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Synthesis of direct and maternal genetic components of economically important traits from beef breed-cross evaluations¹

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ABSTRACT: Published information on relative performance of beef breed crosses was used to derive combined estimates of purebred breed values for predominant temperate beef breeds. The sources of information were largely from the United States, Canada, and New Zealand, although some European estimates were also included. Emphasis was on maternal traits of potential economic importance to the suckler beef production system, but some postweaning traits were also considered. The estimates were taken from comparison studies undertaken in the 1970s, 1980s and 1990s, each with representative samples of beef breeds used in temperate agriculture. Weighting factors for breed-cross estimates were derived using the number of sires and offspring that contributed to that estimate. These weights were then used in a weighted multiple regression analysis to obtain single purebred breed effects. Both direct additive and maternal additive genetic effects were estimated for preweaning traits. Important genetic differ-

ences between the breeds were shown for many of the traits. Significant regression coefficients were estimated for the effect of mature weight on calving ease, both maternal and direct additive genetic, survival to weaning direct, and birth weight direct. The breeds with greater mature weight were found to have greater maternal genetic effects for calving ease but negative direct genetic effects on calving ease. A negative effect of mature weight on the direct genetic effect of survival to weaning was observed. A cluster analysis was done using 17 breeds for which information existed on nine maternal traits. Regression was used to predict breed-cross-specific heterosis using genetic distance. Only five traits, birth weight, survival to weaning, cow fertility, and preweaning and postweaning growth rate had enough breed-cross-specific heterosis estimates to develop a prediction model. The breed biological values estimated provide a basis to predict the biological value of crossbred suckler cows and their offspring.

Key Words: Beef Cattle, Heterosis, Maternal Effects, Regression Analysis

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Introduction

To develop the most effective suckler cow replacement strategies in beef cattle breeding programs it is necessary to have information about breed-specific direct and maternal genetic effects for economically important traits. For the suckler cow, the traits affecting maternal ability and calf production are of primary importance. Consideration must be given also to the

maternal contribution to the calf as a beef production unit.

Several large, multibreed comparison trials have been conducted over the last 30 yr in Canada, the United States, and New Zealand (e.g., Newman et al., 1985; Baker et al., 1990; Cundiff et al., 1996). Smaller trials have taken place in several other countries (e.g., Australia, Morgan and Saul, 1981; France, Vissac et al., 1982). However, the magnitude of differences among beef breeds still remains a subject of contention.

To produce a model for predicting crossbred breed effects, both individual and maternal heterosis must be considered. Several hundred different cattle breeds are recognized worldwide (Mason, 1969). Estimating the breed-cross-specific heterosis levels of a large proportion of these crosses is prohibitive both in terms of time and cost. Long (1980) provided a review of trials using reciprocal crossbreeding to estimate heterosis. Over the last 20 yr a number of diallel experiments

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Table 1. Breeds represented in this report and their abbreviations

Breed	Abbreviation	Genetic distance available ^a
Aberdeen Angus	A	*
Belgian Blue	Be	*
Braunvieh	B	
Blonde D'Aquitaine	BA	*
Brown Swiss	BS	*
Charolais	C	*
Chianina	Ch	*
Devon	D	
Friesian	F	*
Gelbvieh	G	*
Galloway	Ga	*
Hereford	H	*
Holstein	Ho	*
Jersey	J	*
Limousin	L	*
Longhorn	Lo	*
Maine Anjou	MA	*
Pinzgauer	P	
Piedmontese	Pd	*
Polled Hereford	PH	*
Red Angus	RA	
Red Poll	RP	
Simmental	S	*
Salers	Sa	*
South Devon	SD	*
Shorthorn	Sh	*
Tarentaise	T	

^aThe breeds indicated appear in the genetic distance matrix of Blott et al. (1998).

have taken place in the United States to estimate levels of heterosis (e.g., Neville et al., 1984a,b,c; Dearborn et al., 1986).

The aim of this study was to provide a set of breed effects using information on all *Bos taurus* breeds involved in major breed comparison trials that can be used to predict the performance of crossbred cows and offspring. Published estimates of crosses of the breeds compared in trial work were combined, accounting for unequal sampling between trials. In addition, a method, proposed by Goddard and Ahmed (1982), for calculating differential levels of breed-cross-specific heterosis based on genetic distances was investigated.

Materials and Methods

Breeds and Traits

The breeds considered in this study represent *Bos taurus* breeds that have been evaluated in major published breed comparison trials. Amer et al. (1992) undertook a meta-analysis of beef traits but considered only five breeds. In the current study there was much variation in the extent to which breeds were represented for different traits. All breeds that were represented in at least one trait are listed in Table 1. The traits considered were those with important economic

consequences in the suckler cow. The preweaning trait information was considered in terms of direct additive and maternal additive genetic components. The contributions from relatives considered in the study are outlined in Table 2. The maternal additive genetic effect was estimated from the breed being represented by the dam, maternal granddam, or maternal grandsire. The direct additive genetic component was estimated from the breed being represented on both the sire's and dam's side of the pedigree. Postweaning traits have been shown to have maternal effects of variable and reasonably small size (Amer et al., 1992), and therefore only direct effects were considered for this type of trait. Direct effects for calving ease, birth weight, and calf survival were considered to be traits of the progeny and not of the dam, following Amer et al. (1992) (i.e., the breeds were represented as the sire and dam of the progeny).

A summary of the traits considered can be seen in Table 3. The trait × breed combinations for which breed effects were estimated are shown in Table 4, along with the number of sires and trials contributing to the combined estimates.

Experiments Used

To be eligible, breed-cross comparison trials were required to have more than 10 sires for each of at least two of the breeds, randomly sampled from the populations available. Sample sizes were highly variable between trials. In the combination of data, the different sample sizes were accounted for using a weighting approach, which is described later. Trials were required to be conducted under temperate conditions and to be largely of *Bos taurus* × *Bos taurus* comparisons. This resulted in information being used from several breed-cross trials in the United States, breed evaluation work in Canada and New Zealand, an Australian trial, and several small-scale European comparisons.

U.S. Trials

The United States has had a number of large breed-comparison trials. The trials used to obtain estimates of maternal and postweaning traits in the present

Table 2. Assumed genetic contributions from relatives to trait values

Relationship	Contribution to trait value, %	
	Direct additive	Maternal additive
Sire	50	0
Dam	50	100
Paternal grandsire	25	0
Paternal granddam	25	0
Maternal grandsire	25	50
Maternal granddam	25	50

Table 3. Traits reported together with parameters^a assumed in the estimation of weighting factors

Trait	Abbreviation	h ²	Mean	SD	CV, %
Age at puberty, d	AP	0.6	365	36.5	10
Birth weight, kg	BW	0.4	35	3.5	10
Cow fertility, %	CF	0.05	80	40	50
Heifer fertility, %	HF	0.05	75	37	50
Calving ease, %	CE	0.15	85	34	40
Survival to weaning, %	SW	0.1	90	36	40
Gestation length, d	GL	0.5	287	6	2
Mature weight, kg	MW	0.6	580	58	10
Milk yield, kg	MY	0.4	2,000	400	20
Pelvic area, cm ²	PA	0.4	260	5	2
Prewaning growth rate, g/d	PWGR	0.1	900	90	10
Scrotal circumference, cm	SC	0.05	30	15	50
Weight at puberty, kg	WP	0.6	290	30	10
Steer postweaning growth rate, g/d	GR	0.4	1,200	120	10
Steer fatness finish, mm	SFF	0.3	12	2.4	20

^aParameters approximated from Amer et al. (1992), Koots et al. (1994), and Gregory et al. (1999).

study were the USDA Germplasm Study and other experiments from the U.S. Meat Animal Research Center (**USMARC**). In addition, results from the Georgia Diallel Study and several other smaller trials were used.

USMARC. The germplasm study incorporates 26 sire breeds crossed with Hereford (**H**) and Angus (**A**) dams and has been running for the past 30 yr. All aspects of the production cycle have been evaluated in these breed crosses (e.g., Cundiff et al., 1986; Freetly and Cundiff, 1998; Thallman et al., 1999). Three-way breed comparisons were made using the first-cross animals as dams. Further results from USMARC have come from a four-breed diallel experiment involving Brown Swiss (**BS**), Red Poll (**RP**), H, and A breeds, run over 10 yr starting in 1973 (Dearborn et al., 1986; Dearborn et al., 1987; Gregory et al., 1987). At USMARC, four- and five-breed synthetic cows were developed, starting in 1978 and evaluated together with their purebred parents (Gregory et al., 1999).

Georgia. This study was conducted at the University of Georgia Experimental Station in Lexington. It was initiated in the 1977 breeding season and continued for 5 yr. Sires and dams of the Simmental (**S**), Limousin (**L**), H, and Brahman breeds, sampled from herds across the southeastern United States, were combined in a diallel structure (Comerford et al., 1987, 1988). The reproductive performances of dams and birth and survival traits of their calves under pasture conditions have been reported by Comerford et al. (1987). A further study at Georgia University College of Agriculture looked at various degrees of crosses between A, Polled Hereford (**PH**), and Santa Getrudis (**SG**) breeds from the mid-1960s to the mid-1970s (Neville et al., 1984a,b,c).

Other U.S. Sources. Additional sources of information from the United States were included. A crossbreeding experiment involving A, H, and Charolais (**C**) breeds compared breed preweaning traits. This study

was conducted in North Carolina and finished in 1976 (Dillard et al., 1980). A study of pelvic measurements, undertaken in 1983 and 1984 in Colorado and involving A, H, and S breeds, was also included (Green et al., 1988).

Canadian Trials. The results of an experiment run in the early 1970s involving S, L, A, H, and Shorthorn (**Sh**) breeds were reported by Newman et al. (1985). This included calving and preweaning performance results. McKay et al. (1994) and Newman et al. (1994) reported milk yield and postweaning results of a trial run from 1981 to 1985 involving crossbred dams of H, A, C, S, and Sh breeds. Other Canadian results were obtained from a breed-cross trial initiated in the early 1980s at the Elora Beef Cattle Research Centre (Fiss and Wilton, 1992, 1993). This trial involved the comparison of H, A, Gelbvieh (**G**), Pinzgauer (**P**), Tarentaise (**T**), C, Maine Anjou (**MA**), and S breeds in reproductive and preweaning traits.

New Zealand Trials. In New Zealand (**NZ**) a number of experiments have been run over the last 30 yr looking at both the performance of imported European breeds in the Rukarua Beef Breed Evaluation (**BBE**) and beef × dairy cross animals. Results of several experiments that were undertaken during the 1970s were summarized by Baker and Carter (1982). These trials were conducted under a wide variety of different NZ production conditions. A dairy cross beef trial, involving A, J, H, and Friesian (**F**) breeds, recording all aspects of beef production was run from 1978 to 1987 and was reported by Morris et al. (1988). Baker et al. (1990) reported further results from the BBE, of 11 breeds, BA, C, Chianina (**Ch**), L, MA, S, South Devon (**SD**), A, F, H, and J, evaluated from 1973 to 1977. All crossbred cows evaluated were 50% H or A. Information on lifetime production was also presented for the BBE trial (Morris et al., 1993b). Various experiments involving A × H crosses were carried out between 1973 and 1990 (Morris et al., 1987, 1993a, 1994). In addi-

Table 4. Number of sires sampled and number of trial estimates (in parentheses) used to calculate breed trait biological values

Breed	Trait														
	AP	BW	CF	CE	SW	GL	HF	MW	MY	PA	PWGR	SC	WP	GR	SFF
A	260 (6)	476 (15)	267 (7)	368 (12)	217 (9)	139 (6)	92 (2)	283 (8)	112 (4)	10 (1)	425 (11)	98 (2)	192 (5)	173 (7)	204 (8)
Be				20 (2)	25 (1)	10 (1)								10 (1)	10 (1)
B		58 (1)	58 (1)	58 (1)	58 (1)	58 (1)	58 (1)	58 (1)	58 (1)		26 (1)	58 (1)		69 (2)	79 (3)
BA	24 (2)	48 (4)	14 (1)	14 (1)	52 (4)	34 (3)		14 (1)			14 (1)		14 (1)	10 (1)	10 (1)
BS	10 (1)	33 (3)		33 (3)	23 (2)	20 (2)		23 (2)	10 (1)		10 (1)		10 (1)	34 (3)	44 (4)
C	158 (6)	364 (11)	148 (5)	232 (10)	110 (6)	163 (7)	79 (2)	148 (5)	99 (4)		259 (7)	57 (1)	101 (5)	145 (5)	176 (6)
Ch	32 (3)	74 (6)	12 (1)	54 (5)	56 (5)	42 (4)		22 (2)	10 (1)		54 (4)		22 (2)	30 (2)	40 (3)
D	20 (2)			20 (2)	20 (2)	20 (2)		10 (1)			10 (1)		10 (1)	10 (1)	10 (1)
F	22 (2)	96 (7)	22 (2)	86 (6)	46 (4)	64 (4)		22 (2)			34 (3)	20 (1)	32 (2)	10 (1)	10 (1)
G	61 (2)	92 (4)	63 (2)	81 (3)	61 (2)	81 (3)	63 (2)	73 (3)	73 (3)		41 (3)	51 (1)	10 (1)	82 (3)	92 (4)
Ga													27 (1)	31 (1)	41 (2)
H	211 (5)	434 (14)	300 (7)	425 (12)	180 (9)	200 (6)	135 (2)	316 (8)	155 (4)	165 (2)	525 (10)	88 (2)	153 (4)	210 (6)	241 (7)
Ho	10 (1)			10 (1)	10 (1)	10 (1)		10 (1)			10 (1)		10 (1)	12 (1)	10 (1)
J	22 (2)	64 (6)	22 (2)	54 (5)	46 (4)	32 (3)		22 (2)	10 (1)		34 (3)	20 (1)	32 (2)	43 (2)	53 (3)
L	154 (5)	298 (9)	144 (4)	188 (8)	118 (6)	100 (5)	56 (1)	144 (4)	66 (2)	151 (1)	373 (7)	56 (1)	98 (4)	86 (3)	96 (4)
Lo													23 (1)	29 (1)	39 (2)
MA	34 (3)	97 (7)	44 (3)	82 (6)	62 (5)	68 (5)	20 (1)	44 (3)	30 (2)		77 (5)	20 (1)	54 (4)	52 (3)	62 (4)
P	47 (2)	68 (3)	51 (2)	68 (3)	64 (3)	68 (3)	51 (2)	61 (3)	61 (3)		31 (2)	37 (1)	10 (1)	68 (3)	78 (4)
Pd	20 (1)	10 (1)		20 (2)		10 (1)							20 (1)	34 (2)	44 (3)
RP	61 (2)	80 (3)	51 (1)	80 (3)	80 (3)	61 (2)	51 (1)	80 (3)	61 (2)		10 (1)	51 (1)	10 (1)	86 (3)	96 (4)
S	210 (5)	408 (10)	219 (4)	290 (9)	180 (6)	157 (6)	96 (2)	229 (5)	116 (4)	169 (2)	480 (8)	67 (1)	133 (3)	143 (5)	143 (5)
Sa	25 (1)	37 (2)		10 (1)							27 (1)		25 (1)	39 (2)	49 (3)
SD	32 (3)	144 (5)	12 (1)	44 (4)	56 (5)	32 (3)		22 (2)			134 (4)		42 (3)	27 (1)	37 (2)
Sh	22 (1)	23 (1)							10 (1)				22 (1)	26 (1)	36 (2)
T	10 (1)	32 (3)	10 (1)	22 (2)	10 (1)	22 (2)		20 (2)	20 (2)		31 (3)		10 (1)	22 (2)	32 (3)

tion, pubertal traits were evaluated by Morris et al. (1992).

Other Information. Further information was obtained from a number of sources. During the 1970s a four-breed (H, F, C, and Brahman) crossing trial was undertaken at the Pastoral Research Institute, Hamilton, Australia. All cows were managed on pasture (Morgan and Saul, 1981). French data were presented by Vissac et al. (1982), who summarized results of both experimental work and field data of pure and crossbred cows during the 1970s, and by Ménessier et al. (1982), who provided fertility information on the C, MA, and L breeds of cow. A small amount of U.K. data from field estimates during the 1980s and 1990s was also used (Crump et al., 1994; McGuirk et al., 1998).

Combined Estimates of Breed Effects

This section describes the way in which breed and breed-cross information from different experiments was combined to produce single estimates of breed effects.

Accounting for Heterosis When Estimating "Breed" Effects. When trials were composed of a mix of crossbred and purebred animals, a partial account was made of the heterotic advantage of the crossbred animals. Average, across-breed direct and maternal heterosis estimates taken from the literature, including some of the trials used in this study (e.g., Long, 1980; Comerford et al., 1987), were used to correct the mean in the crossbred estimates. This did not take account of differential levels of breed-cross-specific heterosis but avoided, to some extent, the distortion caused by comparing estimates from crossbred animals with estimates from purebred animals.

Trait Means. Trait means used from trials were restricted to those measured on the same scale in all trials (e.g., kilograms of weight at puberty, percentage of easy calving).

Weighting Information from Different Sources. Different trials used different numbers of sires (Table 4) and offspring to compute breed means. A weighting factor was used to ensure that trials that did not widely sample sires from the population, and which only had small numbers of offspring per sire, did not contribute disproportionately to the overall mean. The weighting factor for combining the information in the analysis was $1/SE(Xc)^2$. Approximate standard errors (SE) for each breed cross effect (Xc) were derived using the method of Amer et al. (1992), allowing for the number of sires and progeny sampled:

$$SE(Xc) \cong \sqrt{\frac{\frac{1}{4}h^2CV^2}{n_s} + \frac{\frac{3}{4}h^2CV^2 + (1 - h^2)CV^2}{n_o}}$$

where Xc is the published estimate of the breed-cross effect for the trait considered, h^2 is the heritability,

CV is the coefficient of variation, n_s is the number of sires sampled to produce the breed cross, and n_o is the number of offspring estimated to evaluate Xc. Heritability and CV estimates used were obtained from Amer et al. (1992), Gregory et al. (1997), and Koots et al. (1994) and are presented in Table 3.

Estimates of Breed Effects. A regression procedure, weighted by the factor derived in the previous section, was used to combine the Xc estimates. Two matrices were set up, ADD and MAT with, respectively, dimensions (n,y) and (m,y) where n is the number of breeds, m is the number of breeds represented as a dam, and y is the number of Xc estimates. These matrices represent the proportion of the breeds that contribute to the direct additive and maternal genetic effects of breed-cross estimate Xc. The ADD_{ij} element of matrix ADD represents the proportion of breed i contributing to the direct additive genetic effect in record j . The MAT_{ij} element of matrix MAT represents the proportion of dam breed i contributing to the maternal genetic effect in record j . An illustrative example of these matrices is presented in Appendix 1. For traits that were considered to have only a direct genetic component, the ADD matrix was fitted in the model and the MAT was excluded. The elements of the matrices were, therefore, between 0 and 1 for ADD and between 0 and 1 for MAT. For each record the proportion of the breeds contributing to the direct additive genetic effect summed to 1, with unknown breed accounting for the proportion unaccounted for in any reported estimate. For those traits considered to have a maternal genetic effect, the proportion of breeds contributing to this effect summed to 1. The model was as follows:

$$Y_{jk} = \mu + TRIAL_k + b_i(ADD_{ij}) + c_i(MAT_{ij}) + e_{jk}$$

where Y_{ijk} is the j^{th} record (Xc) from the k^{th} trial, μ is the regression constant, $TRIAL_k$ is the fixed effect of the k^{th} trial, ADD_{ij} is the proportion of breed i contributing to record j ($\sum_{i=1}^n ADD_{ij} = 1.0$, where n is the total number of breeds contributing to Y_{jk}), b_i is the partial regression coefficient for the direct additive effect of breed i , MAT_{ij} is the proportion of the dam of breed i contributing to breed cross j ($\sum_{i=1}^m MAT_{ij} = 1.0$, where m is the total number of dam breeds contributing to Y_{jk}), and c_i is the partial regression coefficient for the maternal additive genetic effect for breed i .

The partial regression coefficients and regression constant obtained from the model were used to calculate the purebred direct additive and maternal genetic effects shown in Tables 5 through 7. The direct additive genetic effects are the sum of the regression constant and the breed direct effect partial regression coefficient (breed i direct additive genetic effect = $\mu + b_i(1)$). In Table 6 the maternal effects are the partial regression coefficients for the breed maternal components (breed i maternal genetic effect = $c_i(1)$).

Table 5. Estimates of breed effects for puberty and fertility traits^a

Breed	Age puberty, d	Weight puberty, kg	Scrotal circumference, cm		Pelvic area, cm ²	Cow fertility, %	Heifer fertility, %
A	379 (18)	267 (9)	29.3 (1.6)	—	249 (8)	79.3 (9.7)	73.0 (43.0)
B	—	—	31.0 (1.6)	—	—	78.7 (9.8)	80.9 (43.0)
BA	465 (26)	373 (42)	—	—	—	80.2 (10.4)	—
BS	327 (28)	277 (17)	—	—	—	—	—
C	419 (19)	356 (9)	29.5 (1.6)	—	—	78.7 (9.8)	67.0 (43.0)
Ch	446 (28)	365 (17)	—	—	—	43.9 (17.1)	—
D	375 (36)	299 (23)	—	—	—	—	—
F	296 (13)	258 (19)	29.8 (1.7)	—	—	84.9 (10.5)	—
G	315 (20)	287 (19)	31.4 (1.6)	—	—	76.5 (9.8)	78.9 (43.0)
Ga	400 (45)	246 (28)	—	—	—	—	—
H	388 (19)	289 (9)	27.6 (1.6)	—	238 (5)	74.9 (9.8)	60.9 (42.6)
Ho	345 (35)	319 (23)	—	—	—	—	—
J	261 (23)	182 (14)	30.5 (1.9)	—	—	85.1 (10.8)	—
L	432 (19)	331 (9)	26.3 (1.6)	—	251 (5)	76.6 (.8)	53.5 (43.0)
Lo	412 (45)	202 (29)	—	—	—	—	—
MA	385 (22)	324 (13)	29.2 (2.2)	—	—	80.8 (10.9)	71.2 (51.2)
P	331 (20)	273 (15)	30.1 (1.6)	—	—	78.7 (9.8)	77.2 (43.1)
Pd	362 (46)	232 (29)	—	—	—	—	—
PH	—	—	—	—	—	77.8 (9.5)	—
RP	337 (20)	245 (19)	30.3 (1.6)	—	—	77.7 (9.8)	75.1 (43.0)
S	384 (19)	321 (9)	31.0 (1.6)	—	253 (5)	75.2 (9.8)	76.9 (42.9)
Sa	408 (45)	312 (28)	—	—	—	—	—
SD	392 (21)	311 (15)	—	—	—	67.2 (11.1)	—
Sh	374 (46)	294 (29)	—	—	—	—	—
T	361 (31)	283 (19)	—	—	—	64.1 (14.7)	—

^aStandard errors presented in parentheses.**Table 6.** Estimates of breed effects for preweaning traits^a

Breed	Gestation length, days		Calving ease, %		Birth weight, kg		Survival to weaning, %		Preweaning growth rate, g/d	
	Direct	Maternal	Direct	Maternal	Direct	Maternal	Direct	Maternal	Direct	Maternal
A	278 (4)	4 (2)	97.0 (4.3)	-1.8 (2.2)	30.7 (1.1)	0.1 (1.1)	88.0 (3.6)	-0.8 (1.5)	648 (67)	96 (39)
B	289 (4)	—	75.6 (6.3)	-10.0 (6.4)	47.4 (2.1)	-7.5 (2.0)	87.1 (3.4)	—	904 (102)	115 (64)
BA	294 (4)	—	88.7 (4.3)	3.2 (3.5)	37.3 (1.6)	3.9 (1.1)	84.1 (3.9)	1.1 (4.4)	1,040 (85)	-41 (77)
Be	283 (6)	—	94.6 (9.7)	—	39.6 (6.7)	—	89.1 (10.1)	—	—	—
BS	285 (4)	—	96.0 (4.4)	-2.7 (3.4)	35.1 (3.5)	5.6 (1.9)	84.7 (5.7)	—	795 (110)	230 (112)
C	288 (4)	-3 (2)	89.0 (4.1)	-5.7 (5.0)	38.5 (1.8)	5.4 (1.2)	72.8 (3.7)	9.1 (2.0)	862 (68)	176 (57)
Ch	294 (4)	—	89.1 (4.9)	0.4 (6.0)	40.1 (1.9)	5.0 (2.5)	85.3 (3.6)	1.1 (4.3)	806 (74)	73 (85)
D	283 (5)	—	105.4 (11.1)	1.9 (10.9)	28.7 (4.8)	2.5 (5.3)	96.9 (6.4)	—	785 (94)	-8 (143)
F	278 (4)	4 (2)	96.0 (4.6)	-10.8 (5.6)	29.5 (1.5)	6.8 (1.0)	92.0 (3.9)	-5.5 (1.8)	607 (90)	294 (89)
G	287 (4)	-2 (3)	94.8 (9.0)	-7.4 (4.8)	35.7 (2.5)	4.6 (2.6)	84.6 (5.8)	3.9 (5.5)	830 (88)	148 (100)
H	285 (4)	2 (2)	95.9 (4.1)	-5.0 (4.5)	30.5 (1.3)	2.5 (1.0)	93.2 (3.6)	-4.6 (1.6)	723 (66)	31 (37)
Ho	279 (5)	—	102.6 (11.0)	-1.4 (10.7)	31.2 (4.5)	6.6 (3.5)	92.5 (6.4)	—	793 (143)	246 (151)
J	281 (4)	—	101.8 (4.8)	-4.4 (6.4)	22.3 (1.8)	5.0 (2.1)	91.2 (3.9)	-0.3 (4.0)	560 (82)	260 (72)
L	292 (4)	-5 (2)	92.9 (4.1)	-7.6 (2.7)	31.7 (1.0)	4.5 (0.9)	85.8 (3.7)	2.6 (2.3)	825 (64)	87 (44)
MA	288 (4)	-2 (2)	77.6 (4.9)	-2.7 (5.1)	39.1 (1.9)	5.4 (2.3)	83.1 (3.9)	0.4 (4.0)	819 (81)	114 (82)
P	287 (4)	-1 (3)	96.7 (8.2)	-5.1 (4.6)	35.7 (2.5)	7.2 (3.0)	92.1 (5.2)	-5.9 (4.5)	734 (70)	122 (124)
Pd	295 (6)	—	—	—	37.8 (6.9)	8.1 (6.4)	87.8 (10.2)	-6.1 (5.1)	—	—
PH	—	—	—	—	30.2 (3.8)	2.9 (2.1)	93.4 (3.3)	3.4 (3.8)	761 (126)	58 (74)
RP	285 (4)	2 (3)	106.5 (7.1)	-7.7 (5.1)	29.4 (2.8)	5.5 (2.6)	101.2 (4.8)	-11.0 (3.5)	709 (70)	149 (114)
S	290 (4)	-5 (2)	90.2 (4.2)	-15.9 (3.7)	37.2 (1.2)	2.4 (1.2)	82.5 (3.7)	0.8 (2.2)	854 (133)	—
Sa	—	—	—	—	33.2 (4.2)	3.8 (2.2)	—	—	930 (65)	141 (45)
SD	289 (4)	—	93.9 (4.7)	-6.3 (4.7)	34.0 (1.8)	8.9 (1.8)	89.1 (3.8)	1.9 (4.0)	740 (81)	147 (71)
Sh	—	—	—	—	33.9 (4.7)	—	—	—	—	—
T	289 (4)	-7 (4)	99.8 (9.5)	-5.4 (9.5)	33.1 (2.9)	2.6 (3.5)	91.3 (5.9)	—	765 (84)	148 (102)

^aStandard errors presented in parentheses.

Table 7. Estimates of breed effects for postweaning traits and milk yield^a

Breed	Postweaning growth rate, g/d	Steer fatness finish, mm	Mature weight, kg	Milk yield, kg
A	1,077 (63)	13.1 (1.2)	502 (47)	1,312 (949)
B	1,125 (64)	6.4 (1.3)	557 (49)	2,180 (952)
BA	1,082 (100)	1.0 (3.3)	659 (52)	—
Be	1,042 (119)	6.1 (4.5)	—	—
BS	1,004 (153)	9.2 (2.6)	553 (57)	2,163 (1,300)
C	1,214 (66)	2.2 (1.3)	620 (49)	1,532 (948)
Ch	1,112 (86)	3.1 (2.3)	640 (68)	1,448 (1,255)
D	808 (124)	14.4 (3.5)	512 (101)	—
F	882 (120)	11.1 (4.6)	542 (50)	—
G	1,116 (64)	5.6 (1.3)	568 (49)	1,912 (952)
Ga	870 (108)	11.9 (3.0)	—	—
H	1,125 (62)	12.0 (1.2)	519 (47)	916 (954)
Ho	1,052 (115)	7.1 (2.5)	616 (100)	—
J	834 (95)	10.0 (2.5)	443 (52)	2,483 (1,297)
L	1,039 (65)	6.2 (1.3)	531 (49)	1,456 (952)
Lo	688 (103)	6.3 (2.8)	—	—
MA	1,118 (87)	7.2 (2.3)	668 (56)	1,837 (1,011)
P	1,068 (66)	7.0 (1.4)	537 (49)	1,977 (958)
Pd	987 (93)	3.4 (2.5)	—	—
PH	1,252 (93)	12.5 (2.8)	—	—
RP	886 (98)	10.6 (1.4)	501 (49)	1,744 (952)
S	1,175 (81)	7.5 (1.2)	572 (48)	1,954 (948)
Sa	1,152 (108)	8.3 (3.0)	—	—
SD	1,088 (102)	12.9 (2.8)	585 (52)	—
Sh	1,143 (82)	12.3 (2.8)	—	1,797 (962)
T	893 (104)	8.2 (2.6)	494 (60)	1,547 (1,013)

^aStandard errors presented in parentheses.

Heterosis

A genetic distance matrix for all cattle breeds registered in the United Kingdom was constructed by Blott et al. (1998) using blood group information; this is shown in Table 8. Nine markers were used, approximately one on every third chromosome. The measure of Reynolds et al. (1983) was used to calculate between-breed distance. This is based on Wright's statistic F_{ST} and assumes that the populations have diverged due to drift alone when there is no selection operating. It also reflects the amount of gene flow between populations and is appropriate for the analysis of the data sampled from a single species (Slatkin and Madison, 1990).

All published breed-cross-specific heterosis estimates for breeds that appear in the U.K. distance matrix were collected. In addition to sources used for estimating breed effects, older studies were used to provide additional heterosis information (Long, 1980; Long et al., 1979a,b). Unfortunately, for a number of traits, very few estimates of heterosis exist. The traits with breed-cross-specific estimates were cow fertility, birth weight, survival to weaning, weaning weight, preweaning growth rate, and postweaning growth rate. For these traits, the method used by Goddard and Ahmed (1982) to predict heterosis level from genetic distance was applied. The first step was to predict the increase in heterozygosity of a cross over the parental

mean. Goddard and Ahmed (1982) proposed the following:

$$F^h = \frac{F_{ST}}{1 - (F_{ST}/2)} \quad [1]$$

where F^h is the increase in heterozygosity resulting from a cross of two breeds with genetic distance F_{ST} . The heterosis estimates were then regressed onto the predicted heterozygosity increases using the following model:

$$Y_i = b(F_i^h) + e_i \quad [2]$$

where Y_i = heterosis estimate i from the literature, F_i^h is the increase in heterozygosity resulting from the breeds contributing to heterosis estimate i , and $b(F_i^h)$ is the linear regression of increase in heterozygosity on the heterosis estimates Y_i .

Cluster Analysis. To determine which breeds were the most similar, based on biological values for suckler cow production traits, a cluster analysis was undertaken. The complete linkage method was used, with the squared Euclidean distance measure. The breeds used in this analysis were those with information on most traits. This resulted in 17 of the breeds being clustered, based on information from nine traits: direct additive genetic effects for age at puberty (**AP**), weight at puberty (**WP**), cow fertility (**CF**), mature weight

Table 8. Genetic distances (below diagonal) with standard errors^a (above diagonal) between breeds of cattle used in the current study (after Blott et al., 1998, unpublished)

Breed	Number of animals	Breed																			
		A	Be	BA	BS	C	Ch	Ho	Ga	G	H	PH	J	L	Lo	MA	Pd	Sa	Sh	S	SD
A	197		0.016	0.022	0.043	0.022	0.044	0.026	0.023	0.041	0.036	0.037	0.045	0.017	0.065	0.022	0.016	0.040	0.029	0.018	0.042
Be	1,242	0.042		0.033	0.033	0.030	0.039	0.013	0.015	0.042	0.025	0.028	0.044	0.018	0.071	0.024	0.026	0.046	0.021	0.017	0.052
BA	304	0.101	0.107		0.033	0.013	0.036	0.030	0.039	0.027	0.026	0.020	0.021	0.012	0.056	0.035	0.019	0.018	0.031	0.018	0.058
BS	68	0.074	0.081	0.129		0.039	0.045	0.041	0.047	0.042	0.063	0.068	0.060	0.032	0.076	0.037	0.038	0.042	0.034	0.060	0.026
C	1,569	0.104	0.106	0.049	0.142		0.047	0.025	0.043	0.029	0.023	0.025	0.029	0.012	0.042	0.030	0.021	0.020	0.037	0.021	0.048
Ch	66	0.176	0.176	0.093	0.188	0.126		0.040	0.038	0.065	0.066	0.070	0.046	0.038	0.060	0.050	0.043	0.064	0.048	0.047	0.050
Ho	7,778	0.046	0.033	0.105	0.110	0.119	0.206		0.017	0.075	0.031	0.028	0.043	0.023	0.072	0.020	0.027	0.043	0.032	0.028	0.105
Ga	64	0.054	0.044	0.156	0.133	0.148	0.254	0.040		0.070	0.024	0.028	0.056	0.036	0.090	0.032	0.036	0.064	0.031	0.040	0.089
G	99	0.110	0.126	0.083	0.147	0.089	0.120	0.142	0.175		0.050	0.052	0.040	0.029	0.051	0.054	0.034	0.044	0.051	0.037	0.068
H	1,034	0.127	0.130	0.119	0.189	0.138	0.232	0.129	0.128	0.168		0.005	0.040	0.028	0.047	0.035	0.033	0.039	0.036	0.027	0.053
PH	1,079	0.104	0.113	0.122	0.182	0.132	0.236	0.111	0.106	0.173	0.011		0.046	0.025	0.049	0.040	0.034	0.042	0.045	0.024	0.044
J	460	0.198	0.173	0.086	0.194	0.132	0.146	0.188	0.239	0.162	0.224	0.227		0.026	0.075	0.044	0.037	0.048	0.042	0.052	0.059
L	1,813	0.098	0.080	0.041	0.112	0.049	0.130	0.099	0.127	0.104	0.158	0.153	0.105		0.043	0.028	0.020	0.018	0.025	0.014	0.046
Lo	66	0.148	0.190	0.168	0.177	0.158	0.289	0.180	0.204	0.214	0.155	0.148	0.252	0.195		0.045	0.051	0.062	0.045	0.064	0.058
MA	86	0.059	0.054	0.095	0.091	0.092	0.152	0.060	0.103	0.140	0.151	0.130	0.178	0.078	0.174		0.038	0.048	0.020	0.032	0.061
Pd	69	0.044	0.056	0.051	0.099	0.066	0.116	0.050	0.078	0.071	0.116	0.105	0.129	0.064	0.171	0.083		0.031	0.024	0.017	0.063
Sa	85	0.140	0.146	0.053	0.193	0.047	0.148	0.140	0.177	0.108	0.178	0.180	0.135	0.055	0.209	0.140	0.089		0.051	0.031	0.083
Sh	64	0.055	0.060	0.091	0.086	0.092	0.168	0.078	0.096	0.128	0.104	0.085	0.170	0.090	0.137	0.055	0.071	0.161		0.032	0.033
S	928	0.069	0.076	0.075	0.124	0.057	0.150	0.079	0.099	0.061	0.140	0.138	0.159	0.069	0.209	0.099	0.040	0.067	0.109		0.062
SD	84	0.084	0.079	0.140	0.111	0.138	0.213	0.133	0.132	0.139	0.168	0.158	0.226	0.106	0.184	0.110	0.104	0.191	0.089	0.130	

^aEstimated using bootstrapping (resampling individuals and loci).

(**MW**), gestation length (**GL**) and maternal and direct additive genetic effects for birth weight (**BW**), calving ease (**CE**), survival to weaning (**SW**), and preweaning growth rate (**PWGR**). Using the same subset of breeds as in the cluster analysis, various relationships between breed effects were investigated with regression analysis.

Results and Discussion

Estimated Biological Values

Tables 5, 6, and 7 present the biological values for different breeds and traits. The effects are presented with their SE obtained directly from the regression model. In order to use these breed effects in different environments it may be necessary to rescale them.

Variable differences were found between the breeds for the traits considered, although associated SE were large for some traits for which little information was available to provide estimates (e.g., heifer fertility). The SE obtained from the regression method used in this study were found to be larger than the approximate SE estimated by Amer et al. (1992).

Using breed effects of the same breeds and traits used in the cluster analysis, associations between traits were investigated. Significant regression coefficients (results not shown) were estimated for the effect of mature weight on calving ease (direct) ($P < 0.001$), calving ease (maternal) ($P < 0.01$), survival to weaning (direct) ($P < 0.05$), and birth weight (direct) ($P < 0.001$). Higher mature weight had a negative effect on calving ease (direct) and survival to weaning (direct). It is intuitive that a breed of larger mature size will be larger at birth, potentially causing calving difficulties and lower survival.

A dendrogram of the similarity between breeds is shown in Figure 1. The cluster analysis identified two largely dissimilar groups of breeds (Figure 1). The first major group encompassed the larger terminal sire breeds. The second group was composed of dairy breeds, (Holstein [**Ho**], F, and Jersey [**J**]) and the small maternal breeds (A, H, T, P, and RP). Further subdivision first isolates the BA and Ch from the first group and the A, H, and T from the second group.

The ranking of breeds across countries was largely consistent, with the exception of growth traits. Given the different production systems that are employed after weaning, this is not surprising. Morris et al. (1993a) also reported evidence of genotype \times environment interactions for reproductive and maternal traits in two contrasting New Zealand environments. The trial compared the effect of 11 terminal sires crossbred with H and A dams. It was found that newly imported continental breeds performed more favorably in less harsh environments and the British breeds ranked more favorably in the harsh environment. The relative performance of crosses in different environments is something that should be considered very carefully when applying the results presented here.

The biological breed potentials presented in this study as purebred estimates provide a very convenient set of parameters for the determination of breed-cross potentials. If this information is combined with estimates of breed-cross-specific levels of direct and maternal heterosis, a reasonable estimate of genetic potential can be obtained. The reliability of such an estimate depends on a number of factors. Errors in the estimation due to different genetic trends in different populations and any interactions of sire or dam breed \times environment, parity of dam, or sex of calf all pose limitations on the use of the breed effects. Management decisions can also affect estimates; for example, post-weaning growth rate and fatness are affected by the slaughter end point of the measurement chosen. Due to this, it is possible that early-maturing breeds such as H and A have had their growth rate underestimated and fat depth overestimated compared to their optimal slaughter time point (Amer et al., 1992).

There is also a danger that for some breeds estimates of breed effects have been obtained that are in fact biased. This situation arises due to the fact that the results presented are a synthesis of all the trials that have taken place and been published since 1980. These results are not the outcome of a complete, balanced diallel design in which every breed is represented as a sire and dam in a cross to every other breed. A situation may arise in which the direct genetic effect of calving ease of a breed was only assessed using dams with high maternal genetic effects for calving ease. This would lead to the result that a high direct effect for

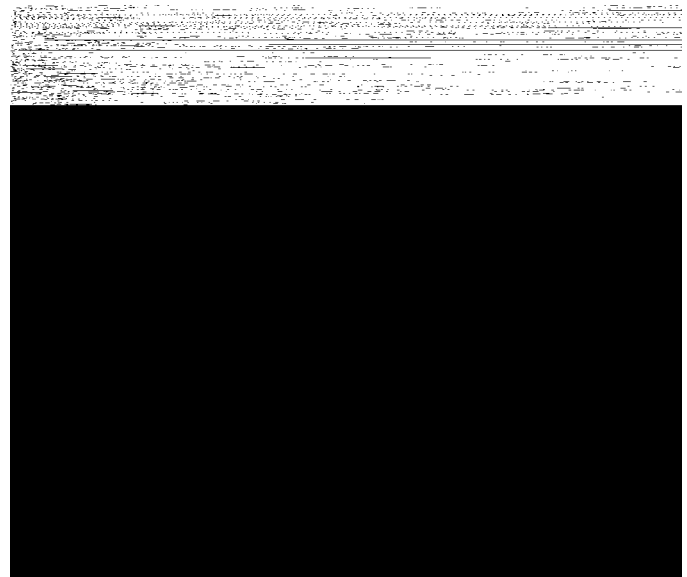


Figure 1. Dendrogram showing the similarity between 17 breeds of cattle based on the following biological values: direct additive genetic effect of age puberty, weight at puberty, cow fertility, mature weight, gestation length, maternal and direct additive genetic effect for birth weight, calving ease, survival to weaning, and preweaning growth rate.

Table 9. Regression coefficients (b) with SD and *P*-value for heterosis on genetic distance^a

Trait	b	SD	<i>P</i> -value
Cow fertility, % of mean ^b	66.7	14.7	0.002
Birth weight, % of mean	24.1	3.1	0.000
Survival to weaning (direct), % of mean	17.3	8.1	0.056
Survival to weaning (maternal), % of mean	17.7	6.6	0.032
Weaning weight, % of mean	32.7	2.4	0.000
Preweaning growth rate, % of mean	36.2	3.5	0.000
Postweaning growth rate, % of mean	40.0	4.0	0.000

^aGenetic distance between breeds ranged from 0.044 to 0.250.

^bHeterosis expressed as a percentage of the trait mean.

calving ease was assigned to the breed when it has not, in fact, been estimated in a fair way. The possibility that there is a reporting bias within the literature, leading to a distorted picture of some breeds, must also be considered.

This study makes no account of genetic trends. The data are derived from experiments that have largely taken place in the 1970s and 1980s. It is possible that differential between-breed genetic progress has been made. If the values are to be used in a specific country, some adjustment for breed genetic trends may need to be applied.

Despite these limitations, these results do provide a basis for comparing many more breeds than is economically feasible in any given crossbreeding trial. Adjustments can be made to this base set of parameters to account for such effects as parity and production system.

Heterosis

An F_1 performance that exceeds the average of the parental performance is generally referred to as hybrid vigor or heterosis. Given the underlying theory of heterosis, it would be possible to use knowledge of the increase in heterozygosity in the F_1 over the level in the parents to predict the level of heterosis, provided that heterosis is under the control of dominance. The regression coefficients (b) of heterosis on genetic distance (Table 8) for the traits with heterosis estimates in the literature are presented in Table 9. One consideration that must be kept in mind is that outcrossing does not always increase performance. There have been suggestions that there is an optimal level of outbreeding (Waser, 1993). The theory underlying this suggestion was born out of the observations that, during experimental outbreeding, the level of heterosis showed an increase as the genetic distance between the parents increased but at a given distance the level of heterosis was seen to fall. Dominance, the interactions of alleles within loci, is believed to be the primary agent responsible for heterosis. However, as the genetic distance is increased, it is believed that there is a break-up of coadapted gene complexes (favorable epistatic interactions) (Lynch and Walsh, 1998). This

shift from dominance to epistasis, interactions among loci, can, therefore, be hypothesized to be responsible for outbreeding depression. This implies that we can predict heterosis providing that the genetic distance does not exceed that level at which favorable epistatic combinations are broken up (i.e., the relationship is linear between heterosis and heterozygosity). Some evidence of this situation was provided by Goddard and Ahmed (1982). They estimated the relationship between the increase in heterozygosity, predicted by genetic distance, and the levels of heterosis reported from breed-cross experiments. It was found that a linear relationship with no constant fitted provided the lowest error mean squares value (**EMS**) when the cross was *Bos taurus* × *Bos taurus* (i.e., the genetic distance was not large). Fitting a line through the origin makes biological sense, because we would expect an average heterosis level to be zero in a purebred mating. However, when *Bos taurus* × *Bos indicus* was investigated it was found that a nonlinear relationship provided the lowest EMS. The nonlinear relationship modelled a decreasing rate of the increase in heterosis as the genetic distance between the parents increased. This relationship did not actually predict any reduction in heterosis at greater genetic distance. The genetic distances used in this study were from Kidd et al. (1974) and were based on cryptic polymorphisms (blood groups, enzymes, and serum proteins). Graml and Pirchner (1984) used data on the dairy performance of cattle breeds in Bavaria. The distance information used was calculated from literature estimates of gene frequencies of six blood group loci, two blood protein loci, and two milk protein loci. They found significant relationships for both milk yield and fat yield heterosis with genetic distance.

In this study the trait with the highest regression coefficient of heterosis on genetic distance was cow fertility, a trait with a low heritability. A low heritability could indicate that the trait is under the control largely of nonadditive genetic effects (i.e., dominance plays a large role). We would expect heterosis to be the result of dominance, and indeed a higher regression coefficient was seen for fertility, a trait expected to have a low heritability, than for those traits in this study, which were expected to have higher heritability.

ies. The magnitude of this coefficient is 66.7, which can be translated into a predicted level of heterosis. For example, we can illustrate this with a H × A cross. The genetic distance between these breeds is estimated to be 0.127 on a scale between 0 and 1.0. This translates into an expected increase in heterozygosity of the F₁ over the parental average of $0.127/(1 - 0.127/2) = 0.136$. We thus predict that the heterosis in this cross would be $66.7 \times 0.136 = 9.07\% \pm 10.7$ at the 95% prediction interval. It can be seen that there is a large degree of error associated with such a prediction. Error can be hypothesized to occur in several aspects of the heterosis prediction model. One potential source of error is in the actual experimental measurement of heterosis. In this study multiple estimates of the same breed-cross-specific level of heterosis were available for a number of traits and variation was seen between these. The second potential error source is the estimation of between-breed genetic distance, obtained in the study of Blott et al. (1998) using a bootstrapping approach. The third potential source of error is the validity of the underlying assumption that heterosis increases in a linear trend with increasing heterozygosity, although this assumption was supported in the case of *Bos taurus* × *Bos taurus* by Goddard and Ahmed (1982). A fourth source of error that can be identified is that due to the genetic distance estimates being obtained from a sample of animals different from that from which the heterosis estimates were obtained. It can be argued that genetic drift could invalidate the mixing of the two pieces of information from different population samples. Studies in the future may be designed to provide heterosis and distance estimates within the same sample populations.

The partitioning of the maternal and direct effects was not always the same in this study as those in the study of Amer et al. (1992). There are two explanations for the difference in partitioning. First, this report considered a much wider range of breeds and experiments from North America, Europe, and New Zealand. Second, in Amer et al. (1992) the maternal and direct effects were calculated separately, whereas in this report the two parameters are calculated simultaneously.

The estimates of breed values obtained here form the basis of predicting the breed effects of planned breed crosses. When estimates of breed-cross-specific levels of heterosis can be predicted a more accurate account can be made of heterosis in both the estimation of breed effects and in the prediction of breed-cross potentials. The additive genetic performance of any individual crossbred group will be the average of the parent breed values, weighted by their genetic contribution. The preweaning traits contain a maternal genetic component in addition to the direct additive genetic component. The procedure can also be applied to a three-breed-cross potential in a similar way. For example, if a SD sire were to be mated to an A × H dam (SD × (A × H)), the breed effect for expected average

survival to weaning of the resulting calf can be predicted using the information in Table 6. The prediction takes the sum of one-half of the direct survival to weaning effect of parent SD, one-quarter of each of the direct effects of an A and H parent, and one-half of each of the maternal effects of an A and H dam. The expected survival to weaning for a (SD × (A × H)) cross would therefore be $0.5(92.8) + 0.25(94.2 + 95.1) + 0.5(-0.2 - 2.7)$, which equals 92.3%. The heterosis, direct and maternal, for calf survival can be predicted using the values in Table 9 and the genetic distances values in Table 8 calculated by Blott et al. (1998). The average genetic distance between SD and H × A is 0.126, and the genetic distance between H and A is 0.127. The direct heterosis is predicted to be $17.3 \times 0.126 = 2.2\%$ and the maternal heterosis to be $17.7 \times 0.127 = 2.2\%$. This increases the predicted calf survival to weaning for the crossbred calf to 96.0%.

This demonstrates the way in which the purebred estimates for direct and maternal effects of a trait can be combined to predict the breed effect for that trait for any breed composition of cow. Heterosis can be combined into this estimate either by using the predictive method described here or by using an average heterosis estimates taken from the literature.

Implications

Estimates of trait breed effects produced by breed comparison experiments in which breeds are represented as both pure and crossbreds can be combined to yield single values of breed by trait potentials. This procedure allows breed effects to be estimated using a larger sample of animals than is possible in any single experiment. The procedure also allows a larger number of breeds to be directly compared, because not all breeds are represented in a single comparison experiment. The use of genetic distance may also provide a predictor of the variation in heterosis levels between specific breed crosses.

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Appendix 1

This example is for illustrative purposes only. There are two breeds for which direct additive genetic effects (b) and maternal genetic effects (c) are being estimated.

Observation (Xc)	% Breed 1	% Breed 2	% Breed 1 as a dam	% Breed 2 as a dam	Trial
10	0	100	0	100	1
11	25	75	50	50	1
12	0	100	0	100	1
5	100	0	100	0	2
7	50	50	50	50	2
6	100	0	100	0	2

$$y = \text{MEAN} + \text{ADD } b + \text{MAT } c + \text{TRIAL } f + e$$

$$\begin{bmatrix} 10 \\ 11 \\ 12 \\ 5 \\ 7 \\ 6 \end{bmatrix} = \begin{bmatrix} 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \end{bmatrix} [\mu] + \begin{bmatrix} 0 & 1 \\ 0.25 & 0.75 \\ 0 & 1 \\ 1 & 0 \\ 0.5 & 0.5 \\ 1 & 0 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} 0 & 0.5 \\ 0.25 & 0.25 \\ 0 & 0.5 \\ 0.5 & 0 \\ 0.25 & 0.25 \\ 0.5 & 0 \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} + \begin{bmatrix} 10 \\ 10 \\ 10 \\ 01 \\ 01 \\ 01 \end{bmatrix} \begin{bmatrix} \text{TRIAL}_1 \\ \text{TRIAL}_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \\ e_5 \\ e_6 \end{bmatrix}$$

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