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Variance Components due to Direct and Maternal Effects for Growth Traits of Australian Beef Cattle

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Abstract

Variance components for birth, weaning, yearling and final weight in Australian Hereford, Angus and Zebu Cross cattle were estimated by Restricted Maximum Likelihood. Six different animal models were fitted for each trait and breed, ranging from a simple model with animals as the only random effect to the most comprehensive model allowing for both genetic and environmental maternal effects and a genetic covariance between direct and maternal effects. The most detailed model generally provided the best fit to the data, though differences between models with at least one maternal effect (genetic or environmental) were often not significant. Ignoring maternal effects, direct heritability (h^2) estimates were inflated substantially, in particular for growth till weaning. Significant maternal effects were found in all analyses except for final weight in Angus. There were marked differences between breeds in the relative magnitude of h^2 and the maternal heritability, and the direct-maternal genetic correlation (r_{AM}). For Angus, r_{AM} was low, positive and not significantly different from zero for all traits. For Hereford and Zebu Cross cattle, r_{AM} was negative, moderate to large for weaning weight (-0.59 and -0.78) and somewhat smaller for yearling weight (-0.48 and -0.39). For Herefords, maternal environmental effects were consistently more important than maternal genetic effects.

Keywords : Beef cattle, growth, maternal effects, genetic parameters.

Introduction

Birth weight of an animal and its early growth rate, in particular till weaning, are determined not only by its own genetic potential but also by the maternal environment. These represent mainly the dam's milk production and mothering ability, though effects of the uterine environment and extra-chromosomal inheritance may contribute. The genotype of the dam therefore affects the phenotype of the young through a sample of half her direct, additive genes for growth as well as through her genotype for maternal effects on growth. Hence, to achieve optimum progress in a selection programme both the direct and maternal component should be taken into account, especially if an antagonistic relationship between them exists; see Baker (1980) and Robison (1981) for reviews concerning the influence of maternal effects on the efficiency of selection.

Detailed models for maternally influenced traits have been presented, including additive genetic, dominance and environmental effects due to the animal and its dam and allowing for covariances between them, and extensions to include grandmaternal effects or recombination loss have been outlined; see Baker (1980) and Willham (1980) for reviews and earlier references. Estimation of maternal effects and their covariance components is inherently problematic since direct and maternal effects are generally confounded (unless embryo transfer or crossfostering has taken place), the expression of the maternal effects is sex-limited, occurs late in life of the female and lags by one generation (Willham, 1980).

Methods to estimate (co)variances and genetic parameters due to maternal effects have been reviewed by Foulley and Lefort (1978). Early work relied on the separate estimation of covariances between various types of relatives, equating these to their expectations and solving the resulting system of linear equations. As emphasized by Foulley and Lefort (1978), such procedures combine information in a non-optimal way as they ignore the fact that the same animals may have contributed to different covariances. Furthermore, sampling variances of estimates cannot be derived. A maximum likelihood approach, as outlined by Thompson (1976), overcomes these problems but estimates are still likely not to be very precise. For optimal experimental designs, Thompson (1976) suggested that in the presence of maternal effects sampling variances of estimates of the (direct) heritability

were roughly three to five times as large as when there were direct effects only.

Estimation of genetic parameters due to maternal effects in beef cattle has generally been restricted to traits describing growth till weaning. In most studies, only additive genetic components have been considered. Some distinguished between a genetic and a permanent environmental effect due to the dam while others ignored the latter. Baker (1980) gave average literature values for direct and maternal heritabilities and the genetic correlation between direct and maternal effects of 0.40, 0.19 and -0.42 for birth weight and 0.30, 0.52 and -0.72 for weaning weight. More recent estimates, including those available for postweaning growth traits, are summarised in Table 1.

With increasing computing power available, linear models employed in the genetic evaluation of animals have become more detailed. To date, the animal model is considered the model of choice for a wide range of applications. Corresponding changes have occurred in the estimation of genetic parameters. As Table 1 demonstrates, during the last decade most estimates of maternal heritabilities and direct-maternal genetic correlations have been obtained by equating variance component estimates from a sire-maternal grandsire and sire-dam model analysis to their expectations, while more recently estimates have been obtained using an animal model incorporating maternal effects.

This paper presents estimates of genetic parameters for growth of Australian beef cattle fitting several animal models, attempting to separate direct genetic, maternal genetic and maternal permanent environmental effects. Since there has been some evidence for maternal effects on postweaning growth (Mavrogenis *et al.* 1978; Mackinnon *et al.* 1991), weights up to 700 days are considered.

Material and Methods

Data

Records for birth weight (BW), weaning weight (WW), yearling weight (YW) and final weight (FW) were obtained for Australian Hereford, Angus and Zebu Cross cattle. Environmentally, production conditions for the three genotypes can be described as temperate

lowlands, dry temperate plains and tropical coast, respectively. Ranges allowed for age at weighing were 120 to 300 days, 301 to 500 days and 501 to 700 days respectively for WW, YW and FW. Other basic edits involved consistency checks of dates, sex at birth and at weighing and range checks for weights and age of dam. For a small proportion of animals, age of dam could not be obtained due to missing birth date of the dam and was replaced by the mean dam age in the respective data set.

The Hereford data originated from four commercial stud herds in south-eastern Australia participating in BREEDPLAN (Nicol *et al.* 1985). This scheme requires the producer to assign cattle at each weighing to so-called management groups to allow for differential treatment of animals, e.g. differences in quality of pasture. Between 7 and 22 years of data were available per herd.

Records for Angus came from the experimental herd maintained at the New South Wales Department of Agriculture and Fisheries' Research Centre in Trangie. This herd, established in 1929, has been 'closed' in 1963. Since 1975, the herd has been divided into 3 lines, two lines selected for high and low growth rate from birth to one year of age, respectively, and a random bred control line. In 10 years of selection a divergence in yearling growth rate of more than 25% has been achieved with correlated changes in WW and YW. Further details on selection strategies and responses are given by Parnell *et al.* (1986). Data and pedigree information utilised in this analysis spanned years of birth from 1963 to 1988.

Weight records for tropical cattle, i.e synthetics between *bos indicus* × *bos taurus*, for animals born from 1976 to 1985 were supplied by the C.S.I.R.O.'s National Cattle Breeding Station Belmont near Rockhampton in Central Queensland. Data were obtained for two genotypes, namely the Africander cross line (AX) with 50% Africander, 25% Hereford and 25% Shorthorn genes on average, and the Africander-Brahman cross line (AXBX) containing equal proportions of genes from Africander, Brahman, Hereford and Shorthorn cattle. These lines have been subject to selection, mainly for weight at weaning or one year of age, tick resistance and heat tolerance. Further details on environment, management, herd structure and selection strategies can be found, for instance, in Turner (1982)

and Mackinnon *et al.* (1991).

Characteristics of the data structure for all breeds and traits together with phenotypic means and standard deviations for weights and ages are summarised in Table 2.

Analyses

Estimates of variance components were obtained by Restricted Maximum Likelihood (REML) using a derivative-free algorithm and fitting an animal model throughout. Maternal genetic or permanent environmental effects were taken into account by including appropriate random effects into the model of analysis (Meyer, 1989). Allowing for and ignoring genetic covariances between direct and maternal effects yielded up to 6 different analyses for each trait and breed.

Let \mathbf{a} and \mathbf{m} denote the vectors of animals' direct and maternal additive genetic effects, respectively, and \mathbf{c} and \mathbf{e} the vectors of maternal environmental effects and residual errors. Further, let \mathbf{A} be the numerator relationship matrix between animals and \mathbf{I} the identity matrix. The (co)variance structure for the analysis can then be described as

$$\begin{aligned} V(\mathbf{a}) &= \sigma_A^2 \mathbf{A} \\ V(\mathbf{m}) &= \sigma_M^2 \mathbf{A} \\ V(\mathbf{c}) &= \sigma_C^2 \mathbf{I} \\ V(\mathbf{e}) &= \sigma_E^2 \mathbf{I} \\ Cov(\mathbf{a}, \mathbf{m}') &= \sigma_{AM} \mathbf{A} \end{aligned}$$

where σ_A^2 is the additive genetic variance, σ_M^2 the maternal genetic variance, σ_{AM} the direct-maternal genetic covariance, σ_C^2 the maternal environmental variance, and σ_E^2 the error variance. Vectors \mathbf{c} and \mathbf{e} were assumed to be uncorrelated with all other effects, i.e. all remaining covariances were assumed to be zero.

Fixed effects fitted were sex, birth type (single *versus* twin) and herd(line)-year-month of weighing. For Herefords, herd-management group subclasses were included in addition and for Zebu Crosses a genotype effect (AX *versus* AXBX) was fitted. For Angus, preliminary analyses identified an interaction between selection line and time of weighing, so

that analyses were carried out within line-year-month subclasses rather than fitting lines as a crossclassified fixed effect. Differences in age at weighing (except for BW) and age of dam were taken into account by fitting these as linear and quadratic covariables.

The first model of analysis fitted, Model 1, was a simple animal model with animals' additive genetic effects as the only random effects, i.e. ignoring any maternal influence. Model 2 allowed for a permanent environmental effect due to the dam, fitting this as an additional random effect, uncorrelated with all other effects in the model. Conversely, Model 3 attributed all maternal effects to the genotype of the dam, fitting the maternal genetic effect as a second random effect for each animal with the same covariance (relationship) structure as the direct additive genetic effects. While Model 3 assumed that direct and maternal effects were uncorrelated, i.e. $\sigma_{AM} = 0$, Model 4 allowed for a covariance between them. Models 5 and 6 then included both a permanent environmental and a genetic maternal effect, ignoring and accounting for a genetic correlation between direct and maternal effects.

With the fixed effects part, $F_{ijk(l)(m)}$, identical for all analyses the 6 models were :

$$Y_{ijk(l)(m)n} = F_{ijk(l)(m)} + a_n + e_n \quad (1)$$

$$Y_{ijk(l)(m)no} = F_{ijk(l)(m)} + a_n + p_o + e_n \quad (2)$$

$$Y_{ijk(l)(m)no} = F_{ijk(l)(m)} + a_n + m_o + e_n \quad (3)$$

$$\text{with } Cov(a_n, m_o) = 0$$

$$Y_{ijk(l)(m)no} = F_{ijk(l)(m)} + a_n + m_o + e_n \quad (4)$$

$$\text{with } Cov(a_n, m_o) \neq 0$$

$$Y_{ijk(l)(m)no} = F_{ijk(l)(m)} + a_n + m_o + p_o + e_n \quad (5)$$

$$\text{with } Cov(a_n, m_o) = 0$$

$$Y_{ijk(l)(m)no} = F_{ijk(l)(m)} + a_n + m_o + p_o + e_n \quad (6)$$

$$\text{with } Cov(a_n, m_o) \neq 0$$

with

$$\begin{aligned}
F_{ijk(l)(m)} = & sx_i + bt_j + hym_k(+hmg_l)(+g_m) \\
& (+b_1 (age_{ijk(l)(m)n(o)} - \overline{age}) + b_2 (age_{ijk(l)(m)n(o)} - \overline{age})^2) \\
& +b_3 (dage_{ijk(l)(m)n(o)} - \overline{dage}) + b_4 (dage_{ijk(l)(m)n(o)} - \overline{dage})^2
\end{aligned}$$

where

$Y_{ijk(l)(m)n(o)}$: the BW, WW, YW or FW record for animal n with dam o and fixed effects combination $F_{ijk(l)(m)}$;

sx_i : the effect of the i th sex of animal;

bt_j : the effect of the j th birth type;

hym_k : the effect of the k th herd-year-month of weighing subclass (line-year-month for Angus);

hmg_l : the effect of the l th herd-management group subclass, fitted for Hereford only;

g_m : the effect of the m th genotype, fitted for Zebu Cross data only;

$age_{ijk(l)(m)n(o)}$: the age at weighing pertaining to $Y_{ijk(l)(m)n(o)}$

\overline{age} : the mean age at weighing

b_1, b_2 : the linear and quadratic regression coefficients of weight on age, not fitted for BW;

$dage_{ijk(l)(m)n(o)}$: the dam age pertaining to $Y_{ijk(l)(m)n(o)}$

\overline{dage} : the mean dam age

b_3, b_4 : the linear and quadratic regression coefficients of weight on dam age;

a_n : the direct additive genetic effect of the n th animal;

m_o : the maternal additive genetic effect of the o th dam;

p_o : the permanent environmental effect due to the o th dam;

$e_{ijk(l)(m)n(o)}$: the random residual error pertaining to $Y_{ijk(l)(m)n(o)}$

All pedigree information available was included in the analysis in order to minimize bias due to selection and to increase the accuracy of estimation through additional ties between animals. For models not fitting a maternal genetic effect (Models 1 & 2), parents not in the data and with links to only one other animal (i.e. offspring) were treated as if they were unknown since they did not contribute any information and only increased the number of effects in the analysis unnecessarily. Conceptually, this is equal to ‘absorbing’ the parent in question.

All calculations were carried out using the DFRML set of programs (Meyer, 1991) employing the Simplex procedure to locate the maximum of the log likelihood (\mathcal{L}) as described by Meyer (1989). Convergence was considered to have been reached when the variance of function values ($-2 \log \mathcal{L}$) in the Simplex was less than 10^{-8} . For Models 4 and 6, a restart was performed to ensure that a global rather than a local maximum had been reached. In no case did the restart change estimates or likelihood values substantially, suggesting that for univariate analyses even with a complicated model involving several highly correlated parameters like Model 6, problems with local maxima may not be frequent.

Depending on the model, the log likelihood function was maximised with respect to the direct heritability (h^2), the maternal heritability (m^2), the permanent environmental variance due to the dam as a proportion of the phenotypic variance (c^2) and the genetic covariance between direct and maternal effects as a proportion of the total variance (c_{AM}), while the error variance (σ_E^2) was estimated directly from the residual sum of squares as suggested by Graser *et al.* (1987). From these parameter estimates, the phenotypic variance (σ_P^2), σ_A^2 , σ_M^2 , σ_C^2 and σ_{AM} were derived at convergence. Furthermore, the genetic correlation (r_{AM}) and ‘total’ heritability (h_T^2) defined as (e.g. Willham, 1972)

$$h_T^2 = (\sigma_A^2 + 0.5\sigma_M^2 + 1.5\sigma_{AM})/\sigma_P^2 \quad (7)$$

were calculated. The numerator in (7) is the covariance of an animal’s phenotypic record with the sum of its genetic effects, i.e. h_T^2 is the regression of an animal’s total genotype

(direct and maternal) on its phenotype.

Approximate sampling errors were calculated for each trait and breed for the model with the highest log \mathcal{L} as suggested by Meyer and Hill (1991), fitting a quadratic function to the profile (log) likelihood for each parameter. The estimate of the sampling variance was then equal to -2 times the reciprocal of the quadratic coefficient. The profile likelihood is the likelihood for a subset of the parameters in the model (of size 1 in this case) with all the remaining parameters equal to their maximum likelihood estimates given the parameter(s) in question. Hence calculation of sampling errors was computationally demanding, requiring remaximization of log \mathcal{L} for at least two numerical values for each parameter, chosen close to the REML estimate and bracketing it.

Results

Birth Weight

Estimates of (co)variance components and genetic parameters for BW together with the maximum (log) likelihood values for each analysis are summarised in Table 3. For both breeds, ignoring maternal effects (Model 1) yielded substantially higher estimates of σ_A^2 and h^2 than for the other models. Fitting a permanent environmental effect (Model 2), increased values of log \mathcal{L} markedly over those for Model 1, i.e. identified a significant maternal effect contributing 8.3 (Angus) to 10.1% (Hereford) of the total variation in BW while reducing estimates of σ_A^2 and σ_E^2 correspondingly.

Fitting a maternal genetic rather than permanent environmental effect, resulted in a considerably bigger increase in log \mathcal{L} (over Model 1) than for Model 2, i.e. Model 3 provided a much better fit to the data than Model 2 for both breeds. With an estimate of the maternal heritability of 13 to 14%, the estimate of the direct heritability was reduced to 40%. However, as likelihood values clearly demonstrate, the data were best described by a model including both genetic and environmental effects. Ignoring permanent environmental effects due to the dam (Models 3 and 4), these tended to be ‘picked up’ in the estimate of σ_M^2 , inflating \hat{m}^2 by 3 to 5%.

For Herefords, estimates of the genetic covariance between direct and maternal effects were essentially zero and changed likelihood values little compared to a model ignoring σ_{AM} . For Angus, estimates for c_{AM} were about 5% with a corresponding estimate of r_{AM} of about 0.3. This resulted in a small but not significant increase in $\log \mathcal{L}$ whether a permanent environmental dam effect was fitted (Model 6 *versus* Model 5) or ignored (Model 4 *versus* Model 3). Allowing for σ_{AM} reduced estimates of both h^2 and m^2 slightly so that the resulting values for h_T^2 differed little between corresponding models.

Estimates of the direct, maternal and total heritabilities are well within the range of literature estimates summarised in Table 1, identifying BW as a highly heritable trait with the maternal genetic variation amounting to about 20% of that due to direct additive genetic effects. While most other studies reported an antagonistic, i.e. negative genetic correlation between direct and maternal effects, results from this analysis suggest that there is little association between them.

Weaning Weight

While estimates for BW were highly consistent across breeds, results for WW given in Table 4 show clear differences. In all cases, the most comprehensive model (Model 6) allowing for both genetic and environmental maternal effects and a direct-maternal covariance provided the best fit to the data.

As clearly demonstrated by likelihood values, WW in Herefords was primarily determined by permanent environmental effects due to the dam. In this breed, milk production — though affected by the dam’s genetic potential but for the trait under analysis an environmental effect — is often considered to be a limiting factor for preweaning growth. Ignoring the dam environmental effect (Models 3 and 4) tended to increase the estimate of the phenotypic variance somewhat over that under the other models, suggesting some influence on the efficacy of correcting for systematic environmental effects in the fixed part of the model. Preliminary analyses of herds individually showed this to hold for 3 out of the 4 herds considered.

Allowing for a direct-maternal covariance yielded a negative estimate amounting to 8% of

the total variance (Model 6) with a corresponding estimate of r_{AM} of -0.6 which increased $\log \mathcal{L}$ significantly. While estimates of σ_P^2 and σ_C^2 were not affected by assumptions about σ_{AM} (Model 5 *versus* Model 6), a negative estimate of σ_{AM} resulted in a corresponding increase in both $\hat{\sigma}_A^2$ and $\hat{\sigma}_M^2$ (Model 4 *versus* Model 3 and Model 6 *versus* Model 5), pointing towards some cross-substitution effect in the partitioning of the total variation when estimating highly correlated parameters. Meyer (1989) found empirical correlations of -0.50 between σ_{AM} and σ_A^2 and of -0.80 between σ_{AM} and σ_M^2 in a simulation study under Model 4 encompassing data from 3 generations of full- and half-sib families.

Except for a more negative direct-maternal genetic correlation, estimates under Model 6 agreed well with results from Koch (*pers. comm.*), given in Table 1, under the same model for the Nebraska Hereford selection experiment. In particular, Koch obtained a similarly large estimate for the importance of maternal environmental effects in this breed.

In contrast, results for Angus indicated that — provided a genetic maternal effect was taken into account — environmental maternal effects on WW were of little importance (increases in $\log \mathcal{L}$ for Models 5 and 6 over Models 3 and 4 respectively being non-significant). Furthermore, estimates of σ_{AM} were small and positive, amounting to 4% of the total variance with a resulting estimate of r_{AM} of 0.2 and did not differ significantly from zero. As for BW, estimates of h_T^2 differed little between Models 3 to 6. The maternal heritability estimate amounted to about 70% of the direct value. Results from a cross-fostering experiment in this herd suggested that 82% of the divergence in WW between the high and low selection lines could be attributed to selection response in the direct additive genetic effects while 18% were due to changes in maternal effects (Herd 1990).

Pronounced differences in estimates for the different models of analysis were found for the Zebu Cross data. Assuming there was no association between direct and maternal genetic effects (Model 5), direct genetic and both maternal effects together seemed to influence WW to the same extent (25% of the total variation) with genetic and environmental effects of the dam about equally important. This resulted in an estimate of h_T^2 of 31% almost identical to that for Angus. Allowing for a non-zero σ_{AM} , however, identified a large negative direct-maternal genetic covariance, 36% of the total variance equivalent to

a genetic correlation close to -0.8, which yielded a substantial increase in $\log \mathcal{L}$. At the same time, estimates of σ_A^2 and σ_M^2 increased dramatically while $\hat{\sigma}_P^2$ remained more or less constant. This resulted in estimates of h^2 and m^2 more than twice as large than for Model 5 while \hat{h}_T^2 dropped to 23%.

As observed above for Herefords, but to a much smaller extent, this can in part at least be attributed to sampling variation in the partitioning of the total variance. Analysing the two Zebu Cross genotypes separately, showed that the large estimate of σ_{AM} with the associated increase in estimates of the direct and maternal variances was due to the AX data set while results for the AXBX gave estimates of c_{AM} and r_{AM} of -4% and -0.26 (for Model 6), respectively, which did not increase $\log \mathcal{L}$ significantly over that for Model 5.

Mackinnon *et al.* (1991), considering a subset of the data (years 1982 to 1986 only) utilised in this study, reported estimates of 0.20, 0.32 and 0 for h^2 , m^2 and c_{AM} , respectively, for an analysis under Model 4. Their analysis not only fitted a considerably more detailed fixed effects model, resulting in a lower estimate of the phenotypic variance than in this analysis, but also did not include pedigree information on parents not in the data. Restricting data to animals born from 1982 to 1986 but including as before all pedigree information available, reduced estimates of c_{AM} , h^2 and m^2 to -0.15, 0.31 and 0.34. With an increase in $\log \mathcal{L}$ of only 1.2, these estimates were not significantly different from corresponding values assuming $\sigma_{AM} = 0$ ($\hat{h}^2 = 0.24$ and $\hat{m}^2 = 0.22$). Ignoring back pedigree information then reduced estimates further to 0.22 (h^2), 0.25 (m^2) and -0.06 (c_{AM}), values comparable to those found by Mackinnon *et al.* (1991).

Yearling Weight

Results for YW are summarised in Table 5. Maternal effects for this trait are often considered negligible though some influence, if only due to a part-whole relationship with growth till weaning is to be expected.

With selection on WW and commercial breeders placing more emphasis on FW than YW, comparatively few YW records were available for Herefords. Hence only estimates from Model 1, ignoring maternal effects altogether, were statistically different from those

under the other models. While estimates for h^2 , m^2 and c_{AM} were comparable to those for WW, the environmental influence of the dam explained only 5% of the phenotypic variation in YW compared to 23% for WW.

For Angus, maternal environmental effects on YW were, as for WW, small and not significant. While the maternal genetic variance was reduced to 4% (compared to 14% for WW), the estimate of the direct heritability increased to 33% (20% for WW). Again, the estimate of σ_{AM} was positive but did not increase the likelihood significantly over a value of zero. Herd (1990) attributed 89% of the divergence in YW between the selection lines to direct and 11% to maternal effects.

Estimates from the different models for the Zebu Cross data exhibited the same pattern as discussed above in detail for WW though less pronounced. As for Herefords, the maternal environmental influence was considerably reduced in importance compared to WW while the dam's genetic effect was still about 60% as important as the direct genetic effect. The estimate of σ_{AM} was negative and significantly different from zero, resulting in a genetic correlation of -0.4. Again, this differed substantially from the results of Mackinnon *et al.* (1991) who found a zero correlation for a subset of the data considering the last 5 years only, probably for similar reasons as for WW.

Final Weight

While some 'carry-over' effect of the maternal influence till weaning on YW was anticipated, this was expected to have become less important for FW. Most studies examining FW have ignored maternal effects. However, as results in Table 6 show, this was only the case for Angus. For both Herefords and Zebu Crosses fitting a maternal effect increased the likelihood significantly over that for a simple animal model.

This was most pronounced for Herefords with an estimate for c^2 of 9% and of m^2 of 3%. With a direct heritability estimate of 22% this implies, somewhat surprisingly, that the dam's environmental effect was about 40% as important as the animals genotype in determining FW. This estimate for c^2 was higher than for YW, but this may well have been due to sampling variation. Again, the estimate for c^2 was consistent with results

from Koch (*pers. comm.*) who reported a value of 8% (see Table 1). For the Zebu Cross data, any remaining maternal influence appeared to be environmental. For this data set, the analysis under Model 6 converged to the bounds of the parameter space. For Model 5, the direct heritability estimate amounted to 24% while the maternal environmental influence explained 5% of the total variance.

Discussion

Estimates from the ‘best’ model for each trait and data set together with their approximate sampling errors are summarised in Table 7. As estimates for WW in Zebu Crosses under Model 6 appeared somewhat questionable, results for Model 5 are given as well for this trait. Clearly, allowing for a covariance between direct and maternal genetic effects increased sampling variances dramatically in that case.

A certain amount of cross-substitution between parameters has been observed above for several traits and data set for Models 4 and 6 compared to Models 3 and 5, respectively. To investigate this further, the additive genetic variance given maternal effects, $\sigma_{A.M}^2 = \sigma_A^2 - \sigma_{AM}^2/\sigma_M^2$, and the conditional direct heritability, $h_{A.M}^2 = \sigma_{A.M}^2/\sigma_P^2$, were calculated. Inspection of the results then suggested to replace $\sigma_{A.M}^2$ by a quantity $\sigma_A^2 + \text{sign}(\sigma_{AM})\sigma_{AM}^2/\sigma_M^2$. As Table 8 shows, values for this statistic and the corresponding heritability were remarkably constant across models of analysis for each trait and data set (ignoring estimates for FW for Model 6 in Zebu Crosses where the analysis converged to the bounds of the parameter space). This provides further evidence for problems of sampling (co)variation encountered when attempting to partition additive genetic effects into their direct and maternal components when these are assumed correlated.

Even the most detailed model considered in this study was a considerable simplification of the model(s) presented by Willham (1972). Not only were grandmaternal and non-additive genetic effects assumed to be absent but the environmental effects of dam and offspring were taken to be independent. Several authors emphasized the possibility of a negative environmental covariance between dam and offspring (σ_{EC}) which was expected to bias the estimate of the direct-maternal genetic correlation downwards. Baker (1980)

summarizing literature results which did not use information from the covariance between dams and their offspring, the only observational component affected by σ_{EC} , gave average values of r_{AM} of 0.0, -0.05 and -0.07 for birth weight, daily gain from birth to weaning and weaning weight, while corresponding values not excluding it were -0.42, -0.45 and -0.72.

Adverse effects of a high plane of nutrition during rearing of beef heifers on the weaning weight of their calves have been reported (see Johnsson and Morant (1984) and earlier references given therein), i.e. daughters of dams with superior maternal abilities may provide an inferior maternal environment for their offspring. Statistically, this is equivalent to a negative covariance between the maternal environmental effects of dams and their daughters. Moderate to large estimates of r_{AM} in this study for WW and YW in Herefords and Zebu Crosses indicate that these may have been inflated by such environmental covariance, i.e. that the model(s) of analysis considered here may not have been comprehensive enough.

Though allowing for a non-zero σ_{EC} , Cantet *et al.* (1988) obtained large negative estimates of σ_{AM} for both BW and WW in Herefords accompanied by positive estimates of σ_{EC} . Falconer (1965) modelled the adverse effect of the dam's maternal environment on that of her daughter through a (negative) regression on the dam's phenotype. Comparing dam-offspring correlations with expected values derived from paternal and maternal half-sib contrasts, Koch (1972) speculated that this was of order -0.1 to -0.2 for gain of beef calves from birth to weaning. Cantet *et al.* (1988) estimated this to be -0.15 and -0.25 for BW and WW, respectively. Correcting for it reduced the estimate of σ_{EC} to close to zero and increased the estimate of σ_{AM} for WW, with a resulting r_{AM} still as large as -0.57, but did not affect results for BW markedly. Lande and Kirkpatrick (1990) argued that Willham's (1972) model(s) or its extensions could not account for cycles of maternal effects as in Falconer's (1965) model. Cundiff (1972) considered a negative genetic relationship between direct and maternal effects logical from an evolutionary point of view.

Aspects of selection bias have been ignored in interpreting results from this study. With selection on WW or gain till one year of age, estimates from univariate analyses of the subsequent weights are likely to be biased, as discussed for direct effect models for instance

by Robertson (1977) or Meyer and Thompson (1984). Lande and Price (1989) evaluated the effects of selection on estimates in a maternal effects model. Thompson (1976) outlined modifications to a maximum likelihood procedure to estimate maternal genetic variances required when parents were selected.

Further research is required into the modelling of maternal effects in beef cattle. There is no animal model equivalent to analyses ignoring the dam-offspring covariance only, but it is conceptually — though not necessarily computationally — easy to allow for a covariance between maternal environmental effects. Furthermore, with increasing availability of data from embryo transfer and crossfostering experiments, field records with additional types of covariances between relatives might allow us to disentangle direct and maternal genetic effects more accurately.

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Table 1 : Selected literature estimates^a for genetic parameters due to maternal effects on growth in beef cattle.

Source	Breed ^b	Co. ^c	Model ^d	h^2	m^2	r_{AM}	c^2	c_{AM}	h^2_T
Birth weight									
Baker 1980				0.40	0.19	-0.42			0.34
Burfening <i>et al.</i> 1981	SIM	USA		0.21	0.11	-0.24			0.21
Quaas <i>et al.</i> 1985	SIM	USA	S-MGS	0.16	0.06	-0.44			0.13
Trus & Wilton 1988	SIM	CAN	S-MGS	0.34	0.20	-0.22			0.36
Garrick <i>et al.</i> 1989	SIM	USA	S-MGS	0.44	0.12	-0.38		-0.09	0.37
Nelson <i>et al.</i> 1984	HEF	USA		0.36	0.82	-0.51			0.35
Cantet <i>et al.</i> 1988	HEF	USA		0.18	0.21	-1.05		-0.21	-0.02
Trus & Wilton 1988	HEF	CAN	S-MGS	0.39	0.13	-0.39			0.32
Brown <i>et al.</i> 1990	HEF	USA	S-D-MGS	0.58	0.22	-0.12	0.03	-0.05	0.62
Trus & Wilton 1988	ANG	CAN	S-MGS	0.37	0.13	-0.34			0.32
Brown <i>et al.</i> 1990	ANG	USA	S-D-MGS	0.42	0.22	-0.12	-0.38	-0.04	0.47
Trus & Wilton 1988	SHH	CAN	S-MGS	0.27	0.20	0.55			0.56
Trus & Wilton 1988	CHA	CAN	S-MGS	0.42	0.17	-0.39			0.35
Bertrand & Benyshek 1987	LIM	USA	S-D-MGS	0.22	0.05	-0.16	0.05	-0.02	0.22
Bertrand & Benyshek 1987	BRN	USA	S-D-MGS	0.25	0.13	-0.12	0.00	-0.02	0.28
Hetzel <i>et al.</i> 1990	AX	AUS	S-D-MGS	0.47	0.05		0.07		0.49
Hetzel <i>et al.</i> 1990	HS	AUS	S-D-MGS	0.23	0.03		0.18		0.24
Hetzel <i>et al.</i> 1990	BX	AUS	S-D-MGS	0.45	0.14		0.00		0.52
Mackinnon <i>et al.</i> 1991	ZX	AUS	AMM	0.61	0.11	0.01		0.02	0.68
Koch 1989 ^e	HEF	USA	AMM	0.43	0.12	0.07	0.02	0.02	0.51
Prewaning gain									
Baker 1980				0.26	0.24	-0.45			0.17
Trus & Wilton 1988	SIM	CAN	S-MGS	0.43	0.20	-0.45			0.37
Trus & Wilton 1988	HEF	CAN	S-MGS	0.30	0.27	-0.42			0.25
Brown <i>et al.</i> 1990	HEF	USA	S-D-MGS	0.58	0.39	-0.05	-0.19	-0.02	0.74
Trus & Wilton 1988	ANG	CAN	S-MGS	0.39	0.21	-0.54			0.26
Brown <i>et al.</i> 1990	ANG	USA	S-D-MGS	0.57	0.15	-0.32	-0.25	-0.09	0.50
Trus & Wilton 1988	SHH	CAN	S-MGS	0.39	0.26	-0.14			0.46
Trus & Wilton 1988	CHA	CAN	S-MGS	0.27	0.16	-0.26			0.27
Hetzel <i>et al.</i> 1990	AX	AUS	S-D-MGS	0.11	0.33		0.06		0.27
Hetzel <i>et al.</i> 1990	HS	AUS	S-D-MGS	0.21	0.15		0.15		0.29
Hetzel <i>et al.</i> 1990	BX	AUS	S-D-MGS	0.11	0.09		0.20		0.15
Mackinnon <i>et al.</i> 1991	ZX	AUS	AMM	0.16	0.31	0.00		0.00	0.32

^asee Table 3 for abbreviations

^bSIM : Simmental, HEF : Hereford, ANG : Angus, LIM : Limousin, BRN : Brangus, AX : Africander Cross, BX : Brahman Cross, HS : Hereford-Shorthorn Cross, ZX : Zebu Cross, SHH : Shorthorn and CHA : Charolais.

^cCountry — AUS : Australia, CAN : Canada

^dAM : simple animal model, AMP : animal model with a permanent environmental dam effect, AMM : animal model with maternal genetic effect, S-MGS : sire-maternal grandsire model, S-D-MGS : combination of S-MGS and sire-dam model.

^epersonal communication

Table 1 continued

Weaning weight									
Baker 1980				0.30	0.52	-0.72			0.25
Quaas <i>et al.</i> 1985	SIM	USA	S-MGS	0.12	0.08	-0.04			0.09
Graser & Hammond 1985	SIM	AUS	S-MGS	0.10	0.13	0.04		0.01	0.17
Wright <i>et al.</i> 1987	SIM	USA	S-MGS	0.12	0.09	0.16	0.07	0.02	0.19
Garrick <i>et al.</i> 1989	SIM	USA	S-MGS	0.36	0.19	-0.32		-0.08	0.33
Mrode & Thompson	SIM	UK	AM	0.32					0.32
1990			AMP	0.19			0.08		0.19
			AMM	0.19	0.07				0.19
Skaar 1985	HEF	USA		0.18	0.24	0.25			0.38
Cantet <i>et al.</i> 1988	HEF	USA		0.32	0.27	-0.57		-0.17	0.20
Brown <i>et al.</i> 1990	HEF	USA	S-D-MGS	0.66	0.43	-0.08		-0.04	0.76
Skaar 1985	ANG	USA		0.24	0.18	0.16			0.38
Brown <i>et al.</i> 1990	ANG	USA	S-D-MGS	0.63	0.16	-0.36		-0.11	0.63
Bertrand & Benyshek 1987	LIM	USA	S-D-MGS	0.16	0.15	-0.30	0.06	-0.05	0.17
Bertrand & Benyshek 1987	BRN	USA	S-D-MGS	0.28	0.20	-0.29	0.04	-0.07	0.28
Hetzel <i>et al.</i> 1990	AX	AUS	S-D-MGS	0.14	0.29		0.06		0.29
Hetzel <i>et al.</i> 1990	HS	AUS	S-D-MGS	0.20	0.12		0.19		0.26
Hetzel <i>et al.</i> 1990	BX	AUS	S-D-MGS	0.12	0.08		0.21		0.16
Robinson 1990	BX	AUS	AMM	0.34	0.16				0.42
Mackinnon <i>et al.</i> 1991	ZX	AUS	AMM	0.20	0.32	0.00		0.00	0.36
Koch 1989	HEF	USA	AMM	0.16	0.19	-0.20	0.26	-0.03	0.20
Yearling weight									
Mrode & Thompson	SIM	UK	AM	0.31					0.31
1990			AMP	0.27			0.05		0.27
			AMM	0.26	0.03				0.27
Robinson 1990	BX	AUS	AMM	0.21	0.12				0.27
Mackinnon <i>et al.</i> 1991	ZX	AUS	AMM	0.25	0.20	0.01		0.01	0.36
Postweaning gain									
Garrick <i>et al.</i> 1989	SIM	USA	S-MGS	0.26	0.01	-0.28		-0.01	0.24
Koch 1989	HEF	USA	AMM	0.37	0.02	0.00	0.02	0.00	0.38
Final Weight									
Mackinnon <i>et al.</i> 1991	ZX	AUS	AMM	0.26	0.09	0.01		0.01	0.33
Koch 1989	HEF	USA	AMM	0.43	0.04	0.24	0.08	0.03	0.50

Table 2 : Characteristics of the data structure.

Trait ^a	Hereford				Angus				Zebu Cross		
	BW	WW	YW	FW	BW	WW	YW	FW	WW	YW	FW
No. records	5488	7003	1449	2783	4036	3465	2374	1254	2842	2480	2121
No. animals ^b	6732	7909	2491	4247	4163	3748	2951	1996	3225	2785	2440
	7379	8579	3033	4861	4173	3756	2959	2002	3483	3052	2669
No. sires ^c	518	541	402	458	374	372	339	334	177	179	176
	240	275	132	186	361	339	288	278	177	179	173
	92	115	19	65	346	304	253		118	121	118
No. dams ^d	2636	2809	1415	1989	1232	1170	863	683	1310	1229	1095
	2145	2416	879	1377	1232	1170	863	683	1308	1227	1093
	1152	1656	198	271	1123	1017	617	511	728	715	604
– 1 calf	793	746	505	636	320	330	285	329	517	555	526
– 2 calv.	484	525	226	353	212	236	168	196	402	343	298
– 3 calv.	337	390	106	217	220	232	159	113	206	177	145
– 4 calv.	229	278	36	104	149	150	110	34	75	86	76
– 5 calv.	147	189	6	47	136	97	74	8	69	41	33
– 6 calv.	92	153		12	97	51	31	3	21	18	11
– 7 calv.	30	79		4	47	39	15		12	5	3
– 8 calv.	16	27		1	25	17	16		6	2	1
– 9 calv.	5	10		1	17	13	3				
– 10 calv.	12	19		2	9	5	2				
No. HYM ^e	210	77	47	60	220	55	47	41	11	11	11
No. HMG ^f	1	53	20	29	1	1	1	1	1	1	1
Weight [kg] :											
Mean	33.42	206.1	324.0	454.5	28.44	187.7	267.4	322.0	163.6	189.9	305.4
SD	5.34	48.3	65.5	83.1	4.75	33.8	49.9	63.3	29.9	33.9	40.0
Age [days] :											
Mean		214.4	419.9	579.4		203.2	366.4	574.2	216.3	376.0	595.6
SD		35.5	39.2	30.0		26.1	20.1	21.6	12.9	28.8	23.7
Dam age [years] :											
Mean	4.66	4.46	4.80	4.71	4.94	4.80	4.51	4.37	5.23	5.26	5.20
SD	2.58	2.13	2.59	2.25	3.04	2.65	2.16	2.02	2.19	2.15	2.09

^aBW : Birth weight, WW : Weaning weight, YW : Yearling weight, FW : Final weight

^bin the analysis; 1st line : for Models 1 & 2, 2nd line : for Models 3 to 6

^c1st line : total no. of sires, 2nd line : no. of sires with progeny in the data, 3rd line : no. of sires in the data which have offspring with records

^d1st line : total no. of dams, 2nd line : no. of dams with progeny in the data, 3rd line : no. of dams in the data which have offspring with records, following lines : distribution of maternal sib group sizes

^eherd(line)-year-month subclasses

^fherd-management group subclasses

Table 3 : Estimates of (co)variance components (in kg²) and genetic parameters^a for BIRTH WEIGHT.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
	Hereford					
σ_A^2	10.539	9.024	7.279	7.035	7.629	7.461
σ_M^2			2.631	2.516	1.599	1.545
σ_{AM}				0.199		0.128
σ_C^2		1.866			0.944	0.935
σ_E^2	8.239	7.626	8.613	8.740	8.199	8.300
σ_P^2	18.779	18.516	18.522	18.490	18.372	18.370
h^2	0.561	0.487	0.393	0.381	0.415	0.406
m^2			0.142	0.136	0.087	0.084
c_{AM}				0.011		0.007
r_{AM}				0.047		0.038
c^2		0.101			0.051	0.051
h_T^2	0.561	0.487	0.464	0.465	0.459	0.459
$\log \mathcal{L}$	-42.76	-12.48	-4.18	-4.14	-0.02	0
	Angus					
σ_A^2	7.669	6.909	5.978	5.104	6.178	5.363
σ_M^2			1.887	1.524	1.240	1.006
σ_{AM}				0.758		0.661
σ_C^2		1.216			0.539	0.500
σ_E^2	7.222	6.573	7.045	7.488	6.821	7.253
σ_P^2	14.890	14.699	14.911	14.873	14.778	14.783
h^2	0.515	0.470	0.401	0.343	0.418	0.363
m^2			0.127	0.102	0.084	0.068
c_{AM}				0.051		0.045
r_{AM}				0.272		0.285
c^2		0.083			0.037	0.034
h_T^2	0.515	0.470	0.464	0.471	0.460	0.464
$\log \mathcal{L}$	-33.30	-10.59	-3.42	-2.00	-1.21	0

^a σ_A^2 : direct additive genetic variance, σ_M^2 :maternal additive genetic variance, σ_{AM} : direct-maternal genetic covariance, σ_C^2 : maternal environmental variance, σ_P^2 : phenotypic variance, h^2 : direct heritability, m^2 : maternal heritability, c_{AM} : σ_{AM}/σ_P^2 , r_{AM} : direct-maternal genetic correlation, c^2 : σ_C^2/σ_P^2 , h_T^2 : total heritability, $\log \mathcal{L}$: log likelihood, expressed as deviation from model with highest value.

Table 4 : Estimates of (co)variance components (in kg²) and genetic parameters^a for WEANING WEIGHT.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
	Hereford					
σ_A^2	223.0	86.5	66.2	130.2	74.3	120.4
σ_M^2			328.2	440.5	58.0	115.5
σ_{AM}				-142.2		-69.2
σ_C^2		251.5			207.8	201.3
σ_E^2	648.4	527.7	561.8	525.4	531.7	505.6
σ_P^2	871.3	865.8	956.3	953.9	871.7	873.6
h^2	0.256	0.100	0.069	0.137	0.085	0.138
m^2			0.343	0.462	0.065	0.132
c_{AM}				-0.149		-0.079
r_{AM}				-0.594		-0.587
c^2		0.291			0.238	0.230
h_T^2	0.256	0.100	0.241	0.144	0.119	0.085
$\log \mathcal{L}$	-236.90	-15.14	-67.55	-52.81	-6.90	0
	Angus					
σ_A^2	179.2	124.4	87.9	77.3	90.7	79.1
σ_M^2			80.2	71.7	61.9	53.6
σ_{AM}				14.7		14.5
σ_C^2		49.1			13.9	14.0
σ_E^2	230.1	218.0	235.0	240.9	231.2	236.9
σ_P^2	409.3	391.4	403.1	404.7	397.8	398.1
h^2	0.438	0.318	0.218	0.191	0.228	0.199
m^2			0.199	0.177	0.156	0.135
c_{AM}				0.036		0.037
r_{AM}				0.198		0.223
c^2		0.125			0.035	0.035
h_T^2	0.438	0.318	0.318	0.334	0.306	0.321
$\log \mathcal{L}$	-44.64	-14.16	-1.83	-1.16	-0.72	0
	Zebu Cross					
σ_A^2	168.2	133.2	117.3	301.2	124.8	294.9
σ_M^2			118.2	247.8	55.5	182.2
σ_{AM}				-203.1		-181.4
σ_C^2		115.0			68.2	53.6
σ_E^2	322.9	244.4	266.2	163.0	246.8	155.7
σ_P^2	491.5	492.6	503.5	508.9	495.2	505.0
h^2	0.343	0.270	0.234	0.592	0.252	0.584
m^2			0.236	0.487	0.112	0.361
c_{AM}				-0.399		-0.359
r_{AM}				-0.743		-0.783
c^2		0.233			0.138	0.106
h_T^2	0.343	0.270	0.350	0.237	0.308	0.226
$\log \mathcal{L}$	-98.24	-37.30	-32.49	-5.40	-29.93	0

^asee Table 3 for abbreviations

Table 5 : Estimates of (co)variance components (in kg²) and genetic parameters^a for YEARLING WEIGHT.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
Hereford						
σ_A^2	219.4	143.1	131.8	163.4	128.2	164.7
σ_M^2			101.9	154.5	69.8	115.5
σ_{AM}				-64.4		-66.4
σ_C^2		98.4			45.1	52.8
σ_E^2	849.3	815.3	834.0	813.6	819.4	795.4
σ_P^2	1068.7	1056.8	1067.8	1067.1	1062.6	1062.0
h^2	0.205	0.135	0.124	0.153	0.121	0.155
m^2			0.096	0.144	0.066	0.109
c_{AM}				-0.060		-0.063
r_{AM}				-0.405		-0.481
c^2		0.093			0.042	0.050
h_T^2	0.205	0.135	0.171	0.135	0.153	0.116
$\log \mathcal{L}$	-4.29	-1.51	-0.87	-0.42	-0.56	0
Angus						
σ_A^2	381.3	334.2	304.4	240.3	304.3	246.6
σ_M^2			61.5	43.3	40.9	28.1
σ_{AM}				45.6		40.7
σ_C^2		44.0			21.3	18.6
σ_E^2	388.1	375.8	396.3	424.0	386.6	414.6
σ_P^2	769.4	754.1	762.2	753.2	753.1	748.6
h^2	0.496	0.443	0.399	0.319	0.404	0.329
m^2			0.081	0.058	0.054	0.038
c_{AM}				0.061		0.054
r_{AM}				0.447		0.489
c^2		0.058			0.028	0.025
h_T^2	0.496	0.443	0.440	0.439	0.431	0.430
$\log \mathcal{L}$	-6.92	-2.22	-1.28	-0.47	-0.69	0
Zebu Cross						
σ_A^2	179.6	149.2	117.7	164.2	120.2	166.6
σ_M^2			77.8	111.3	64.6	96.7
σ_{AM}				-51.2		-49.5
σ_C^2		65.42			17.2	16.5
σ_E^2	496.7	458.8	476.8	449.1	469.7	442.5
σ_P^2	676.3	673.4	672.3	673.4	671.7	672.7
h^2	0.266	0.222	0.175	0.244	0.179	0.248
m^2			0.118	0.165	0.096	0.144
c_{AM}				-0.076		-0.074
r_{AM}				-0.379		-0.390
c^2		0.097			0.026	0.025
h_T^2	0.266	0.222	0.233	0.212	0.227	0.209
$\log \mathcal{L}$	-17.14	-7.94	-2.50	-0.29	-2.15	0

^asee Table 3 for abbreviations

Table 6 : Estimates of (co)variance components (in kg²) and genetic parameters^a for FINAL WEIGHT.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
Hereford						
σ_A^2	413.0	310.2	308.6	311.9	291.8	312.0
σ_M^2			94.2	98.8	28.2	39.9
σ_{AM}				-6.7		-22.3
σ_C^2		142.0			123.0	125.2
σ_E^2	1047.7	992.2	1051.3	1048.0	999.0	990.1
σ_P^2	1460.7	1444.3	1454.1	1453.0	1442.1	1444.9
h^2	0.283	0.215	0.212	0.215	0.202	0.216
m^2			0.065	0.068	0.020	0.028
c_{AM}				-0.005		-0.015
r_{AM}				-0.038		-0.200
c^2		0.098			0.085	0.087
h_T^2	0.283	0.215	0.245	0.242	0.212	0.207
$\log \mathcal{L}$	-8.98	-0.59	-4.68	-4.67	-0.11	0
Angus						
σ_A^2	370.5	371.2	370.5	367.0	<i>not fitted</i>	
σ_M^2			0.0	0.0		
σ_{AM}				3.0		
σ_C^2		0.0				
σ_E^2	432.8	431.2	433.2	436.5		
σ_P^2	802.9	803.2	803.7	806.6		
h^2	0.461	0.462	0.461	0.455		
m^2			0.000	0.000		
c_{AM}				0.004		
r_{AM}				0.914		
c^2		0.000				
h_T^2	0.461	0.462	0.461	0.461		
$\log \mathcal{L}$	-0.01	-0.01	-0.01	0		
Zebu Cross						
σ_A^2	287.5	254.6	236.4	195.4	246.6	203.0
σ_M^2			46.8	24.1	12.8	5.4
σ_{AM}				41.2		33.0
σ_C^2		56.5			47.7	41.4
σ_E^2	740.5	710.8	735.2	761.2	714.9	737.3
σ_P^2	1027.9	1021.8	1018.4	1021.8	1022.1	1020.2
h^2	0.280	0.249	0.232	0.191	0.241	0.199
m^2			0.046	0.024	0.013	0.005
c_{AM}				0.043		0.032
r_{AM}				0.600		1.000
c^2		0.052			0.047	0.041
h_T^2	0.280	0.249	0.255	0.264	0.248	0.277
$\log \mathcal{L}$	-2.98	-0.62	-2.49	-0.87	-0.55	0

^asee Table 3 for abbreviations

Table 7 : Parameter^a estimates from ‘best’ model with approximate sampling errors.

	Model No.	h^2		m^2		c_{AM}		c^2	
		est. ^b	s.e. ^c	est.	s.e.	est.	s.e.	est.	s.e.
Birth Weight									
Hereford	6	0.406	0.041	0.084	0.023	0.007	0.035	0.051	0.018
Angus	6	0.363	0.053	0.068	0.026	0.045	0.026	0.034	0.017
Weaning Weight									
Hereford	6	0.138	0.031	0.132	0.031	-0.079	0.025	0.231	0.020
Angus	6	0.199	0.052	0.135	0.039	0.037	0.028	0.035	0.024
Zebu Cross	6	0.584	0.111	0.361	0.084	-0.359	0.080	0.106	0.048
	5	0.251	0.055	0.112	0.048	—		0.138	0.047
Yearling Weight									
Hereford	6	0.155	0.070	0.109	0.058	-0.063	0.058	0.050	0.051
Angus	6	0.329	0.084	0.038	0.034	0.054	0.043	0.025	0.025
Zebu Cross	6	0.248	0.052	0.144	0.044	-0.074	0.041	0.025	0.031
Final Weight									
Hereford	6	0.216	0.048	0.028	0.029	-0.015	0.037	0.087	0.029
Angus	1	0.461	0.069	—		—		—	
Zebu Cross	5	0.241	0.055	0.013	0.034	—		0.047	0.032

^a h^2 : direct heritability, m^2 : maternal heritability, c_{AM} : direct-maternal covariance as proportion of phenotypic variance, c^2 : maternal environmental variance as proportion of phenotypic variance
^bestimate
^csampling error

Table 8 : Estimates of additive genetic variances(σ) given maternal genetic effects, $\sigma_A^2 - \sigma_{AM}^2/\sigma_M^2$, and of $\sigma_A^2 + \sigma_{AM}^2/\sigma_M^2$ (second line) for analyses with positive estimates of σ_{AM} , together with resulting heritabilities(h^2); corresponding unconditional values are given for comparison.

		Additive given Maternal ^a				Additive genetic	
		Model 3	Model 4	Model 5	Model 6	Model 4	Model 6
Birth Weight							
Hereford	σ^2	7.279	7.019	7.629	7.450	7.035	7.461
	h^2	7.279	7.051	7.629	7.472		
Angus	σ^2	0.393	0.380	0.415	0.406	0.381	0.406
	h^2	0.393	0.382	0.415	0.407		
Angus	σ^2	5.978	4.646	6.178	4.929	5.104	5.363
	h^2	5.978	5.481	6.178	5.797		
		0.401	0.312	0.418	0.333	0.343	0.363
		0.401	0.371	0.418	0.392		
Weaning Weight							
Hereford	σ^2	66.2	84.3	74.3	78.9	130.2	120.4
	h^2	0.069	0.088	0.085	0.090	0.137	0.138
Angus	σ^2	87.9	74.3	90.7	75.2	87.9	90.7
	h^2	87.9	80.3	90.7	83.0		
		0.218	0.184	0.228	0.189	0.191	0.199
		0.218	0.198	0.228	0.209		
Zebu Cross	σ^2	117.3	134.7	124.8	114.3	301.2	294.9
	h^2	0.234	0.265	0.252	0.226	0.592	0.584
Yearling Weight							
Hereford	σ^2	131.8	128.2	128.2	126.5	163.4	164.7
	h^2	0.124	0.120	0.121	0.119	0.153	0.155
Angus	σ^2	304.4	192.3	304.3	187.7	240.3	246.6
	h^2	304.4	288.3	304.3	305.5		
		0.399	0.255	0.404	0.251	0.319	0.329
		0.399	0.383	0.404	0.408		
Zebu Cross	σ^2	117.7	140.6	120.2	141.3	164.2	166.6
	h^2	0.175	0.209	0.179	0.210	0.244	0.248
Final Weight							
Hereford	σ^2	308.6	311.4	291.8	299.5	311.9	312.0
	h^2	0.212	0.214	0.202	0.207	0.215	0.216
Zebu Cross	σ^2	236.4	125.0	246.6	1.3	195.4	203.0
	h^2	236.4	265.8	246.6	404.7		
		0.232	0.122	0.241	0.001	0.191	0.199
		0.232	0.260	0.241	0.397		

^aIdentical to additive genetic variance for Models 3 and 5.