian Simmental associations in the early nineties. As a result, the first US national multibreed genetic evaluation was conducted by researchers of Cornell University (Klei and Quaas, 1995; Klei et al., 1996), and was published in 1997 (Pollak and Quaas, 1998; Quaas and Pollak, 1999). In 2004 University of Georgia researchers implemented a multibreed system similar to the one developed at Cornell University. Colorado State University uses models that include (fixed) breed group and heterosis effects. Iowa State University uses intrabreed genetic evaluation procedures. The best alternative would be for *all* breed associations in the US to agree to conduct a single joint US multibreed genetic evaluation that incorporated data from all sources. This would permit comparisons of purebred and crossbred sires mated to dams of any breed composition.

In Brazil, the size of many cattle operations, whether purebred or multibreed is very large. Cattle operations involving 10,000 or more cows are not uncommon (e.g., Fazendas Paquetá Limitada, 2004; GAP Genética Agropecuária Limitada, 2004). Groups of cattle operations have formed alliances to improve the marketability of their products. Many of these operations have agreements with researchers in private and semiprivate organizations to conduct genetic evaluations (e.g., EMBRAPA, 2004; GENSYS, 2004; ANC "Herd-Book Collares", 2004). Brazilian breed associations (ABCZ, 2004; ANCP, 2004) play an important role in national genetic evaluations for a number of breeds (e.g., Brahman, Gir, Guzerat, Indubrasil, Nelore, Tabapua). Based on the current organizational structure of the cattle industry in Brazil, the following levels of multibreed genetic evaluations could be considered: 1) local genetic evaluations within large individual multibreed cattle operations, 2) local or national genetic evaluations within alliances (groups of purebred and multibreed cattle operations), 3) national genetic evaluations within breed associations, 4) national genetic evaluations within groups of breed associations and(or) groups of alliances, 5) complete national genetic evaluation using all purebred and crossbred data in Brazil. Perhaps a two-stage program of research and development of multibreed genetic evaluations could be attempted. First, develop

multibreed genetic evaluations within currently existing organizational levels 1, 2, and 3, and, if successful, then consider their implementation at levels 4 and 5. In order to carry out any of the across organization multibreed genetic evaluations, a global agreement on organizational, technical, and marketing aspects would need to be worked out. Long-term cooperation among participating institutions would be required. It might also be advantageous to create a global organization with representatives from all interested parties to establish norms for and to facilitate the development of uniform national genetic evaluations, in much the same way as the Beef Improvement Federation does in the US.

Basic Multibreed Genetic Evaluation Model

Multibreed genetic evaluation models are simply extensions of unibreed genetic models that account for intrabreed and interbreed additive and nonadditive genetic effects. In multibreed models, additive genetic effects are the result of the combined intrabreed and interbreed additive genetic effects. The term interbreed additive genetic effects refers to segregation effects (Wright, 1968; Lande, 1981; Lo et al., 1993), and they exist only when parents are crossbred. For computational simplicity, nonadditive intrabreed and interbreed genetic effects here refer to regression effects due to intralocus intrabreed and interbreed interactions within breed-group-of-sire × breed-group-of-dam subclasses for (fixed) group nonadditive genetic effects ("heterosis"), and within sire × breed-group-of-dam subclasses for random nonadditive genetic effects ("random heterosis"). More complex nonadditive regression models can be written (Elzo, 1990b), but confounding and(or) multicollinearity may prevent successful computations.

The basic structure of multibreed models will be illustrated with the sire-maternal grandsire model used to evaluate the Chilean Holstein-Other breeds multibreed population (Elzo et al., 2004). Thus,

$$y = Xb + Z_{ga}g_a + Z_{gn}g_n + Z_{gmgd}g_{mgd} + Z_a s_a + Z_n s_n + v$$

$$
\begin{bmatrix} y \\ s_a \\ s_n \\ v \end{bmatrix} \sim MVN
\begin{bmatrix} Xb + Z_{ga}g_a + Z_{gn}g_n + Z_{gmgd}g_{mgd} \\ 0 \\ 0 \\ 0 \end{bmatrix},
\begin{bmatrix} Z_a G_a Z_a' + Z_n G_n Z_n' + R & Z_a G_a & Z_n G_n & R \\ G_a Z_a' & G_a & 0 & 0 \\ G_n Z_n' & 0 & G_n & 0 \\ R & 0 & 0 & R \end{bmatrix}
$$

where, using the notation H = Holstein, and O = Other breeds,

    y   =   vector of cow records for milk yield, fat yield, and protein yield ordered by traits within cows,

    b   =   vector of herd-year-seasons,

    g_a =   vector of sire-maternal grandsire intrabreed H additive direct genetic group effects,

    g_n =   vector of sire H/O nonadditive direct genetic group effects,

g_{mgd} = vector of maternal granddam intrabreed H additive direct genetic group effects,

s_a = vector of sire and maternal grandsire additive direct genetic effects,

s_n = vector of sire H/O interbreed intralocus nonadditive direct genetic effects,

v = vector of residuals,

X = matrix that relates cow records to elements of b (1's and 0's),

Z_{ga} = matrix that relates cow records to elements of g_a through the expected fraction of H alleles in the sire and the maternal grandsire of a cow ($p_{Hs} + .5p_{Hm}$), where p = probability, and the subscripts s = sire, and m = maternal grandsire,

Z_{gn} = matrix that relates cow records to elements of g_n through the probability of intralocus H and O alleles in the cow ($p_{Hs} p_{Od} + p_{Os} p_{Hd}$), where the subscript d = dam,

Z_{gmgd} = matrix that relates cow records to elements of g_{mgd} through the expected fraction of H alleles in the maternal granddam,

Z_a = matrix that relates cow records to elements of s_a through the sire (1) and the maternal grandsire (.5),

Z_n = matrix that relates cow records to elements of s_n through the probability of intralocus H and O alleles in the cow ($p_{Hs} p_{Od} + p_{Os} p_{Hd}$),

MVN = multivariate normal,

G_a = matrix of multibreed additive genetic variances of and covariances between elements of s_a,

G_n = matrix of multibreed nonadditive genetic variances of and covariances between elements of s_n, and

R = block-diagonal matrix of multibreed residual variances of, and covariances between, elements of v.

Multibreed additive genetic variances and covariances explain the intrabreed and interbreed additive genetic variation that exists among sires and maternal grandsires. They are computed as linear combinations of base intrabreed and interbreed additive genetic variance components, where "base" refers to the parental populations: Holstein and Other breeds. Nonadditive genetic variances and covariances explain the variation due to intralocus intrabreed and interbreed interactions within sire × breed-group-of-dam subclasses. Multibreed residual variances and covariances contain all multibreed additive, nonadditive, and environmental variation not accounted for by the model. Multibreed environmental variances and covariances are modeled in a similar fashion to multibreed additive genetic variances and covariances. For a complete description of the basic model in a beef cattle situation with direct and maternal genetic effects see Elzo and Wakeman (1998).

Computational strategies needed to build multibreed mixed model equations are more complex than those of intrabreed models. However, the general strategy is the same: computation of individual animal contributions to the various effects in the model. The main difference is the heterogeneity of genetic and environmental variances and

covariances. The required inverses of the multibreed additive and nonadditive covariance matrices are computed using simple algorithms (Elzo, 1990a,b). The inverse of the residual matrix is accomplished by direct inversion of individual blocks. Multibreed additive and nonadditive genetic, and environmental variances and covariances are estimated using multibreed restricted maximum likelihood procedures that utilize a generalized expectation-maximization algorithm (MREMLEM; Elzo, 1994, 1996). For additional information on multibreed models and estimation of multibreed variances and covariances in beef and dairy cattle refer to Elzo and Famula (1985), Elzo and Bradford (1985), Arnold et al. (1992), Cantet and Fernando (1995), Elzo and Wakeman (1998), Elzo et al. (1998a,b, 2001, and 2004), Birchmeier et al. (2002), and Koonawootrittriron et al. (2002). A more theoretical development of multibreed models can be found in Lo et al. (1993, 1995). For a Bayesian perspective on multibreed models refer to Jara et al. (2001a,b), and Cardoso and Tempelman (2004).

Applied Multibreed Genetic Evaluation Models

The form that multibreed genetic evaluation models take will depend on the multibreed population to be analyzed. In large multibreed beef cattle populations composed of two to four parental breeds and their crossbreds, it may be feasible to predict intrabreed and interbreed additive and nonadditive genetic effects if there are sufficient numbers of sires mated across breed groups of dams, and multibreed contemporary groups are appropriately connected. Beyond four breeds, more sweeping assumptions are likely to be required.

Grouping strategies may need to be modified according to the representation of particular breeds in the multibreed population. If a multibreed population contains a large number of breeds, then genetic groups could be created with animals from all breed of similar origin (e.g., African, British, Continental, Zebu). If one of the breeds is present in all animals and all other breeds have substantially smaller representation, then two genetic groups could be defined (e.g., Holstein and Other breeds).

Heterogeneity of additive genetic, nonadditive genetic, and environmental variances will be easier to estimate in reasonably well-balanced multibreed populations, but perhaps impossible to compute in highly unbalanced multibreed populations where sires are poorly represented across breed groups of dams. In extreme cases, for simplicity or for computational reasons, a single set of additive genetic variances and covariances and only fixed group nonadditive genetic effects would be considered in the multibreed model.

The Cornell national multibreed model is a good example of what can be accomplished and the compromises that need to be made in a large multibreed population. Simmental, Simbrah, and Canadian Simmental data contribute to this multibreed genetic evaluation. The Cornell system: 1) defines four genetic groups: British, Continental, Zebu, and Other breeds), 2) uses a Bayesian approach for heterosis and genetic group effects to prevent drastic changes of estimates of these effects across years, and 3) utilizes a single

variance-covariance matrix for all purebred and crossbred animals (Quaas and Pollak, 1999). The Cornell system is now part of the Beef Improvement Federation guidelines for national cattle evaluation in the US (BIF, 2004). The multibreed system developed at the University of Georgia in 2004 follows the strategy used by Cornell. Colorado State University version of multibreed evaluation accounts for fixed breed group and heterosis effects. Because these three universities are in charge of the genetic evaluation of most of the beef breeds in the US, it could be said that multibreed genetic evaluation procedures have become the procedure of choice for national beef cattle evaluation in the US.

Because 80% of cattle in Brazil has some Zebu influence, and a large fraction of multibreed cattle operations have Zebu × British and(or) Zebu × Continental, sizable amounts of *Bos indicus* × *Bos taurus* intralocus interactions could be expected. The distribution of these interactions would need to be determined. If there is little variation around the mean of particular interaction, then fitting only breed-group-of-sire × breed-group-of-dam interactions (as in the Cornell model) may suffice. However, if there were ample variation among sire × breed-group-of-dam interaction effects due to intralocus interactions (intrabreed or interbreed), then sire × breed-group-of-dam interaction effects would need to be included in the multibreed model. There is some evidence that nonadditive variation due to *Bos indicus* × *Bos taurus* intralocus interactions may be comparable to additive genetic variation for various growth (Elzo and Wakeman, 1998; Elzo et al., 1998a; Elzo et al., 2001), carcass (Elzo et al., 1998b), and dairy (Koonawootrittriron et al., 2002) traits (Table 5). However, these studies were conducted in small multibreed populations and need to be reconfirmed with substantially larger multibreed datasets, which Brazil appears to possess in abundance.

A multibreed genetic model for research and development purposes in Brazil could have the following structure:
   1) multibreed contemporary groups (e.g., herd × season × sex × management group),
   2) regression of age of dam × sex of calf on breed fraction(s) of dams (e.g., a fourth degree polynomial as suggested by BIF, 2004),
   3) other relevant fixed effects,
   4) breed group of animal (as a regression on breed fractions),
   5) breed-group-of-sire × breed-group-of-dam interaction (as a regression on intralocus interbreed interactions),
   6) random animal additive genetic effect,
   7) random sire × breed-group-of-dam interaction (as a regression on intralocus interbreed interactions),
   8) residual.

This model would be for multiple traits, and it would account for heterogeneity of variances and covariances.

Table 5. Ratios of additive (heritabilities) and intralocus interbreed nonadditive (interactibilities) variances to multibreed phenotypic variances for growth, carcass, and dairy traits in several small multibreed populations

Breed Group	Trait	Heritability		Interactibility	
		Direct	Maternal	Direct	Maternal
Angus × Brahman	Birth Weight	0.19	0.15	0.15	0.16
	Weaning Weight	0.22	0.16	0.18	0.20
	Carcass Weight	0.30		0.27	
	Loin Muscle Area	0.34		0.28	
	Marbling	0.13		0.12	
	Shear Force	0.17		0.07	
Romosinuano × Zebu	Birth Weight	0.20	0.16	0.21	0.26
	Weaning Weight	0.09	0.11	0.05	0.04
	Postweaning Gain	0.14	0.15	0.12	0.11
Sanmartinero × Zebu	Birth Weight	0.28	0.27	0.22	0.25
	Weaning Weight	0.09	0.10	0.08	0.08
	Postweaning Gain	0.40	0.42	0.30	0.35
Holstein × Other breeds	Milk yield	0.38		0.17	
	Fat yield	0.34		0.20	

Multibreed Expected Progeny Differences

Multibreed genetic evaluation models yield predictions of additive and nonadditive genetic effects. Thus, three types of multibreed expected progeny differences (MEPD) can be computed for an animal: additive (AMEPD), nonadditive (NMEPD), and total (TMEPD = AMEPD + NMEPD). Additive MEPD are the multibreed equivalent of intrabreed additive EPD. Nonadditive MEPD are due to intralocus interactions created anew when sperm and ova unite, thus it would be ill advised to use them alone. Both commercial producers and purebred breeders would be able to take advantage of MEPD. Purebred breeders can use AMEPD to further their additive selection goals, and TMEPD to give them information on the combining ability of their sires when mated to specific breed groups of dams, thus improving the marketability of their sires for use in commercial cattle operations. Commercial producers involved in crossbreeding will be able to increase the reproductive and productive level in their herds by choosing sires that are not only good additively but that combine well with the breed groups of cows present in the herd. As a general rule it would be advisable to choose sires in two sequential

steps: first select a preliminary group of sires by their AMEPD, and second, *within the group of chosen sires by AMEPD*, select the final set of sires according to their TMEPD. This is a safe approach to sire selection in multibreed populations in that permanent additive genetic changes are given priority over temporary nonadditive genetic changes. Its purpose is to move a population in the desired direction in both additive and nonadditive terms (Elzo et al., 1998b). Because many breed groups of cows may be present in a commercial operation, sires from a wide range of breed compositions would need to be chosen. In practice, however, a workable mating system may require a mixture of artificial insemination (to create multibreed contemporary groups) and natural service.

Implementation Factors

Application of multibreed genetic evaluation models to field datasets will need to deal with the following aspects:
1) connectedness among multibreed contemporary groups,
2) estimation of multibreed variances and covariances,
3) choosing a multibreed genetic base,
4) deciding what specific MEPD to compute,
5) development of appropriate means of delivery for MEPD, and
6) explaining the differences between additive, nonadditive, and total genetic predictions and their use for selection and genetic management decisions.

Connectedness. In multibreed populations connectedness needs to be considered at two levels: connectedness by breed groups and connectedness by animals present across multibreed contemporary groups (Elzo, 1995). Ideally all breed groups of sires and dams would be represented in all multibreed contemporary groups. Clearly this would be impossible to accomplish even in experimental settings, except perhaps for simple two-breed designs. However, connectedness across multibreed contemporary groups should be given by animals (sires, dams, maternal grandsires) from as many breed groups as possible. This will help avoid problems of confounding and multicollinearity in multibreed models with fixed and random additive and nonadditive genetic effects. Connectedness in current field multibreed populations is probably given mostly by purebred sires and(or) sires from composite breeds (e.g., Brangus, Girolando). Field research is needed to determine if additional connections may be required to implement multibreed models with random additive and nonadditive genetic effects, else compromises (e.g., drop random nonadditive genetic effects from the model, discard multibreed contemporary groups with few breed groups represented), and appropriate simplifying assumptions (e.g., common covariance matrices for all breed groups) will need to be made.

Estimation of Multibreed Variances and Covariances. Successful estimation of variance and covariance components will largely depend on how well balanced the structure of a field multibreed population is, the level of connectedness (breed groups and animals), and the amounts of information available per animal. Because of goal

specificity (upgrading, creation of specific crossbred group) many, if not most, field multibreed populations will be highly unbalanced, they will have animals from few breed groups, and contemporary groups are likely to be connected by animals from few breed groups. Thus, heavy editing may be needed to estimate genetic parameters. In the Chilean Holstein-Other breeds multibreed population, a small well-balanced subset was required to be extracted from the complete dataset to be able to compute additive and nonadditive genetic parameters for three dairy traits (Elzo et al., 2004). Cardoso and Tempelman (2004) faced a similar situation when computing genetic parameters in a highly unbalanced Brazilian Nelore-Hereford beef cattle dataset using Bayesian procedures.

Confounding and multicollinearity are the two main factors contributing to difficulties in estimation of genetic parameters in multibreed populations. Although improvements in breed group and animal connectedness may help to some extent, judicious editing of field datasets will always be an important factor to obtain credible estimates of multibreed genetic parameters, regardless of estimation methodology.

It should be emphasized that although a very large number of different additive genetic variances and covariances are needed in multibreed genetic evaluations, only a small fraction of them need to be estimated using multibreed restricted maximum likelihood procedures (Elzo, 1994, 1996). These are the additive variances and covariances for the base breeds. Multibreed additive variances and covariances for all crossbred groups are computed as linear combinations of these base breed additive variances and covariances. A similar situation exists for multibreed environmental variances and covariances.

Multibreed Genetic Base. A multibreed genetic base should be chosen to facilitate comparisons of purebred and crossbred animals across breed groups and mating types (breed-group-of-sire × breed-group-of-dam combinations). It will have two components: one additive genetic, similar to intrabreed genetic bases, to compare animals for AMEPD, and one nonadditive genetic to compare mating combinations for NMEPD or TMEPD. To compare animals for AMEPD, a genetic base could be constructed using animals from any breed composition because multibreed genetic evaluation procedures can fairly compare animals of all breed compositions for additive multibreed genetic effects.

The comparison of animals (probably sires in most instances) for NMEPD and TMEPD is somewhat more involved. Comparisons among sires for NMEPD and TMEPD could be done using the maximum NMEPD and TMEPD values produced by multibreed genetic evaluation models. However, these maximum values, in practice, apply only to first generation crossbred matings. Another alternative would be to choose a breed group of dam that yielded the same expected fraction of nonadditive genetic effects in the progeny for all sire × breed-group-of-dam comparisons. For example, in a two-breed multibreed population, such breed group of dam could be F1 individuals (all progeny would be expected to show 50% intralocus nonadditive genetic effects). These alternatives rank sires for NMEPD and TMEPD in a generic fashion that may be of limited use to commercial producers that have cows of several breed groups in their herds. Thus, a more useful alternative would be to develop flexible computer programs

that rank sires for AMEPD, NMEPD, and TMEPD given the breed composition of cows in a herd. Even further, if dam AMEPD were available, then matings could be based on the total multibreed genetic prediction of the future progeny, where TMEPD of future progeny = ½ AMEPD of sire + ½ AMEPD of dam + NMEPD of sire × breed-group-of-dam.

Computation of Specific NMEPD and TMEPD. The decision to regularly compute NMEPD and TMEPD will largely depend on the expected mating frequency of sires and dams of particular breed compositions. Because of the large number of potential sire × breed-group-of-dam combinations, even in a two-breed multibreed population, and the likelihood that many sires will only be mated to cows from some breed groups, it is unlikely that complete lists of NMEPD or TMEPD will ever be produced. Purebred breeders supplying sires to commercial operations may include, in addition to AMPED, NMEPD and TMEPD for some sire × breed-group-of-dam combinations that are popular with commercial producers to gain an edge over the competition.

A more likely scenario would be for both purebred breeders and commercial producers to have access to software that will enable them to compute NMEPD and TMEPD on demand, such that short list of sires chosen based on some minimum value of AMEPD and TMEPD using the two-step procedure outlined above could be produced. Lists like this will help the identification of suitable sires and facilitate commercial transactions.

Development of appropriate means of delivery for MEPD. Publication of sire summaries for AMEPD on paper, may in many instances, still be an appropriate and cost-effective alternative. However, publication of NMEPD and TMEPD on paper will likely be limited to small groups of highly used sires (e.g., sires used to connect multibreed herds). Electronic publication of complete sire summaries for AMEPD would seem to be the most cost effective alternative. Electronic publication of NMEPD and TMEPD will likely be limited to frequently used sires, and only for the most common sire × breed-group-of-dam combinations.

The most useful means of publication of AMEPD, NMEPD, and TMEPD would be easy-to-use computer software with access to the complete list of additive and nonadditive genetic predictions of all sires. This will allow users to choose the best sires for the cows to be mated according to the predicted additive and total genetic values of their future progeny.

Explaining the differences between AMEPD, NMEPD, and TMEPD, and their use for selection and genetic management decisions. This is an aspect whose importance should not be underestimated. Multibreed genetic predictions are only one more tool to help purebred breeders and commercial producers to make appropriate production and economic decisions. Needless to say, to be effectively used, AMEPD, NMEPD, and TMEPD must be understood properly. It is the responsibility of the organizations that conduct and supply multibreed evaluations to clearly explain their proper use for selection and marketing purposes.

Additive MEPD should be used in much the same way as additive intrabreed EPD are used: to select animals for additive genetic effects. The main differences between the two is that AMEPD are computed relative to a broader genetic base, and they can be used to compare animals of all possible breed fractions of the base breeds in a multibreed population. However, AMEPD of animals from different multibreed populations with at least one different base breed *cannot* be compared, even if they have the same breed composition. Also, because of differences in genetic bases, even if two multibreed populations had the same base breeds, AMEPD from one evaluation *cannot* be compared to AMEPD from the other evaluation.

The maximum NMEPD computed in a multibreed genetic evaluation refers to intralocus interactions between alleles from a particular sire and from dams of all breed groups mated to a sire. Nonadditive MEPD computed for specific sire $\times$ breed-group-of-dam combinations are intralocus interactions between alleles from a particular sire and from dams of a single breed group. Notice that these intralocus interactions will be realized in the future progeny of these planned matings. Specific NMEPD will always be less than or equal to the maximum NMEPD.

Total MEPD are simply the sum of AMEPD + NMEPD, i.e., they are a combination of additive and nonadditive genetic effects, thus their main use will likely be for planning crossbred matings. From a usability standpoint, TMEPD should be used in conjunction with AMEPD, e.g., as part of the two-step procedure to select sires in multibreed populations. These TMEPD would be the most comprehensive prediction of the outcome of crossbred matings. They would be useful to purebred breeders to promote sires for their combining ability, and will enable commercial producers to choose sires that are expected to produce the best crossbred progeny given their cowherd breed composition.

Final Remarks

Brazil has a very large national cattle population that is largely crossbred, thus suitable to be considered for genetic evaluation using multibreed genetic evaluation procedures. Advantages of multibreed genetic evaluation procedures include higher accuracy for additive genetic predictions, direct comparison of animals of different breed composition, availability of nonadditive and total (additive + nonadditive) genetic predictions for individual sires permitting better prediction for the outcome of crossbred matings, and improvement of a multibreed population in additive and nonadditive genetic terms. Disadvantages include heavier computational loads, larger number of genetic parameters to be estimated, and problems of confounding and multicollinearity.

A key factor for a successful implementation of multibreed genetic evaluation procedures is the existence of representative and well-connected multibreed contemporary groups. In addition, location, climate, nutrition, management, reproduction practices, and the type and number of base breeds will directly impact the form and complexity of the multibreed model. It is possible that provided a suitable set of assumptions could be

found, even highly unbalanced multibreed populations could be evaluated using multibreed procedures.

Lastly, however feasible multibreed genetic evaluation procedures may be from a technical standpoint, it is likely that cost-benefit factors will eventually determine whether and how they will be implemented in Brazil.

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