

## Estimates of the complete genetic covariance matrix for traits in multi-trait genetic evaluation of Australian Hereford cattle

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**Abstract.** Estimates of covariance components among all 22 traits considered in the current multi-trait genetic evaluation of Australian Hereford cattle were obtained. Traits included 5 weight traits, 8 traits measured through live ultrasound scanning, 3 traits related to reproductive performance, and 6 carcass traits. Estimates were obtained by restricted maximum likelihood, carrying out a series of bivariate analyses. Data for each analysis were selected attempting to maximise the number of animals or animal–parent pairs that had both traits recorded. Estimates were pooled using a weighted ‘iterative summing of expanded part matrices’ procedure, which ensured positive semi-definite covariance matrices. Models of analyses for individual traits closely resembled those used in genetic evaluation. Results generally agreed with literature results, although estimates of genetic parameters for carcass traits that had few records available tended to fluctuate. Except for ‘days to calving’, heritability estimates were moderate to high for all traits. Genetic parameters for early growth were different to those for other breeds, with maternal effects for weaning weight being considerably more important and the heritability somewhat lower.

**Additional keywords:** beef cattle, genetic parameters, growth, carcass, fertility.

### Introduction

Today’s genetic evaluation schemes for beef cattle generally involve multi-trait analyses. The Australian system, known by the trade name of BREEDPLAN, carries out an animal model analysis for more than 20 traits. From its beginnings, considering weight traits and individual herds only (Graser and Hammond 1985; Nichol *et al.* 1985), BREEDPLAN has evolved into a complex system incorporating weights, traits measured via live ultrasound scanning, reproductive traits and abattoir carcass traits, and all records for a breed (Schneeberger *et al.* 1991; Johnston *et al.* 1999). Additional traits describing feed efficiency or temperament are included on a trial basis for some breeds, and calving ease is considered separately.

Prediction of breeding values requires covariance matrices, specific to each breed, for the traits considered, and all random effects fitted as input parameters. Ideally, these should be estimated for each breed and all traits in the analysis. Whilst there are a plethora of genetic parameter estimates for weights of beef cattle, relatively few analyses consider cross-correlations between groups of traits introduced more recently, i.e. ultrasound scan measurements, reproductive traits, and carcass records (Koots *et al.* 1994b). Hence covariance matrices required are often constructed

from estimates of variances and correlations from various analyses available for the breed, and literature values for correlations that are not available, but may have been estimated for other breeds or locations. Commonly, this involves several *ad hoc* decisions, both on which estimates to select and the procedure used to ensure that the resulting matrices are valid, i.e. positive definite or semi-definite.

This paper presents estimates of the complete covariance and correlation matrices for Australian Hereford cattle, for the 22 traits included in the multi-trait genetic evaluation for this breed under BREEDPLAN version 4.1, employing a new method to obtain consistent, pooled covariance matrices.

### Materials and methods

#### *Data and traits*

Data were extracted from the National Beef Recording System (NBRS) database, considering combined records for Hereford and Polled Hereford. Initially, data extracted in September 1999 were considered, with an update to May 2000 and March 2001 (and May 2002 for intra-muscular fat content records) extracts later. Raw data included pedigree information for 923050 animals, 1447065 weight records, 79394 scan records, 95618 days to calving records, and 40455 gestation length records, but only 1388 abattoir carcass trait records.

Basic edits eliminated small proportions of records for animals with missing birth date or date of recording, unknown sex, and records before 1980, as well as any erroneous records identified by range and

validity checks of dates, records, and, where applicable, ages at recording.

In total, 22 traits were considered, consisting of weights at different ages, scan traits, reproductive performance traits, and carcass traits.

#### *Weights*

There were 5 weights, namely birthweight (BW), weaning or 200-day weight (WW), yearling or 400-day weight (YW), final or 600-day weight (FW), and weights of cows recorded at weaning of their calves, referred to henceforth as mature cow weights (MCW). Permissible ages for WW, YW, FW, and MCW were 80–300 days, 301–500 days, 501–700 days, and 701–4500 days, respectively. Repeated records were allowed only for MCW. If an animal had more than one record in the age range allowed for WW, YW, or FW, only the record closest to the target age of 200, 400, or 600 days was retained.

#### *Scan traits*

Real-time ultrasound scanning of live animals by accredited scanners is widely used to obtain measurements of fat thickness and intramuscular fat content or marbling (Graser *et al.* 1998). Scan measurements on heifers or steers and on bulls were considered to be different traits. This yielded 8 traits, namely eye muscle area for heifers/steers (EMA.H) and bulls (EMA.B), fat depth at the 12th/13th rib for heifers/steers (RIB.H) and bulls (RIB.B), P8 fat depth for heifers/steers (P8.H) and bulls (P8.B), and percentage intra-muscular fat for heifers/steers (IMF.H) and bulls (IMF.B). Ages at scanning from 300 to 700 days were considered, with a single record per trait.

#### *Reproductive traits*

Three traits describing reproductive performance were analysed. Scrotal circumference (SS) records for bulls were selected analogously to scan traits. Gestation length (GL) was considered to be a trait of the calf born at the end of gestation. Repeated records per cow were considered for days to calving (DC). Records in contemporary groups (CG) with calving rates of <60% were excluded, assuming that this reflected a flaw in reproductive performance of the service sire. Only records for cows mated by natural service were used. Records for cows with a successful calving were the number of days from the date the bull entered the mating paddock to the calving date. Cows not calving were assigned the highest value in their CG plus a penalty of 21 days (Johnston and Bunter 1996).

#### *Carcass traits*

Carcass records were collected from abattoirs under the meat quality research project conducted by the Australian Cooperative Research Centre for Cattle and Beef Industry ('Beef CRC'). Traits considered were carcass weight (CWT), percentage retail beef yield (CRBY), percentage intra-muscular fat (CIMF), eye muscle area scanned pre-slaughter (CEMA), and subcutaneous fat depths at the 12th/13th rib (CRIB) and the P8 site (CP8), respectively. Only records for animals with CWT recorded were retained. Further details on trait definition and data collection are given by Reverter *et al.* (2000, 2003).

#### *Model of analysis*

The model of analysis for all traits adhered closely to the corresponding BREEDPLAN model. All analyses fitted CG as fixed effects, and assumed an animal model, i.e. fitted animals' additive genetic effects as random effects. Additional random effects fitted, i.e. genetic and permanent environmental maternal effects and animals' permanent environmental effects were fitted as appropriate for individual traits. Preliminary, univariate analyses were carried out for all traits, fitting the same model as used for multivariate analyses as well as a model including the random effects due to sire  $\times$  herd (S  $\times$  H) subclasses in

addition. Pedigree records for all animals with records and 2 further generations backwards were utilised, i.e. parents and grand parents of parents not in the data were included in the analysis.

#### *Weights*

CG for early weights were defined as herd–sex of calf–management group–date of weighing subclasses. For BW, year–month rather than actual date was used. In addition, an 'age slicing' of 45 days (WW) or 60 days (YW and FW) was applied, i.e. CG classes were subdivided further, if the range in ages at weighing exceeded the given number of days. Other fixed effects fitted were birth type (single *v.* twin), and the so-called 'heifer factor', i.e. an age of dam status effect (heifer *v.* cow). Age at weighing was fitted as a linear covariable for each sex (heifers, bulls, steers), and age of dam was taken into account as a linear and quadratic covariable. Both genetic and permanent environmental maternal effects were fitted as additional random effects.

For MCW, CG were defined as herd–herd of origin–lactation status–management group–date subclasses, with 2 classes for lactation status, wet or dry. Age at weighing was fitted as a linear and quadratic covariable. With up to 6 repeated records per animal, direct permanent environmental effects were fitted as additional random effects.

#### *Scan traits*

Fixed effects in the model for scan traits were the same as weights taken at corresponding ages, i.e. YW or FW. Sex effects were accounted for by the trait definition. No additional random effects were included in the analysis.

#### *Reproductive traits*

The model for SS was the same as for scan traits. For GL, CG defined as herd–year/season of birth–birth type–sex of calf subclasses, with seasons classified as 'autumn' (January–June) and 'spring' (July–December) calvings, were the only fixed effects fitted. With GL treated as a trait of the calf, both genetic and permanent environmental effects of the dam were important, and fitted as additional random effects. CG for DC were defined as herd–service sire–'bull in' date–previous lactation status  $\times$  age subclasses. There were 4 categories for the latter, namely 2-year-olds ('dry'), 3-year-olds with a previous calf ('wet'), 3-year-olds without a previous calf ('dry'), and others. Again, no other fixed effects were fitted.

#### *Carcass traits*

Carcass records were pre-adjusted for age or weight using linear and quadratic regression coefficients given by Reverter *et al.* (2000). CWT was adjusted to an age at slaughter of 650 days and the remaining traits were adjusted to a carcass weight of 300 kg. CG for carcass traits were defined as herd of origin–'kill regime'–sex of animal subclasses, where 'kill regime' encompasses date of kill, abattoir, finishing regimen (pasture *v.* grain), and target market (domestic, Korea, or Japan). No other fixed or additional random effects were fitted.

#### *Statistical analyses*

Covariance components were estimated by restricted maximum likelihood (REML), employing an average information algorithm together with an additional derivative-free search step to check for convergence. All calculations were carried out using DFREML v.3.0 (Meyer 1998), using a combination of derivative-free and average information algorithms. Whilst approximate sampling variances of estimates were available for some individual analyses, approximation for others failed. Hence no sampling errors are given. Pedigrees were 'pruned' for analyses not fitting maternal genetic effects, i.e. parents without records, a single offspring only, and no pedigree information

**Table 1. Characteristics of the data structure for univariate analyses**

BW, birthweight; WW, weaning weight; YW, yearling weight; FW, final weight; MCW, mature cow weight; IMF.H, intra-muscular fat content for heifers or steers; IMF.B, intra-muscular fat content for bulls; P8.H, fat depth at P8 site for heifers or steers; P8.B, fat depth at P8 site for bulls; RIB.H, fat depth at the 12/13th rib for heifers or steers; RIB.B, fat depth at the 12/13th rib for bulls; EMA.H, eye muscle area for heifers or steers; EMA.B, eye muscle area for bulls; SS, scrotal circumference; GL, gestation length; DC, days to calving; CWT, carcass weight; CEMA, carcass eye muscle area; CIMF, carcass intra-muscular fat content; CP8, carcass fat depth at P8 site; CRIB, carcass fat depth at the 12/13th rib; CRBY, carcass retail beef yield

Trait	Records	Animals <sup>A</sup>	No. of:				Trait		Age	
			Sires <sup>B</sup>	Dams <sup>B</sup>	Sire × herd ef.	Contemp. groups	Mean	s.d.	Mean	s.d.
BW	31756	47305	1073	11070	1432	1365	37.60	5.91		
WW	36228	49889	1016	11796	1292	2048	228.4	52.3	212.5	39.4
YW	33410	49408	1315	12170	1486	1338	343.9	83.2	399.7	38.9
FW	31369	47576	1407	13025	1696	1650	406.5	114.6	587.0	39.9
MCW	10536 <sup>C</sup>	21605	1297	5351	1605	460	545.8	88.2	1767.5	804.8
IMF.H	10274	40314	1391	8229	1721	716	3.415	1.563	523.4	81.0
IMF.B	10992	46370	1626	9019	2160	1035	2.611	1.441	525.8	87.1
P8.H	23855	57728	2318	16147	2925	1491	6.143	3.577	505.3	79.2
P8.B	35338	88859	3740	23914	5121	2836	4.986	2.651	516.7	84.5
RIB.H	23705	53544	2316	16080	2923	1482	4.097	2.086	505.4	79.1
RIB.B	35249	88733	3735	23880	5114	2831	3.468	1.553	516.4	84.5
EMA.H	23843	53705	2318	16134	2926	1493	53.20	10.23	505.5	79.2
EMA.B	35367	88872	3736	23899	5116	2837	76.89	13.72	516.7	84.5
SS	27007	70003	3293	18608	4178	2103	34.71	3.56	493.0	99.4
GL	33006	93922	1388	23765	4052	2880	284.8	5.2		
DC	71328 <sup>D</sup>	88320	7145	27541	11016	10035	315.5	26.7		
CWT	1036	2300	58	831	92	179	272.7	54.1	649.9	132.2
CEMA	867	2048	58	716	91	156	62.67	11.13	651.3	135.4
CIMF	1001	2252	58	805	92	176	3.94	1.68	653.2	130.7
CP8	1002	2576	58	801	92	178	10.29	4.76	654.7	131.1
CRIB	1012	2621	58	812	92	177	7.39	4.00	650.1	133.2
CRBY	372	1288	32	344	47	83	67.13	3.35	619.0	124.4

<sup>A</sup>In the analysis, including parents without records. <sup>B</sup>With progeny in the data. <sup>C</sup>On 7382 cows. <sup>D</sup>On 40977 cows.

themselves, were treated as unknown. Covariances between direct and maternal genetic effects were assumed to be zero throughout.

#### Univariate analyses

Two univariate analyses, including and excluding  $S \times H$  effects, were carried out for each trait. For traits with comparatively few observations, all records available were considered. For traits with large numbers of observations, i.e. BW, WW, YW, and FW (with a total of 260004, 544212, 309991, and 215682 valid records available), records in the largest herds only were selected for analysis. Records in small CG classes were disregarded, requiring a minimum of 2 records per subclass for carcass traits and live intramuscular fat percentage, and 3 records for all other traits. Characteristics of the data structure for univariate analyses are given in Table 1.

#### Multivariate analyses

In total, 231 bivariate analyses were carried out to estimate all covariances and correlations between the 22 traits. Bivariate analyses ignored  $S \times H$  effects. In addition, a multivariate analysis considering all 6 carcass traits simultaneously was performed.

With greatly differing numbers of records per trait, different strategies had to be employed in extracting datasets for individual analyses. In doing so, the aim was to maximise number of 'pairs' of records for the traits considered, whilst keeping the total number of animals in the analysis reasonable—about 50000 or less if maternal effects were fitted and about 80000 or less otherwise. To accommodate

traits measured on a distinct subset of animals and to utilise information on relatives, 'pairs' were defined to include both traits measured on the same animal as well as one trait measured on the animal, the other on one of its parents. If few animals had records for both traits (less than 60) in an analysis, records for one of the traits were deleted for these animals, usually records for the trait with more information, to avoid spurious estimates of environmental covariances based on few observations.

For the traits with relatively few observations, i.e. the carcass traits, live intra-muscular fat percentage, and MCW, all records available were utilised throughout. In bivariate analyses of these traits with scan traits and SS, all observations for the latter were included. Whilst this resulted in analyses with large numbers of animals and imbalance in the number of records per trait, it was considered necessary in order to maximise the amount of information on genetic covariances available through pairs of relatives, especially if traits were measured on distinct subsets of animals. Similarly, for bivariate analyses of these traits together with weights (except MCW), all weight records in herds (herds of origin for carcass traits) that had records for the former trait were used. There were 'pairs' of records (as defined above) for joint analyses with GL or DC. Hence, these analyses utilised all records for GL in herds with any 'pairs' as well as all records in herds with at least 10 observations for GL or 50 observations for DC, respectively.

For bivariate analyses among scan traits (except IMF.H/IMF.B) and SS, again all records in herds with 'pairs' of records were extracted. For joint analyses of these traits together with weights (except MCW) and GL or DC, or GL/DC together with a weight (except MCW), parents

without records for the second, more numerous trait were ignored in counting 'pairs'. Records extracted for the latter were then restricted to those part of a 'pair', and all records in the same CG as these records. Finally, for analyses involving 2 weight traits (except MCW), a similar strategy was applied, restricting records to those being part of a pair for both traits, and additional records in the same CG for the weight with more records were only added until a CG size of 10 was reached. Whilst this maximised information for genetic covariances between traits while restricting the size of analyses, it resulted in some distortion of sex ratios in the resulting datasets. If the first trait, i.e. the trait with fewer observations available, was measured on both sexes, there were more records on females than on males for the second trait (as we added more dams than sires). If the first trait was sex-limited, most records for the second trait (weight) were records for that sex.

Numbers of records for each trait in bivariate analyses with the 21 other traits are summarised in Table 2. Corresponding numbers of animals in each analysis in total, i.e. including parents without records, and numbers of animals with records for both traits are given in Table 3. Fluctuations in numbers can be attributed to using records from different data extracts, or elimination of records for small numbers of animals with records for both traits. In addition, selected analyses—with small numbers of 'pairs' of records—were repeated including an additional generation of pedigree information.

#### Combining results

Results from bivariate analyses and the 6-variate analysis were combined using the 'iterative summing of expanded part matrices' approach suggested by Mäntysaari (1999), extended to allow for differential weighing of results from individual analyses, as implemented in program ITSUMCOV (Henshall and Meyer 2002). This was carried out separately for each source of variation. For residual covariances, it was applied to the sum of temporary and permanent environmental covariances (analyses involving MCW and DC). Phenotypic covariances were calculated as the sum of direct and maternal genetic, maternal permanent environmental, and residual components.

#### Algorithm

Consider  $q$  traits, and let  $\mathbf{V}^t$  of size  $q \times q$  denote the covariance matrix among all traits for the  $t$ th iterate. Furthermore, let  $\mathbf{C}_s$  represent the matrix of covariance estimates from the  $s$ th analysis, of size  $k_s \times k_s$  ( $k_s = 2$  for bivariate analyses). Define a transformation matrix  $\mathbf{P}_s$ , of size  $q \times k_s$ , which has  $k_s$  elements of unity,  $p_{ij} = 1$ , if the  $i$ th trait overall is the  $j$ th trait in the  $s$ th analysis, and zero otherwise. Pre- and post-multiplying  $\mathbf{C}_s$  with  $\mathbf{P}_s$  and its transpose,  $\mathbf{P}_s \mathbf{C}_s \mathbf{P}_s'$ , yields the part matrix expanded to full size ( $q \times q$ ), with rows and columns of zeros for the traits not included in the analysis. The iterative summation scheme is then given as:

$$\mathbf{V}^{t+1} = \sum_{s=1}^S w_s \left\{ \mathbf{V}^t (\mathbf{P}_s \mathbf{P}_s' \mathbf{V}^t \mathbf{P}_s \mathbf{P}_s')^{-1} \mathbf{P}_s \mathbf{C}_s \mathbf{P}_s' (\mathbf{P}_s \mathbf{P}_s' \mathbf{V}^t \mathbf{P}_s \mathbf{P}_s')^{-1} \mathbf{V}^t \right. \\ \left. + [(\mathbf{I} - \mathbf{P}_s \mathbf{P}_s') (\mathbf{V}^t)^{-1} (\mathbf{I} - \mathbf{P}_s \mathbf{P}_s')]^{-1} (\mathbf{I} - \mathbf{P}_s \mathbf{P}_s') \right\} / \sum_{s=1}^S w_s$$

with  $\mathbf{I}$  an identity matrix of size  $q$ ,  $w_s$  the weight for the  $s$ th analysis, and  $^{-1}$  denoting a generalised inverse.  $\mathbf{P}_s \mathbf{P}_s'$  is a diagonal matrix with elements of unity for the traits represented in the  $s$ th analysis. Hence, pre- and post-multiplying  $\mathbf{V}^t$  with this matrix yields the submatrix of  $\mathbf{V}^t$  for the traits in the analysis, with the remaining rows and columns zero. Analogously, pre- and post-multiplication with  $(\mathbf{I} - \mathbf{P}_s \mathbf{P}_s')$  selects the submatrix corresponding to the traits not included in the  $s$ th analysis.

#### Initial values

Starting values for the overall covariance matrix were obtained by first averaging variance component estimates for each trait over all analyses (21 estimates for each trait). Estimates of correlations (single estimate for each correlation) were then combined in a  $q \times q$  correlation matrix, and an eigenvalue decomposition of this matrix was carried out. If the combined matrix was not positive definite, all eigenvalues were regressed to their mean, choosing the regression coefficient so that, after regression, the smallest eigenvalue was equal to an operational zero of  $10^{-8}$ , a procedure generally referred to as 'bending' (Hayes and Hill 1981). Pre- and post-multiplying the diagonal matrix of regressed eigenvalues with the corresponding matrix of eigenvectors and its transpose, respectively, then yielded a modified correlation matrix that was (semi-)positive definite. This was multiplied with the appropriate average standard deviations to yield an initial covariance matrix,  $\mathbf{V}^0$ , for the iterative summation scheme.

#### Weighing factors

A weighted summation was chosen since individual analyses differed substantially in the amount of records included, the number of animals with pairs of records, and the amount of genetic links available. Whilst some measure of accuracy of estimates derived from the inverse of the average information matrix (= lower bound sampling covariance matrix) for each analysis would have been desirable, this was not available for all analyses. Hence, weights chosen were the number of records per analysis (total number for both traits) plus the number of records multiplied with the ratio of the number of animals with pairs of traits to the number of animals represented in the data.

## Results

#### Univariate analyses

Results from univariate analyses are summarised in Table 4. Approximate lower bound sampling errors for estimates of genetic parameters are given for analyses omitting  $S \times H$  effects. Corresponding values for analyses fitting  $S \times H$  effects (not shown) were similar, albeit generally slightly larger, due to the extra parameter estimated. Estimates of the variance due to  $S \times H$  effects ( $s^2$ ) explained up to 10% of the phenotypic variation, with significantly increased likelihoods except for carcass traits. On the whole, estimates of genetic parameters for weights and scan traits agreed well with corresponding literature values.

The model for genetic evaluation employed by BREEDPLAN includes a  $S \times H$  effect (Graser *et al.* 1999). This is fitted primarily to account for non-genetic similarities among progeny of a bull when management group recording has been inadequate or cows and calves remain in the same groups as at mating, rather than true genotype  $\times$  environment interactions. Estimation of the variance due to  $S \times H$  effects is often problematic, as genetic sire effects and environmental sire group effects can only be separated for sires used in multiple herds, i.e. in the main, bulls used via artificial insemination (AI). If the proportion of AI usage is low, too large a proportion of the variance between sires tends to be interpreted as variance due to  $S \times H$  effects rather than genetic variance, leading to underestimates of the genetic variance and heritability estimates that are biased downwards. As shown in more



**Table 3. Total numbers of animals including parents without records (lower triangle; number divided by 1000) and number of animals in the data with records for both traits (upper triangle) in multivariate analyses**

See headline of Table 1 for definitions of trait acronyms

	BW	WW	YW	FW	MCW	IMFH	IMFB	P8.H	P8.B	RIB.H	RIB.B	EMA.H	EMA.B	SS	GL	DC	CWT	CEMA	CIMF	CP8	CRIB	CRBY
BW	29372	29401	24325	2583	6455	5504	11804	14507	11722	14476	11822	14645	12993	6268	7185	0	0	0	0	0	104	0
WW	60.5	31512	28576	5069	0	0	14481	20104	14374	20083	14494	20164	18736	8737	18813	746	646	723	726	736	277	0
YW	75.2	73.5	27625	4206	7695	8783	15757	21628	15647	21610	15757	21692	19151	6118	11745	944	730	828	829	851	311	0
FW	75.2	77.7	67.8	3777	6396	6544	12932	18637	12887	18573	12966	18689	16045	8372	10257	860	554	653	657	658	245	0
MCW	68.9	84.0	71.6	70.6	280	0	3057	0	3065	0	3068	0	0	63	1489	0	0	0	0	0	0	0
IMFH	88.2	97.9	88.8	83.0	47.9	0	9744	0	9744	0	9603	0	0	991	492	0	0	0	0	0	0	0
IMFB	99.6	99.7	102.1	92.5	52.9	58.1	0	10528	0	10525	0	10525	5528	1137	0	0	0	0	0	0	0	0
P8.H	49.2	49.3	50.8	47.9	74.4	73.8	81.0	0	18682	0	18773	0	0	1330	3483	1019	853	984	986	997	363	0
P8.B	68.3	75.3	75.5	73.7	90.0	97.3	118.8	80.6	0	26067	0	26105	14396	2857	0	0	0	0	0	0	0	0
RIB.H	49.1	49.1	50.7	47.9	74.2	73.6	80.8	41.6	80.5	0	18694	0	0	1321	3432	1019	853	984	986	997	363	0
RIB.B	68.1	75.2	75.4	73.6	89.9	95.8	118.6	80.3	64.0	80.2	0	26052	14331	2843	0	0	0	0	0	0	0	0
EMA.H	49.2	49.2	50.8	48.0	73.9	73.8	80.8	41.7	80.6	41.6	80.3	0	0	1342	3484	997	843	971	964	975	343	0
EMA.B	69.1	75.3	75.5	73.7	90.0	102.2	118.8	80.7	64.1	80.6	64.0	80.6	14392	2853	0	0	0	0	0	0	0	0
SS	64.7	74.1	69.0	69.3	66.3	86.2	99.1	80.8	51.4	80.7	51.3	80.8	51.3	1741	0	0	0	0	0	0	0	0
GL	51.9	60.8	53.9	86.5	72.5	85.8	93.6	79.8	76.8	79.6	76.7	79.7	76.9	87.0	758	0	0	0	0	0	0	0
DC	116.9	108.5	109.0	100.6	95.1	106.1	110.6	105.8	113.1	105.6	113.0	105.7	113.1	113.5	109.1	0	0	0	0	0	0	0
CWT	37.7	63.7	40.2	37.2	19.7	37.1	42.0	53.8	67.1	53.6	67.0	53.8	90.2	59.6	74.0	71.9	849	979	988	1000	360	0
CEMA	34.9	58.3	39.3	36.3	19.4	36.9	41.8	53.8	66.9	53.6	66.8	53.7	66.9	59.3	73.6	71.7	1.9	829	815	844	310	0
CIMF	35.1	58.4	39.3	36.4	19.6	37.0	41.9	53.8	67.0	53.6	66.9	53.7	67.1	59.5	90.5	71.8	1.9	1.8	946	956	345	0
CP8	37.6	63.7	43.3	38.5	19.6	37.1	42.0	53.8	67.0	53.6	66.9	53.8	67.1	59.5	73.9	71.8	1.9	1.9	967	967	352	0
CRIB	99.2	63.7	43.3	38.5	19.6	37.1	42.0	53.8	67.0	53.6	67.0	53.8	67.1	59.6	73.9	71.8	1.9	1.9	1.9	1.9	1.9	0
CRBY	32.7	50.6	35.2	27.8	18.6	36.2	41.0	53.7	66.3	47.1	79.6	53.7	66.3	58.7	72.7	71.0	1.9	1.7	1.8	1.9	1.9	0

**Table 4. Estimates of phenotypic ( $\sigma_p^2$ ) and error ( $\sigma_E^2$ ) variances and genetic parameters ( $h^2$ , direct heritability;  $m^2$ , maternal heritability;  $s^2$ , sire  $\times$  herd variance as proportion of  $\sigma_p^2$ ;  $c^2$ , maternal, permanent environmental variance as proportion of  $\sigma_p^2$ ;  $p^2$ , direct, permanent environmental variance as proportion of  $\sigma_p^2$ ; all  $\times 100$ ) from univariate analyses, together with approximate lower band sampling errors (s.e.;  $\times 100$ ) and likelihood ratio test criterion (LRT) for sire  $\times$  herd effects**

See headnote of Table 1 for definitions of trait acronyms

Trait	Analyses omitting sire $\times$ herd effects					Analyses fitting sire $\times$ herd effects						LRT
	$\sigma_p^2$	$\sigma_E^2$	$h^2 \pm$ s.e.	$m^2 \pm$ s.e.	$c^2/p^{2A} \pm$ s.e.	$\sigma_p^2$	$\sigma_E^2$	$h^2$	$m^2$	$s^2$	$c^2/p^2$	
BW	20.09	8.99	42.1 $\pm$ 1.5	10.3 $\pm$ 1.1	2.8 $\pm$ 0.8	20.49	9.42	35.2	8.1	7.1	3.6	202.2
WW	742.1	410.4	12.7 $\pm$ 1.0	11.0 $\pm$ 1.0	20.9 $\pm$ 1.0	740.0	427.8	7.3	10.4	3.0	21.5	81.3
YW	1045.1	679.9	19.7 $\pm$ 1.3	6.2 $\pm$ 0.8	9.1 $\pm$ 0.8	1044.4	704.1	14.2	5.1	3.4	9.9	87.4
FW	1288.2	834.8	26.5 $\pm$ 1.7	4.2 $\pm$ 0.8	4.5 $\pm$ 0.8	1290.6	855.4	22.1	3.5	3.2	4.9	75.3
MCW	2775.3	626.7	38.7 $\pm$ 2.8		39.3 $\pm$ 2.7	2812.3	625.2	27.7		9.4	40.8	72.4
IMF.H	1.077	0.732	32.6 $\pm$ 4.6			1.077	0.777	24.3		3.6		10.7
IMF.B	0.634	0.470	25.9 $\pm$ 4.1			0.637	0.493	17.4		5.3		27.0
P8.H	4.276	2.560	40.1 $\pm$ 2.0			4.309	2.600	36.1		3.5		47.0
P8.B	2.908	2.029	30.2 $\pm$ 1.6			2.916	2.069	26.1		3.0		49.0
RIB.H	1.574	1.071	32.0 $\pm$ 1.8			1.583	1.101	26.5		3.9		50.7
RIB.B	0.993	0.721	27.4 $\pm$ 1.6			0.994	0.731	24.4		2.1		28.5
EMA.H	30.42	20.79	31.5 $\pm$ 1.8			30.41	21.22	27.8		2.4		20.3
EMA.B	45.02	33.50	25.6 $\pm$ 1.5			45.15	33.91	22.4		2.5		38.6
SS	453.8	233.8	48.5 $\pm$ 2.0			454.8	237.7	46.0		1.7		12.6
GL	23.60	13.00	37.9 $\pm$ 2.4	4.8 $\pm$ 1.1	2.3 $\pm$ 1.2	23.73	13.51	30.4	4.8	4.6	3.2	86.3
DC	566.8	466.9	3.9 $\pm$ 0.6		13.7 $\pm$ 0.8	568.7	467.9	1.9		1.8	14.0	40.60
CWT	638.6	251.8	60.6 $\pm$ 15.0			640.9	286.8	51.4		3.9		1.8
CEMA	35.72	11.61	67.5 $\pm$ 18.9			35.71	11.61	67.5		0.0		0.0
CIMF	1.481	0.950	35.8 $\pm$ 14.3			1.481	0.950	35.8		0.0		0.0
CP8	29.17	23.13	20.7 $\pm$ 9.4			29.15	25.25	9.5		3.8		1.3
CRIB	8.552	6.833	20.1 $\pm$ 9.8			8.552	6.845	19.9		0.1		0.0
CRBY	4.594	3.370	26.6 $\pm$ 17.2			4.594	3.370	26.6		0.0		0.0

<sup>A</sup> $p^2$  for MCW and DC.

detail for weights of Australian Hereford cattle in Meyer (2003), this bias can be substantial, especially for weaning weight and analyses with <50% of records on progeny of AI sires.

Emphasis in the present study was on estimation of genetic correlations. Extracting datasets suitable for reliable separation of S  $\times$  H and genetic sire effects in bivariate analyses would have lost considerable information on 'pairs' of traits. Whilst S  $\times$  H effects significantly affected most traits in univariate analyses, bivariate analyses were thus carried out omitting S  $\times$  H effects. This was expected to yield estimates of genetic variances slightly inflated by S  $\times$  H effects (Meyer 2003), but considered much less of a problem than substantial underestimates found in preliminary, bivariate analyses between weights and other traits that included S  $\times$  H effects. Furthermore, both estimates of genetic variances and covariances were expected to be inflated in proportion, i.e. estimates of correlations were presumed to be little affected.

#### Multivariate analyses: pooled variances and variance ratios

Mean estimates (simple average) and ranges of variance components and genetic parameters for individual traits for the 21 bivariate analyses that each trait was included in are

summarised in Table 5. With non-independent datasets, variances of estimates across analyses do not give an indication of sampling variances. Where approximate sampling errors of estimates of genetic parameters were obtained, these were generally larger than their counterparts from univariate analyses given in Table 4. Figure 1 shows the spread of estimates from individual analysis for one trait from each group. Clearly, estimates were most variable for traits with large numbers of records available, such as WW, and thus different subsets extracted for individual bivariate analyses. For traits where all records available were used in each analysis, such as CP8, fluctuations in estimates of variance components were much smaller.

Estimates of variance components and their ratios, pooled over multivariate analyses, are given in Table 6. Using a weighted summation procedure as described above, values show slight deviations from the simple averages over analyses (Table 5), but deviations were generally well within the range of estimates across analyses.

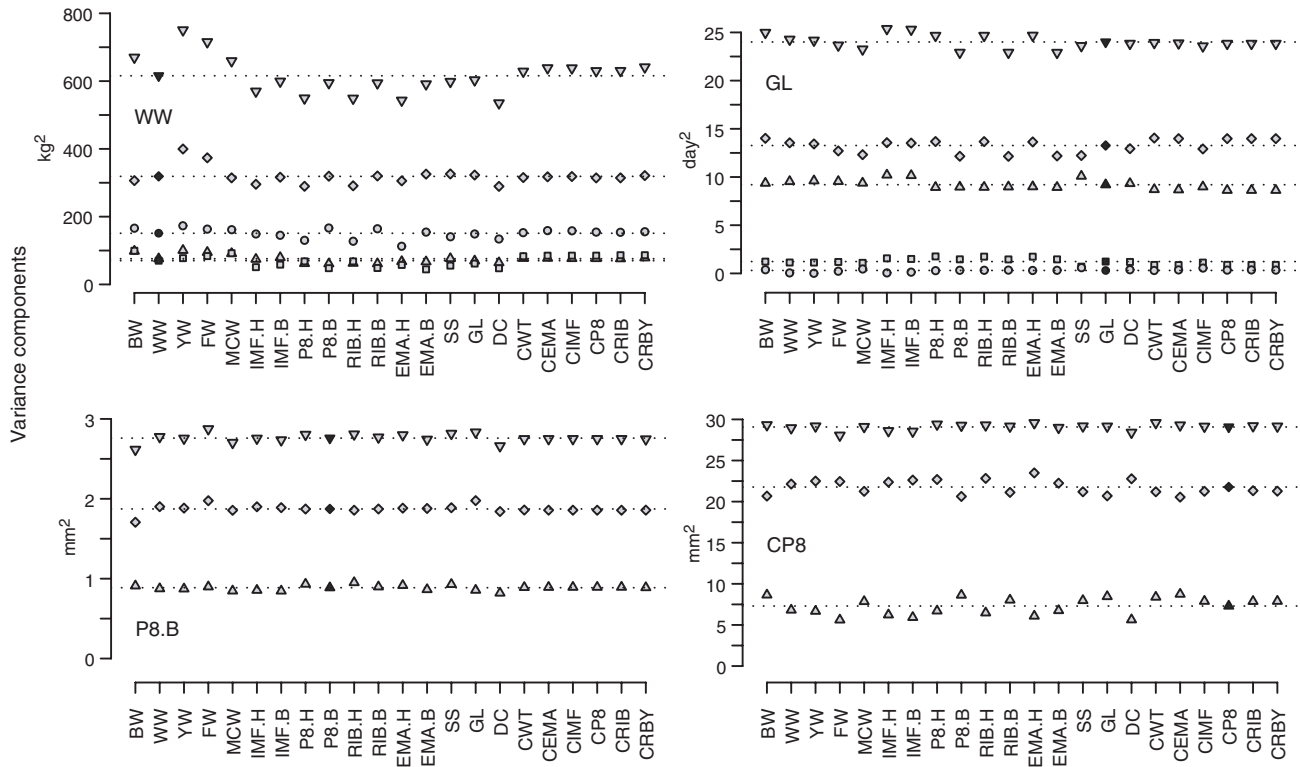
#### Weights

Estimates of variance ratios for weight traits were well within the range of literature values; see, for instance, Mohuiddin (1993) or Koots *et al.* (1994a) for reviews. As

**Table 5. Mean and ranges for estimates of genetic and phenotypic variance components and genetic parameters ( $\times 100$ ), from multivariate analyses**  
See headline of Table 1 for definitions of trait acronyms

Trait	Variance			Heritability			Variance ratio			
	Direct genetic	Phenotypic	Permanent env. <sup>A</sup>	Direct	Maternal	Mean	Range	Mean	Range	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
BW	7.26	5.51–9.22	17.71	16.44–19.43	41.0	32.6–47.5	8.5	6.5–9.9	2.8	1.2–5.9
WW	75.9	61.0–100.7	615.8	535.2–750.7	12.3	10.3–14.7	11.3	7.5–14.8	24.5	20.7–28.0
YW	220.5	148.7–257.2	968.7	836.2–1120.5	22.8	16.6–27.5	5.8	2.3–9.6	9.8	5.3–13.2
FW	365.7	310.1–438.2	1315.8	1068.9–1501.6	28.0	23.5–35.8	6.1	3.7–7.7	4.3	0.6–7.0
MCW	1104.7	1044.2–1222.2	2808.7	2778.6–3016.3	39.3	35.8–43.2			37.9	34.6–42.7
IMFH	33.80	31.50–34.96	107.22	105.23–107.90	31.5	29.9–32.5				
IMFB	16.30	14.68–18.84	63.20	61.78–63.90	25.8	23.8–29.5				
P8.H	1.679	1.580–1.830	4.252	4.128–4.387	39.5	37.4–42.1				
P8.B	0.887	0.821–0.952	2.760	2.617–2.875	32.1	30.2–34.8				
RIB.H	0.490	0.431–0.572	1.541	1.468–1.6244	31.7	29.0–35.5				
RIB.B	0.266	0.245–0.320	0.979	0.927–1.037	27.2	24.9–30.9				
EMA.H	9.46	8.26–10.05	30.49	28.69–31.67	31.0	28.7–32.0				
EMA.B	12.01	10.97–12.95	45.27	42.32–47.22	26.5	25.4–27.4				
SS	220.2	211.6–235.3	449.2	443.2–467.9	49.0	47.6–50.5				
GL	9.20	8.63–10.21	24.01	22.91–25.38	38.3	36.2–42.7	5.1	3.0–7.1	1.3	0.0–2.5
DC	22.1	19.6–28.0	572.7	566.5–588.9	3.9	3.5–4.8			13.8	12.5–14.7
CWT	365.5	181.2–467.3	627.5	508.8–679.0	58.0	35.6–68.8				
CEMA	24.67	20.60–28.46	35.67	35.02–36.77	69.1	58.5–77.4				
CIMF	0.522	0.412–0.621	1.460	1.337–1.502	35.7	29.6–41.6				
CYLD	1.283	0.998–1.892	4.416	4.207–4.703	29.0	23.4–43.0				
CP8	7.30	5.61–8.75	29.08	28.06–29.59	25.1	19.8–29.9				
CRIB	1.96	1.47–2.98	8.48	8.20–8.84	23.1	17.6–33.7				

<sup>A</sup>Direct component for MCW and DC; maternal component otherwise.



**Fig. 1.** Estimates of variance components ( $\nabla$  phenotypic;  $\triangle$  direct, additive genetic;  $\square$  maternal, additive genetic;  $\circ$  maternal, permanent environmental;  $\diamond$  residual) from individual analyses and corresponding means (shown as closed symbols for the trait considered) for weaning weight (WW), gestation length (GL), P8 fat depth measured on bulls (P8.B), and carcass P8 fat depth (CP8).

found in other studies on Hereford cattle, estimates of the variance due to permanent environmental effects for WW were higher than in other breeds, amounting to 22% of total in this case. Whilst the estimate of the phenotypic variance ( $\sigma_p^2$ ) for WW was comparable with that reported for Herefords in other countries (e.g. de Mattos *et al.* 2000), the estimate of the direct heritability ( $h^2$ ) was lower, amounting to only 13%. For YW,  $\sigma_p^2$  was highest for a joint analysis with WW, suggesting a small effect of selection on the basis of WW, but this did not hold for subsequent weights.

Heritability for MCW was moderately high, with 39% and a corresponding repeatability of 77%. This is at the lower end of  $h^2$  estimates for cow weights, with values of 50% or higher reported by various authors (e.g. Kaps *et al.* 1999; Arango *et al.* 2002; Rumph *et al.* 2002).

#### Scan traits

As reported previously (Meyer and Graser 1999), live ultra-sound scan traits measuring 'fatness' recorded on heifers and steers were consistently more variable and heritable than those recorded on bulls. This was accompanied by higher means, indicating that bulls might not have achieved a sufficient degree of finish to express full genetic variation at the time of scanning. Heritabilities overall were moderate and, on the whole, somewhat lower

than comparable literature values (e.g. Crews and Kemp 2001; Devitt and Wilton 2001; Kemp *et al.* 2002; Stelzleni *et al.* 2002; Crews *et al.* 2003; Hassen *et al.* 2003). It should be borne in mind though, that some of the latter were obtained using relatively small numbers of observations, whereas our estimates are based on a substantial body of field records.

#### Reproductive traits

In line with most other studies considering this trait,  $h^2$  for SS was high, amounting to 50%. Koots *et al.* (1994a) reported a corresponding average literature value of 48%. For DC, however,  $h^2$  was considerably lower than estimates of 12% and 11% obtained for Angus in Australia (Johnston and Bunter 1996) and New Zealand (Morris and Cullen 1995), but was close to an earlier estimate for Herefords of 5% (Meyer *et al.* 1991). Koots *et al.* (1994a) gave an average literature value of 8% for the analogous trait 'Date of Calving'. Direct heritability estimates for GL, treated as a trait of the calf, are generally moderate to high, whereas corresponding maternal heritability estimates ( $m^2$ ) are low. Our estimates of 39% ( $h^2$ ) and 5% ( $m^2$ ) agreed well with values of 36–42% ( $h^2$ ) and 2–13% ( $m^2$ ) reported by Azzam and Nielsen (1987), and values of 37% ( $h^2$ ) and 9% ( $m^2$ ) obtained by Wray *et al.* (1987).

**Table 6. Pooled estimates of variance components ( $\sigma_A^2$ , direct, additive genetic;  $\sigma_M^2$ , maternal, additive genetic;  $\sigma_C^2$ , maternal, permanent environmental;  $\sigma_E^2$ , residual<sup>A</sup>;  $\sigma_P^2$ , phenotypic variance) and resulting genetic parameters ( $h^2$ , direct heritability;  $m^2$ , maternal heritability;  $c^2$ , maternal, permanent environmental variance as proportion of  $\sigma_P^2$ ) from multivariate analyses**

See headnote of Table 1 for definitions of trait acronyms. Values for MCW and DC include direct, permanent environmental variances

Trait	$\sigma_A^2$	$\sigma_M^2$	$\sigma_C^2$	$\sigma_E^2$	$\sigma_P^2$	$h^2$	$m^2$	$c^2$
BW	7.17	1.46	0.57	8.36	17.56	0.408	0.083	0.032
WW	78.9	70.1	131.6	324.8	605.4	0.130	0.116	0.217
YW	211.3	59.2	98.7	599.1	968.3	0.218	0.061	0.102
FW	379.6	75.0	65.5	814.8	1335.0	0.284	0.056	0.049
MCW	1079.4			1669.3	2748.7	0.393		
IMF.H	0.332			0.735	1.067	0.311		
IMF.B	0.163			0.468	0.631	0.258		
P8.H	1.663			2.583	4.246	0.392		
P8.B	0.888			1.871	2.759	0.322		
RIB.H	0.485			1.049	1.535	0.316		
RIB.B	0.264			0.710	0.975	0.271		
EMA.H	9.37			21.10	30.46	0.308		
EMA.B	11.93			32.91	44.84	0.266		
SS	223.1			225.9	449.0	0.497		
GL	9.40	1.31	0.29	13.18	24.18	0.389	0.054	0.012
DC	23.2			502.9	526.1	0.044		
CWT	364.8			247.5	612.3	0.596		
CEMA	23.48			11.33	34.81	0.675		
CIMF	0.563			0.933	1.496	0.376		
CP8	7.13			21.72	28.85	0.247		
CRIB	2.028			6.477	8.505	0.238		
CRBY	1.411			3.158	4.569	0.309		

### Carcass traits

Carcass records utilised in this study were essentially the same as analysed by Reverter *et al.* (2000, 2003). Some differences in estimates highlight the sensitivity of analyses considering such small numbers of records to small differences in the subset of records used, and the traits considered jointly. Corresponding literature values are generally based on similarly small datasets, and fluctuate over a wide range, with the consensus that heritabilities of carcass traits are moderate to high. Recent estimates can be found, for instance, in Crews and Kemp (2001), Devitt and Wilton (2001), Kemp *et al.* (2002), Splan *et al.* (2002), and Crews *et al.* (2003).

### Multivariate analyses: pooled correlations

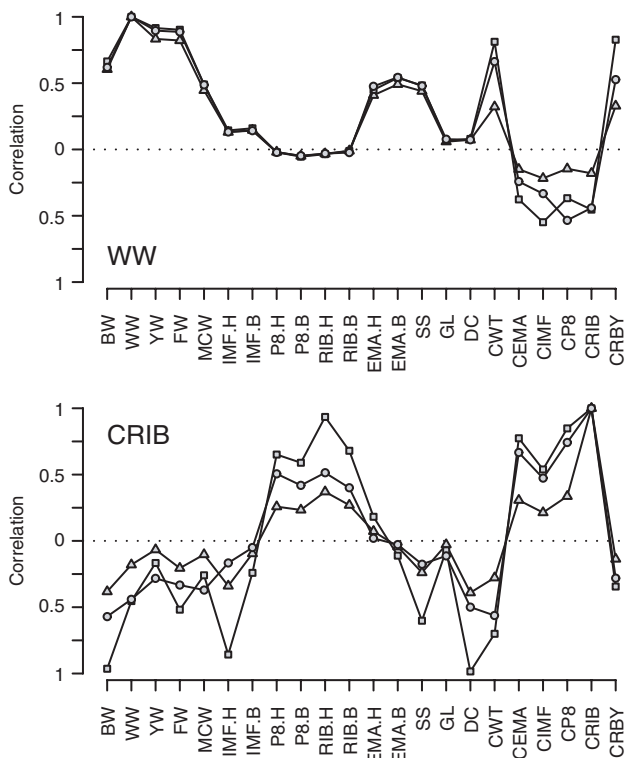
Estimates of additive genetic correlations obtained from the pooled additive genetic covariance matrix are given in Table 7, together with their counterparts from individual analyses. With 22 traits, some of which were highly correlated and some of which had very few records available, the matrix of original correlation estimates was highly inconsistent, with 5 negative eigenvalues, the smallest value of  $-1.63$  being substantially below zero. Hence a bending factor of 0.380

would have been required to regress eigenvalues to their mean (1.000 for a correlation matrix) to ensure that all regressed values were non-negative. This was predominantly due to erratic results from analyses involving carcass traits; considering the other 16 traits only, corresponding values were  $-0.099$  and  $0.910$ . The summation procedure used was dependent on starting values. Furthermore, weights assigned to individual analyses only approximately reflected the information available and accuracy of estimates.

An initial attempt at pooling genetic covariances components for all 22 traits using a severely modified correlation matrix to obtain a positive definite matrix of starting values yielded implausible changes in some estimates of correlations based on relatively large amounts of data. Hence, pooled genetic covariances were derived in a 2-step procedure. First estimates from 120 bivariate analyses of the 16 weight, scan, and reproductive traits were pooled, as described above. In the second step, these were treated as if they were results from a 16-trait, multivariate analysis with a very large weight assigned, and combined with estimates from the 6-trait analysis of carcass traits and the remaining 96 bivariate analyses between carcass and other traits. This yielded very few changes in correlations among the 16 non-carcass traits from step 1 to step 2, whereas some

**Table 7. Estimates of direct additive genetic correlations ( $\times 100$ ) from individual, multivariate analyses (above diagonal) and from pooled covariance matrix (below diagonal)**  
See headnote of Table 1 for definitions of trait acronyms

Trait	BW	WW	YW	FW	MCW	IMFH	IMFB	P8.H	P8.B	RIB.H	RIB.B	EMA.H	EMA.B	SS	GL	DC	CWT	CEMA	CIMF	CP8	CRIB	CRBY
BW	66	54	61	62	-16	-16	-16	-26	-29	-25	-24	15	14	19	9	33	53	-31	-79	-63	-96	70
WW	62	92	90	49	14	16	16	-2	-5	-4	-1	45	54	48	6	8	81	-38	-55	-37	-45	83
YW	51	90	97	68	3	11	3	3	4	0	5	47	44	36	6	1	89	-30	-26	-52	-17	51
FW	59	89	96	77	-3	7	-2	-2	1	-5	0	41	41	39	7	2	100	-36	-24	-54	-52	38
MCW	56	49	66	75	-19	3	-33	-13	-13	-31	-18	1	1	1	1	14	100	-67	-65	-75	-26	83
IMFH	-16	13	4	-2	-20	80	47	29	29	49	22	1	-2	6	10	-23	-59	-100	97	-23	-86	-48
IMFB	-16	14	11	8	-1	78	29	40	40	28	41	-8	-7	8	2	-50	-4	-2	59	-18	-24	52
P8.H	-27	-2	3	-3	-30	45	31	77	77	80	61	7	6	3	4	-33	16	31	74	47	65	-50
P8.B	-29	-5	5	0	-14	30	42	76	60	58	89	-2	-5	2	0	-10	7	12	50	26	59	29
RIB.H	-25	-3	0	-6	-30	46	30	81	60	68	68	8	10	9	7	-35	12	30	66	57	93	-42
RIB.B	-24	-2	5	0	-16	26	40	63	89	67	5	5	-10	6	-1	-3	-13	9	46	1	68	11
EMA.H	14	48	45	40	2	1	-7	7	-1	8	3	86	86	13	12	4	43	53	0	-11	18	39
EMA.B	15	54	45	40	1	-1	-9	7	-6	9	-9	85	85	6	5	8	72	35	-47	-72	-11	49
SS	18	48	36	37	2	5	9	3	1	10	6	12	7	7	6	-14	35	47	-10	-41	-60	-7
GL	10	8	6	7	2	10	1	5	0	7	-1	12	5	5	5	23	43	34	-21	-50	-7	7
DC	32	7	1	3	14	-24	-49	-32	-12	-34	-5	4	8	-14	22	8	15	-27	-39	-100	-98	38
CWT	57	66	67	70	59	-15	-11	-18	-12	-19	-12	35	38	24	21	28	28	-52	-52	-77	-70	56
CEMA	-37	-24	-19	-23	-37	-24	-15	32	26	33	26	22	17	6	10	-26	-41	58	42	42	77	-21
CIMF	-51	-33	-31	-37	-44	44	37	48	41	47	39	-11	-17	-6	-6	-32	-45	47	32	32	54	-42
CP8	-53	-53	-42	-46	-40	-6	1	37	25	37	23	-21	-25	-24	-26	-50	-66	33	28	85	85	-42
CRIB	-57	-44	-28	-33	-37	-17	-5	51	42	51	40	2	-3	-18	-11	-50	-56	67	47	74	74	-34
CRBY	47	53	55	58	52	-27	-6	-22	-2	-24	1	36	37	8	10	23	51	-16	-36	-36	-28	-28



**Fig. 2.** Estimates of direct, genetic correlations for weaning weight (WW) and carcass rib fat (CRIB) from bivariate analyses ( $\square$ ), and after ‘bending’ of the combined correlation matrix ( $\Delta$ ), and after iterative summing of expanded part matrices ( $\circ$ ).

correlations with the carcass traits changed markedly. As shown in Table 7, pooled estimates are by and large plausible, with the biggest changes from individual results for carcass traits.

Figure 2 illustrates the effects of the procedure used to obtain a pooled, positive semi-definite covariance matrix on individual correlation estimates in more detail, and contrasts it with a simple manipulation of the eigenvalues of the matrix. Regressing eigenvalues towards their mean resulted in a reduction in magnitude (absolute value) of most correlations, substantially so for correlations close to unity. Values shown for WW and other non-carcass traits are those obtained by ‘bending’ the  $16 \times 16$  for these traits;

considering all 22 traits would have resulted in correlations considerably closer to zero. For WW, the trait with most data available, pooled correlations with other weights and those close to zero are virtually indistinguishable from original values. For CRIB, a carcass trait with few records available, most pooled correlations are quite different from the individual estimates, with the estimate between CRIB and IMF.B showing the largest change in the complete matrix.

Estimates of maternal genetic and permanent environmental correlations among the 5 traits (BW, WW, YW, FW, GL) for which corresponding effects were fitted are given in Table 8. Table 9 finally, summarises estimates of residual and phenotypic correlations. Note that with sex-limited traits, several analyses involved pairs of traits measured on distinct subsets of animals. For these analyses, residual covariances were assumed to be zero and no residual correlation estimates are given. Corresponding phenotypic correlations then merely reflect the genetic covariance, ‘diluted’ by environmental variances.

*Weight traits*

In line with numerous other studies, estimates of genetic correlations ( $r_A$ ) between birth and later weights were moderate, and correlations among WW, YW, and FW were high (Koots *et al.* 1994b). Both genetic ( $r_M$ ) and permanent environmental ( $r_C$ ) maternal correlations between the 3 weights were very high, whereas estimates of  $r_M$  and  $r_C$  with BW were moderate (0.29–0.44) and low (0.22).

Estimates of  $r_A$  between MCW and earlier weights were moderate to high, ranging from 0.49 to 0.75. Bullock *et al.* (1993) obtained estimates of 0.64, 0.80, and 0.89 for  $r_A$  between mature weight of Polled Hereford cows and BW, WW, and YW, respectively, and Northcutt and Wilson (1993) found corresponding values for Angus of 0.57, 0.62, and 0.45. Kaps *et al.* (1999) reported higher values of 0.69 and 0.85 for  $r_A$  between WW and repeated records for MCW in Angus for analyses in, and excluding, a direct-maternal genetic correlation.

WW, YW, and FW showed a moderate genetic association with the size-related traits SS and live-ultrasound eye muscle area. Corresponding estimates for weights and CEMA as well as carcass fat depth and fat content measurements were

**Table 8.** Estimates of maternal genetic and permanent environmental correlations ( $\times 100$ ) from individual bivariate analyses (above diagonal) and from pooled covariance matrix (below diagonal)

See headnote of Table 1 for definitions of trait acronyms

Trait	Genetic					Permanent env.				
	BW	WW	YW	FW	GL	BW	WW	YW	FW	GL
BW		43	40	52	53		33	33	28	100
WW	33		95	81	40	22		100	100	-90
YW	29	94		95	48	22	100		100	-97
FW	44	81	94		43	22	100	100		-34
GL	54	52	59	55		67	-58	-58	-57	

**Table 9. Estimates of residual (above diagonal) and phenotypic (below diagonal) correlations ( $\times 100$ ) from pooled covariance matrices**  
See headnote of Table 1 for definitions of trait acronyms

Trait	BW	WW	YW	FW	MCW	IMF.H	IMF.B	P8.H	P8.B	RIB.H	RIB.B	EMA.HEMA.B	SS	GL	DC	CWT	CEMA	CIMF	CP8	CRIB	CRBY	
BW	21																					
WW	30	61																				
YW	29	73	69																			
FW	31	63	79	48																		
MCW	30	29	45	54	14																	
IMF.H	-8	3	8	7	-6	2																
IMF.B	-6	3	10	10	0	22																
P8.H	-13	15	26	24	2	32	10															
P8.B	-11	6	13	14	-5	10	35	27														
RIB.H	-10	17	27	25	2	31	8	72	19													
RIB.B	-7	8	15	16	-5	8	32	21	74	19												
EMA.H	9	36	48	47	17	13	-2	25	0	24	1											
EMA.B	9	24	35	37	0	4	4	2	9	3	11	24										
SS	14	24	31	28	1	2	7	1	5	4	8	5	17									
GL	17	2	-1	1	-15	3	3	-2	1	-1	0	-2	0	1								
DC	3	1	0	2	4	-1	-5	-6	-1	-5	-1	-3	1	-2	6							
CWT	28	47	53	56	28	-6	-4	7	-5	10	-5	42	15	13	10	5						
CEMA	-20	-6	-7	-8	-19	-11	-6	4	12	0	11	20	7	4	5	-4	-19					
CIMF	-20	-17	-19	-22	-17	15	12	4	14	3	12	-23	-5	-3	-2	-4	-28	7				
CP8	-31	-61	-60	-51	-23	-3	0	23	13	11	11	-50	-12	-16	-15	-10	-77	12	39			
CRIB	-14	-14	-12	-10	-11	-5	-1	25	12	21	10	-13	-1	-6	-3	-5	-23	6	26	69		
CRBY	17	17	26	30	18	-8	-2	-11	-1	-11	0	33	11	3	4	3	32	8	-30	-55	-36	

small and negative, presumably reflecting that CEMA measurements were adjusted to a standard carcass weight. In contrast, Splan *et al.* (2002) reported small positive genetic correlations between WW and eye muscle area or fat depth. Correlation between liveweights and CWT ranged from 0.57 to 0.70, and corresponding values for CRBY from 0.47 to 0.58.

Whilst estimates of  $r_A$  between weights and GL as a trait of the calf were close to zero, corresponding values for maternal genetic effects were consistently moderately high, ranging from 0.52 to 0.59 (Table 8). In contrast, pooled estimates of  $r_C$  for the 3 later weights were of similar magnitude, but negative. Estimates from individual bivariate analyses were close to unity (absolute value) and, to some extent at least, presumably an artefact of estimates of maternal permanent environmental variances for GL, which were close to zero.

#### Scan traits

Estimates of  $r_A$  for the same scan trait measured on different sexes were moderately high, ranging from 0.67 to 0.85, and were comparable with earlier estimates for several breeds of Australian cattle obtained by Meyer and Graser (1999). There were strong genetic correlations between the 2 fat depth measurements (P8 and RIB) within sex; 0.81 for heifers or steers and 0.89 for bulls. EMA showed no association with the other live scan traits. Intra-muscular fat levels (IMF) had low to medium  $r_A$  with fat depth.

Fat depth and fat content measurements had low, but consistently negative estimates of genetic correlations with DC, with fat depth measurements on heifers showing a stronger relationship than scans on bulls. This implies that genetically 'fatter' cows tended to have better reproductive performance. DC records considered in this study used records on all cows, whilst genetic evaluation under BREEDPLAN requires cows to have a DC record corresponding to a first mating between 271 and 1730 days of age. Analyses considering this subset of DC records only, yielded estimates of  $r_A$  from individual, bivariate analyses of  $-0.65$  for P8.H and  $-0.85$  for RIB.B, albeit with large sampling errors (Meyer and Johnston 2003), indicating a somewhat stronger genetic association between 'fatness' and DC for heifers than for older cows.

Pooled genetic correlations between live-scan traits, adjusted to a constant age, and their carcass counterparts, adjusted to a constant carcass weight, ranged from 0.26 to 0.51 for fat content and fat depths, and from 0.17 to 0.22 for eye muscle area. Corresponding estimates from individual bivariate analyses were consistently higher, although on the whole not as high as found in other recent studies. Clearly, these values based on few records for the carcass measurements were given little weight and were thus reduced in the process of pooling covariances. For instance, Devitt and Wilton (2001) obtained estimates of  $r_A$  between

age-constant steer carcass and bull ultrasound measurements of 0.66 for eye muscle area and 0.88 for backfat thickness, and slightly higher values of 0.75 and 0.91, respectively, when considering weight-constant carcass measurements. Corresponding estimates reported by Kemp *et al.* (2002) were 0.69 (EMA) and 0.82 (RIB), and Crews *et al.* (2003) found  $r_A$  of 0.80 (heifers) and 0.54 (bulls) for EMA and 0.83 (heifers) and 0.79 (bulls) for fat thickness.

#### Reproductive traits

Estimates of correlations among reproductive traits were low. GL is a component of DC. However,  $r_A$  was only 0.2, i.e. variation in GL explained little variation in DC. As for 'fatness' traits measured by live ultrasound scanning, estimates of  $r_A$  between DC and fats measured on the carcass were consistently negative, moderate at  $-0.5$  for fat cover (CRIB and CP8), and somewhat weaker at  $-0.3$  for marbling (CIMF).

#### Carcass traits

Correlations between carcass traits were estimated in an analysis considering all 6 traits, i.e. the corresponding block of the covariance matrix was positive definite. Due to highly variable and sometimes inconsistent estimates of  $r_A$  between carcass and other traits, however, most correlations were reduced in size by the pooling procedure. Even more so than heritability estimates, estimated genetic correlations for carcass traits available are highly variable. In contrast to literature results (Moser *et al.* 1998; Pariacote *et al.* 1998; Devitt and Wilton 2001; Kemp *et al.* 2002) and results for Angus in the same research project (Reverter *et al.* 2000), estimates of  $r_A$  between CEMA and carcass fat cover (CRIB and CP8) were positive and moderate. Reverter *et al.* (2000) attributed this to the sampling of sires used. Similarly, estimates of  $r_A$  between CWT and backfat were about  $-0.6$ , whilst Koots *et al.* (1994b) reported a weighted literature average of 0.29. More consistent estimates, pooling data from several temperate breeds in the 'beef CRC' research project, including those on Herefords used here, are given by Reverter *et al.* (2003).

#### Discussion

Estimation of a complete genetic covariance matrix for numerous traits is an arduous task. High-dimensional multivariate analyses considering all traits are computationally infeasible at the present time. Not only that, disregarding computational constraints, analyses of more than 3 or 4 traits are notorious for producing erratic estimates on occasions, in particular where the estimation procedure converges at the boundary of the parameter space. The chances for the latter increase with the number of traits. Hence, bivariate or trivariate analyses are commonly chosen for routine estimation of genetic parameters. Using a series of bivariate analyses in this study ignored any selection on the

basis of traits recorded early in life. However, as comparisons of variance component estimates for later weights from univariate analyses and analyses together with weaning weight showed, effects of selection on variance components were small to negligible. For traits with many records, analyses of only two traits together readily allowed extraction of subsets of records with a high number of animals or parent–offspring pairs that had records for both traits.

Reliable estimation of genetic parameters requires good data, i.e. sufficient amounts of reliable measurements and good pedigree structure. Estimates of covariances among weight, live ultrasound scan, and reproductive traits by and large agreed with expectations and literature values. Clearly, however, estimates of genetic correlations for carcass traits were severely afflicted by the small number of records available for these traits and, moreover, as noted by Reverter *et al.* (2000), suffered from problems associated with a sample of sires that might not have been fully representative of the population for these traits. In addition, fixed effects may not have been estimated reliably. Estimates involving these traits should hence be regarded with caution, and estimation should be repeated when more data for these traits become available.

For multivariate analyses involving many highly correlated traits, a substantial reduction in dimensionality can be achieved by re-parameterising to principal components corresponding to the dominating eigenvalues of the covariance matrices. An eigenvalue decomposition of the  $16 \times 16$  genetic covariance matrix for weight, scan, and reproductive traits showed that the linear combination of the 16 traits given by the eigenvector corresponding to the largest eigenvalue explained 72.0% of the total genetic variation. Similarly, the second and third largest eigenvectors and eigenvalues explained 16.9% and 5.7%, respectively. Considering that the first 11 largest eigenvalues captured 99.9% of total genetic variance, the number of genetic effects estimated in a multivariate analysis could be reduced by ~30% without any essential loss of estimation. Considering the estimated genetic covariance matrix for all 22 traits, the first and second eigenvalue explained 68.4% and 15.1% of the total genetic variation, whilst eigenvalues 1–9 accounted for 99.1% and 1–14 for 99.9% of genetic variance, respectively.

## Conclusions

With some exceptions, such as weaning weight, genetic parameters for Hereford cattle in Australia are comparable with those for other breeds and countries. Except for days to calving, traits included in the multivariate genetic evaluation are moderately to highly heritable, and there are sizable genetic correlations among related traits or groups of traits. More carcass data are needed to determine the genetic relationships between carcass and other traits with confidence.

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