Estimates of genetic parameters for weaning weight of beef cattle accounting for direct-maternal environmental covariances

Karin Meyer

Animal Genetics and Breeding Unit, University of New England,
Armidale, NSW 2351, Australia

Abstract

Restricted Maximum Likelihood algorithm estimates of (co)variance components due to maternal effects as well as a regression on maternal phenotype were obtained for seven weaning weight data sets of Australian and New Zealand beef cattle. Fitting such regression, analyses accounted for environmental covariances between dams and their offspring.

Results show a substantial, negative regression on maternal phenotype (up to -0.2) for Hereford field data, accompanied by small, negative estimates of a direct-maternal genetic covariance. In contrast, for Angus and Limousins, the direct-maternal genetic covariance was clearly more important than its environmental counterpart, i.e. for these breeds an estimate of the direct-maternal genetic correlation of about -0.5 could not be attributed to a negative environmental relationship which previously had not been modeled correctly.

Fitting a sire × herd-year interaction as an additional random effect increased the likelihood dramatically for all data sets. While estimates of the regression on maternal phenotype were little affected, fitting the interaction reduced estimates of the direct-maternal genetic covariance, substantially so for Angus and Limousin, reducing (absolute value) estimates of the corresponding correlations to -0.3 to -0.2.

Key words : Beef cattle, Genetic parameters, Weaning weight, Direct-maternal environmental covariance

Introduction

Estimation of maternal effects and the corresponding genetic parameters has always been considered inherently problematic. Not only are direct and maternal effects generally confounded (unless embryo transfer or crossfostering has taken place), but the expression of maternal effects is sex-limited, occurs late in life of the female and lags by one generation (Willham, 1980). Early methods to estimate (co)variance components due to maternal effects relied on equating different types of covariances between relatives to their expectations; see, for instance, Foulley and Lefort (1978) for a review. More recently, the availability of Restricted Maximum Likelihood (REML) algorithms for analyses fitting an animal model including maternal effects, genetic or permanent environmental, as additional random effects has made this task less arduous.

Nevertheless, the problems of imprecise estimates and high sampling correlations (Thompson, 1976; Foulley and Lefort, 1978) between parameters remain. A simulation study illustrated that even for data structures which were specifically designed to allow maternal components to be estimated (with many relatives, including unsual types of relatives), large data sets were necessary to ensure reasonably accurate parameter estimates (Meyer, 1992). Even then sampling correlations remained strong and negative (-0.8 or stronger), in particular for models fitting a direct-maternal genetic covariance.

Numerous studies, in particular of preweaning growth of beef cattle but, to a lesser extent, also in sheep, have found an antagonistic correlation between direct and maternal genetic effects (r_{AM}), often as strong as -0.5 or higher (in absolute value). While a weak adverse genetic relationship between direct and maternal effects has been considered plausible (Cundiff, 1972), such strong, negative estimates have been met with justified scepticism.

Several authors (e.g. Koch, 1972) emphasized the possibility of a negative direct-maternal environmental covariance which, if not modeled, is expected to bias the estimate of the direct-maternal genetic covariance and correlation. Such environmental covariance only affects the covariance between dams and their offspring. Summarising literature estimates for r_{AM} for weaning weight of beef cattle, Baker (1980) reported an average value of -0.72 for estimates considering all sources of information and of -0.07 for estimates excluding dam-offspring covariances.

A potential source of a negative direct-maternal environmental covariance is the level of nutrition available to the dam during early growth. An adverse effect of a high plane of nutrition during rearing of heifers on the weaning weight of their calves has been reported, see, for instance, Johnson and Morant (1984). This is commonly referred to as “fatty udder syndrome”. It causes daughters of dams with high maternal ability to provide a worse maternal environment for their offspring than dictated by their (maternal) genetic potential. It gives rise to a negative, environmental covariance between dams and their offspring, and, over several generations, results in a ‘cyclic’ maternal environmental effect.

The animal models commonly fitted when estimating maternal effects include maternal genetic and permanent environmental effects, i.e. are the models suggested by Willham (1963) (omitting dominance effects). While it is conceptually easy to extend these to allow for direct-maternal, permanent environmental covariances, this might impose computational problems, especially for large, ‘unstructured’ (field) data sets. A more appealing alternative is the approach taken by Falconer (1965) who modeled maternal effects on litter size in mice by fitting a regression on maternal phenotype. Thompson (1976) showed that the ‘Falconer model’ (F) performed better in terms of sampling errors and correlations than the ‘Willham model’ (W). However, Falconer’s (1965) model did not allow for a separate maternal genetic effect. Recently, Koerhuis and Thompson (1997) described an ‘integrated Falconer-Willham model’ (IFW), i.e. an animal model fitting both genetic and environmental maternal effects as well as a regression on maternal phenotype.

This paper outlines a derivative-free REML algorithm to estimate the parameters of the IFW model, and shows its application for several data sets of weaning weight in beef cattle. In addition, the effects of extraneous variation, for instance due to inappropriate definition of contemporary groups, on parameter estimates are examined.

Material and Methods

REML algorithm

Consider the ‘usual’ mixed linear model,

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{e} \tag{1}$$

with $\mathbf{y}$ the vector of observations, $\mathbf{b}$ the vector of fixed effects (including regression coefficients) fitted, $\mathbf{u}$ the vector of random effects in the model, $\mathbf{e}$ the vector of residuals, and $\mathbf{X}$ and $\mathbf{Z}$ the incidence matrices pertaining to $\mathbf{b}$ and $\mathbf{u}$, respectively.

Under an animal model, $\mathbf{u}$ always contains the vector of animals' direct additive genetic effects, $\mathbf{a}$. If traits(s) analysed are subject to maternal effects, this is usually taken into account by fitting vectors of maternal additive genetic effects ($\mathbf{m}$) and maternal permanent environmental effects ($\mathbf{c}$) in addition, i.e.,

$$\mathbf{u} = \begin{pmatrix} \mathbf{a} \\ \mathbf{m} \\ \mathbf{c} \end{pmatrix} \tag{2}$$

with corresponding partitioning $\mathbf{Z} = (\mathbf{Z}_A \mid \mathbf{Z}_M \mid \mathbf{Z}_C)$. This is a reduced version (ignoring dominance effects) of the model formulated by Willham (1963) to describe the mode of inheritance of maternal effects.

Further, let $\mathbf{A}$ denote the numerator relationship matrix between animals. While maternal genetic effects are assumed to have the same correlation structure as direct additive genetic effects, maternal permanent environmental effects are usually taken to be independently distributed. Hence, in the univariate case,

$$\mathbf{G} = \mathrm{V}\begin{pmatrix} \mathbf{a} \\ \mathbf{m} \\ \mathbf{c} \end{pmatrix} = \begin{pmatrix} \sigma_A^2\mathbf{A} & \sigma_{AM}\mathbf{A} & \mathbf{0} \\ \sigma_{AM}\mathbf{A} & \sigma_M^2\mathbf{A} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \sigma_C^2\mathbf{I} \end{pmatrix} \tag{3}$$

where $\mathbf{I}$ denotes an identity matrix. Similarly, under (1) residuals are assumed to be *i.i.d.*, i.e.

$$\mathbf{R} = \mathrm{V}(\mathbf{e}) = \sigma_E^2\mathbf{I} \tag{4}$$

This gives the phenotypic variance of individual observations as

$$\sigma_P^2 = \sigma_A^2 + \sigma_M^2 + \sigma_{AM} + \sigma_C^2 + \sigma_E^2 \tag{5}$$

Falconer's model and beyond. An alternative formulation is due to Falconer (1965) who modeled maternal effects by fitting a linear regression of phenotype of the individual on the phenotype of the dam. In addition, Falconer (1965) allowed for litter effects, i.e., environmental effects common to full-sibs which were not explained by the regression on maternal phenotype.

Let $\mathbf{y}_M$ denote the vector of dams' records pertaining to $\mathbf{y}$, i.e. for animal i with dam j the i-th element of $\mathbf{y}_M$ is y_j, the record for animal j, or 0 if a record for j is not available or the animal's dam is unknown. Correspondingly, let $\mathbf{X}_M$ be the incidence matrix for fixed effects pertaining to $\mathbf{y}_M$. The i-th row of $\mathbf{X}_M$ is equal to the j-th row of $\mathbf{X}$, or zero for unknown dams or missing dams' records.

The "Falconer model" (ignoring dominance effects) can then be written as (Koerhuis and Thompson, 1997)

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \beta\,(\mathbf{y}_M - \mathbf{X}_M\mathbf{b}) + \mathbf{e}^* \tag{6}$$

where β denotes the linear regression on maternal phenotype. Falconer's (1965) formulation did not include a separate maternal genetic effect, i.e., in the linear model notation $\mathbf{u}' = (\mathbf{a}' \mid \mathbf{c}')$ in this case. However, (6) extends readily to an "integrated Falconer-Willham model" (Koerhuis and Thompson, 1997) by including $\mathbf{m}$ in $\mathbf{u}$, as above, in addition.

Note that β in (6) is not a regression coefficient in the usual sense (i.e., a fixed or random effect in the linear model), but a ratio of variance components, namely the direct-maternal environmental covariance expressed as a proportion of the phenotypic variance. While it has an interpretation as the regression on maternal phenotype, it is a parameter to be estimated, in addition to σ_A^2, σ_M^2, σ_{AM}, σ_C^2 and σ_E^2, which affects the log likelihood. The IFW model thus provides an alternative to the 'extended' Willham model (Koerhuis and Thompson, 1997) which allows for non-zero direct-maternal environmental covariances. In contrast to (1), (6) is a linear model for which $V(\mathbf{y})$ is not linear in the parameters to be estimated.

As shown by Koerhuis and Thompson (1997), under (6) the covariances between animals' direct and maternal genetic effects and their dams' phenotypes are given by geometric series in the genetic (co)variance components with a common ratio of $\frac{1}{2}\beta$, and can be summarised as $4\frac{\beta}{2-\beta}\,(\frac{1}{2}\sigma^2_A+\frac{1}{4}\sigma_{AM})$ and $4\frac{\beta}{2-\beta}\,(\frac{1}{2}\sigma^2_M+\sigma_{AM})$, respectively. This gives the variance of individual observations as

$$\sigma^{2\,*}_P = \left[\sigma^2_A+\sigma^2_M+\sigma_{AM}+\sigma^2_C+4\frac{\beta}{2-\beta}(\frac{1}{2}\sigma^2_A+\frac{5}{4}\sigma_{AM}+\frac{1}{2}\sigma^2_M)+\sigma^2_E\right]/(1-\beta^2) \tag{7}$$

The term $(\frac{1}{2}\sigma^2_A+\frac{5}{4}\sigma_{AM}+\frac{1}{2}\sigma^2_M)$ is the dam-offspring covariance under the 'Willham model'.

Unknown maternal phenotype. In each data set there are animals, such as base animals, with unknown dams or missing maternal phenotypes. The residual variance for these is

$$\sigma^{2\,*}_E = \left[\beta^2(\sigma^2_A+\sigma^2_M+\sigma_{AM}+\sigma^2_C)+4\frac{\beta}{2-\beta}(\frac{1}{2}\sigma^2_A+\frac{5}{4}\sigma_{AM}+\frac{1}{2}\sigma^2_M)\right]/(1-\beta^2) \tag{8}$$

Hence, the residual covariance matrix under the IFW model is

$$\mathbf{R}^* = \mathrm{V}(\mathbf{e}^*) = \sigma^2_E\mathbf{D} \tag{9}$$

where $\mathbf{D}$ is a diagonal matrix with elements $d_i = 1$ for animals with dams' records available, and $d_i = \sigma^{2\,*}_E/\sigma^2_E$ otherwise.

In addition, unavailability of a maternal phenotype gives rise to small, non-zero genetic covariances between animals with 'uncorrected' phenotypes and their offspring. As outlined by Koerhuis and Thompson (1997), these can be taken into account by regressing the records for such animals on the accumulated genotypes of their dams instead of their unknown phenotypes, with the accumulated genotype of an animal defined as the sum of genotypes of maternal ancestors, each weighed by β^t for $t = 0,1,\ldots$ the number of generations separating the animal and its ancestor, i.e. for an animal with genotype a, dam with genotype a_D, maternal granddam with genotype a_{DD}, etc., the accumulated genotype is $a+\beta a_D+\beta^2 a_{DD}+\beta^3 a_{DDD}+\ldots$. Similarly, the maternal genotype for animals with unrecorded dams is replaced by the accumulated maternal genetic value of the dam, defined analogously. This slightly changes the genetic relationship structure. A modified numerator relationship matrix $\mathbf{A}^*$ and its inverse can be obtained applying standard rules (e.g. Henderson, 1976) with some adjustment to the coefficients for dams with unknown phenotypes and those relating them to their offspring; see the Appendix of Koerhuis and Thompson (1997) for details. If $\mathbf{A}^*$ rather than $\mathbf{A}$ is used, $\sigma^{2\,*}_E$ above (8) is reduced accordingly. In the following, $\mathbf{A}$ denotes either $\mathbf{A}$ or $\mathbf{A}^*$, calculations are the same whether the covariances between unrecorded dams and their offspring are taken into account or ignored.

Calculating the likelihood. REML estimation of variance components and genetic parameters for models of form (1) using a derivative-free algorithm has been described in detail by Meyer (1989). This can readily be adapted to include the regression on maternal phenotype by noting that (6) can be rewritten to have the same form as (1), namely

$$\mathbf{y}-\beta\,\mathbf{y}_M = (\mathbf{X}-\beta\,\mathbf{X}_M)\,\mathbf{b}+\mathbf{Z}\mathbf{u}+\mathbf{e}^* \tag{10}$$

or

$$\mathbf{y}^* = \mathbf{X}^*\mathbf{b}+\mathbf{Z}\mathbf{u}+\mathbf{e}^* \tag{11}$$

with $\mathbf{y}^* = \mathbf{y}-\beta\,\mathbf{y}_M$ and $\mathbf{X}^* = \mathbf{X}-\beta\,\mathbf{X}_M$. While the columns of $\mathbf{X}$ pertaining to fixed effects have elements 0 or 1, corresponding values in $\mathbf{X}^*$ are 0, 1, $-\beta$ and $1-\beta$.

Let N_M and N_0 denote the number of records with and without maternal records available, $N = N_M+N_0$, N_A be the total number of animals (including parents without records), and N_C denote the number of dams with progeny in the data. The REML log likelihood ($\mathcal{L}$) for (6) is then

$$\begin{aligned}\log\mathcal{L} \quad = \quad & -\frac{1}{2}\left[const+N_A\log(\sigma^2_A\sigma^2_M-\sigma_{AM}{}^2)+2\log|\mathbf{A}|+N_C\log(\sigma^2_C)\right.\\ & +N_0\log(\sigma^{2\,*}_E)+(N_M-r(\mathbf{X}^*)-2N_A-N_C)\log(\sigma^2_E)\\ & \left.+\log|\mathbf{C}^*|+\mathbf{y}^{*'}\mathbf{P}\mathbf{y}^*/\sigma^2_E\right] \end{aligned} \tag{12}$$

where $\mathbf{C}^*$ is the coefficient matrix in the mixed model equations pertaining to (6),

$$\mathbf{P} = \mathbf{V}^{-1} - \mathbf{V}^{-1}\mathbf{X}^*(\mathbf{X}^{*'}\mathbf{V}^{-1}\mathbf{X}^*)^{-}\mathbf{X}^{*'}\mathbf{V}^{-1} \tag{13}$$

for $\mathbf{V} = \mathrm{V}(\mathbf{y}) = \mathbf{ZGZ}' + \mathbf{R}^*$, and $\mathbf{y}^{*'}\mathbf{P}\mathbf{y}^*$ is the residual sum of squares. For the straight Falconer model ($\mathbf{m}$ not fitted), (12) reduces to

$$\begin{aligned}\log \mathcal{L} \quad &= -\frac{1}{2}\left[const + N_A \log(\sigma_A^2) + \log|\mathbf{A}| + N_C \log(\sigma_C^2) + N_0 \log(\sigma_E^{2\,*})\right.\\ &\left.+(N_M - r(\mathbf{X}^*) - N_A - N_C)\log(\sigma_E^2) + \log|\mathbf{C}^*| + \mathbf{y}^{*'}\mathbf{P}\mathbf{y}^*/\sigma_E^2\right]\end{aligned} \tag{14}$$

Since β is included in the design matrix for fixed effects, it does not enter the likelihood explicitly, but (12) and (14) depend on it via the last two terms, $\log|\mathbf{C}^*|$ and $\mathbf{y}^{*'}\mathbf{P}\mathbf{y}^*$. As shown by Graser *et al.* (1987) these can be evaluated simultaneously by factoring the mixed model matrix, i.e. the coefficient matrix augmented by the vector of right hand sides and its transpose and the weighted sum of squares in the data vector. For the Falconer-Willham model (6) and the likelihood given in (12), this matrix is

$$\begin{pmatrix} \mathbf{y}^{*'}\mathbf{D}^{-1}\mathbf{y}^* & \mathbf{y}^{*'}\mathbf{D}^{-1}\mathbf{X}^* & \mathbf{y}^{*'}\mathbf{D}^{-1}\mathbf{Z}_A & \mathbf{y}^{*'}\mathbf{D}^{-1}\mathbf{Z}_M & \mathbf{y}^{*'}\mathbf{D}^{-1}\mathbf{Z}_C \\ \mathbf{X}^{*'}\mathbf{D}^{-1}\mathbf{y}^* & \mathbf{X}^{*'}\mathbf{D}^{-1}\mathbf{X}^* & \mathbf{X}^{*'}\mathbf{D}^{-1}\mathbf{Z}_A & \mathbf{X}^{*'}\mathbf{D}^{-1}\mathbf{Z}_M & \mathbf{X}^{*'}\mathbf{D}^{-1}\mathbf{Z}_C \\ \mathbf{Z}_A'\mathbf{D}^{-1}\mathbf{y}^* & \mathbf{Z}_A'\mathbf{D}^{-1}\mathbf{X}^* & \mathbf{Z}_A'\mathbf{D}^{-1}\mathbf{Z}_A + \alpha^{11}\mathbf{A}^{-1} & \mathbf{Z}_A'\mathbf{D}^{-1}\mathbf{Z}_M + \alpha^{12}\mathbf{A}^{-1} & \mathbf{0} \\ \mathbf{Z}_M'\mathbf{D}^{-1}\mathbf{y}^* & \mathbf{Z}_M'\mathbf{D}^{-1}\mathbf{X}^* & \mathbf{Z}_M'\mathbf{D}^{-1}\mathbf{Z}_A + \alpha^{12}\mathbf{A}^{-1} & \mathbf{Z}_M'\mathbf{D}^{-1}\mathbf{Z}_M + \alpha^{22}\mathbf{A}^{-1} & \mathbf{0} \\ \mathbf{Z}_C'\mathbf{D}^{-1}\mathbf{y}^* & \mathbf{Z}_C'\mathbf{D}^{-1}\mathbf{X}^* & \mathbf{0} & \mathbf{0} & \mathbf{Z}_C'\mathbf{D}^{-1}\mathbf{Z}_C + \frac{\sigma_E^2}{\sigma_C^2}\mathbf{I} \end{pmatrix} \tag{15}$$

where α^{ij} is the ij-the element of

$$\alpha = \sigma_E^2 \begin{pmatrix} \sigma_A^2 & \sigma_{AM} \\ \sigma_{AM} & \sigma_M^2 \end{pmatrix}^{-1} \tag{16}$$

With $\mathbf{D}$ a diagonal matrix, incorporating $\mathbf{D}^{-1}$ into the data part of the mixed model matrix merely amounts to including a scaling factor for animals with unknown maternal phenotype. Hence, apart from the latter (15) can be set up in the same way as under model (1) by simply substituting $\mathbf{X}^*$ and $\mathbf{y}^*$ for $\mathbf{X}$ and $\mathbf{y}$.

Maximising the likelihood. As for the Willham model (1), the likelihood can be maximised — including β as an additional parameter — with respect to all parameters simultaneously using a suitable derivative-free optimisation procedure such as Nelder and Mead's (1965) simplex algorithm or Powell's (1965) method of conjugate directions; see Meyer (1989) for details. As before, σ_E^2 can be estimated directly from the residual sum of squares. Adding the regression on maternal phenotype as an extra parameter thus increases the dimension of search to a maximum of 5, for the 'full' Falconer-Willham model.

Alternatively, as done by Thompson (1976) for the Falconer model and Koerhuis and Thompson (1997) for the IFW model, the maximum of the likelihood can be located in a nested, two-step procedure. The external step in this case involves a quadratic approximation of the profile likelihood function for β. Evaluating each point on the latter (internal step) is equivalent to an analysis under the Willham model, requiring maximisation of $\log \mathcal{L}$ with respect to the remaining parameters for given values of β. This procedure is advantageous if it is desired to use information from derivatives of $\log \mathcal{L}$. For instance, the powerful "average information" REML algorithm (Johnson and Thompson, 1995) can be employed in the internal maximisation step. In this way, we can utilise the advantages of methods requiring derivatives of $\log \mathcal{L}$ for those parameters for which derivatives are easy to derive, but avoid the need to differentiate $\log \mathcal{L}$ with respect to β. Moreover, approximate sampling errors can be determined from the inverse of the Hessian matrix (or its approximation) at convergence, and a quadratic or higher order approximation of the profile likelihood for β.

Data

Records for weaning weight of calves from several beef breeds were analysed, considering a total of seven different data sets. Characteristics of the data structure are summarised in Table 2.

Table 1 : Genetic parameters[a] estimated for different models of analysis.

	2	2^{β}	5	5^{β}	6	6^{β}	7	7^{β}	7_a	7_a^{β}	8	8^{β}
h^2	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
m^2			✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
r_{AM}					✔	✔	✔	✔	✔	✔	✔	✔
c^2	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔	✔
s^2							✔	✔			✔	✔
p^2									✔	✔	✔	✔
β		✔		✔		✔		✔		✔		✔

[a] h^2: direct heritability, m^2: maternal heritability, r_{AM}: direct-maternal genetic correlation c^2: permanent environmental maternal variance as proportion of the phenotypic variance, s^2: variance due to sire × year effect as proportion of the phenotypic variance, p^2: variance due to paddock × year effect as proportion of the phenotypic variance, and β : regression on maternal phenotype

The first two data sets originated from the 'Wokalup' selection experiment in Western Australia. This comprised two herds of about 300 cows, the first purebred Polled Herefords and the other so-called Wokalups, a four-breed synthetic, with selection carried out for preweaning growth rate. Records spanned 1974 to 1990. These data have been analysed previously not accounting for maternal phenotype; see Meyer *et al.* (1993) for details and further information on the experiment.

The third and fourth data set were subsets of field records for Australian (AUS) and New Zealand (NZ) Angus, analysed previously under the assumption that direct-maternal genetic covariances were zero (Meyer, 1995). For this study, only herds with at least 200 and 100 records, respectively, with maternal phenotype available were considered. This yielded data sets with more than 50% of dams' records known.

The other data sets consisted of records for Australian Polled Herefords, Herefords and Limousin, respectively, extracted from the National Beef Recording data base. Basic edits included consistency and range checks for birth and weighing dates and weights. As actual weaning dates were not available, weights within the range allowed by (Group)BreedPlan (the Australian genetic evaluation scheme for beef cattle), 80 to 300 days, closest to to target weaning age of 200 days (for animals with multiple weights in the permissible range) were selected. For Herefords and Polled Herefords only calves born form 1980 onwards were considered, and, as above, only herds contributing at least 200 weaning weights with maternal phenotype known were included.

Analyses

Estimates of genetic parameters and variance components were obtained by REML, using a derivative-free algorithm. An animal model including maternal genetic and permanent environmental maternal effects as additional random effects was fitted for all data sets. As done by Koerhuis and Thompson (1997), the unmodified numerator relationship matrix between animals was used. Analyses were carried out assuming direct and maternal genetic effects were uncorrelated as well as allowing for a direct-maternal genetic covariance. Ignoring maternal phenotype, these were Models 5 and 6, respectively, of previous analyses (e.g. Meyer *et al.*, 1993), and this nomenclature is retained here for consistency. Model 7, not used previously, was as Model 6 (allowing for a non-zero σ_{AM}) but fitted a sire × herd-year interaction as an additional random effect $\mathbf{h}$, with assumed covariance matrix $\sigma^2_{SH}\mathbf{I}$.

All three models were augmented by fitting a regression on maternal phenotype in addition as described above, yielding models 5^{β}, 6^{β} and 7^{β}, respectively. Furthermore, an animal model including maternal permanent environmental effects only, Model 2 of previous studies, was fitted for the experimental data sets. Including the regression on maternal phenotype as an extra parameter then yielded Model 2^{β}, the 'Falconer model'. In addition, Models 7a and $7a^{\beta}$ were as model 7 and 7^{β} but included a paddock × year effect instead of a sire × year interaction. Models 8 and 8^{β} finally were as 7 and 7a (or 7^{β} and $7a^{\beta}$) combined, i.e. included both the paddock × year and sire × year effects. Table 1 shows the genetic parameters estimated under the 12 different models.

For Limousins and the experimental data sets, all pedigree information available was included in the analyses. For the remaining large data sets, only one (Herefords) or two (Angus) passes through the pedigree were performed to locate parental identities for animals not in the data, in order to restrict the total number of animals in the analysis.

For the field data sets, fixed effects fitted were similar to those used in genetic evaluation under (Group)BreedPlan,

Table 2 : Characteristics of the data structure for weaning weight

		Experimental data		Field data				
		Polled Heref.s	Wokalups	Polled Heref.s	Herefords	Angus AUS	Angus NZ	Limousin
No. of records		3088	3191	61,787	79,434	87,389	57,375	16,635
. . . with dam's rec.		2284	2254	23,234	33,426	46,274	29,319	3926
No. of animals[a]		3426	3851	84,520	107,154	109,841	69,817	28,236
No. of sires[b]		174	189	2089	2689	2589	1819	1086
No. of dams[b]		946	1189	23,967	30,866	31,272	19,456	8502
No. of CG[c]		151	139	6224	6551	6903	2553	4304
No. of S×HY[d]		433	287	7337	7837	7719	3776	3291
Weight[e]	$\overline{x}$[f]	234.0	264.3	221.9	219.0	232.9	216.6	232.3
	sd[g]	48.1	48.5	50.4	55.7	47.3	50.5	49.4
Age[h]	$\overline{x}$	219.5	215.9	218.2	214.1	214.6	201.8	215.4
	sd	25.4	26.6	42.0	39.1	32.6	39.8	40.1
Dam age[i]	$\overline{x}$	4.46	4.59	5.33	4.91	4.88	5.41	–
	sd	1.87	2.05	2.30	2.38	2.29	2.57	–

[a] in the analysis, including parents without records
[b] with progeny in the data
[c] contemporary group classes
[d] sire × herd-year interaction effects
[e] in kg
[f] mean
[g] standard deviation
[h] at weighing, in days
[i] at calving, in years

though no precorrection of data was performed. Analyses were carried out within contemporary groups, defined as herd-year-management group-sex subclasses, with an "age slicing" of 45 days, i.e. for herds with long calving seasons subclasses were divided further, so that only calves born not more than 45 days apart were directly compared with each other.

Additional differences in age at weighing were taken into account by fitting a linear regression on age within sex. Age of dam was fitted as a linear and quadratic covariable (except for Limousins). Furthermore, an age status of dam (heifers : 28 month or less at calving *vs.* cows : older than 28 months), the so-called "heifer factor" and birth type (single *vs.* twin) were fitted as crossclassified fixed effects. For the Hereford and Angus data sets, a small proportion of dam ages were missing and, for the purpose of analysis, replaced by the mean dam age in the respective data set. For Limousins, insufficient dam ages were available, and the regression on age of dam and the "heifer factor" were omitted from the model of analysis.

For the experimental data, fixed effects for analyses under models 2, 5 and 6 were sex (at weighing), birth type, year-paddock and year-month of weighing subclasses, as fitted in previous analyses (Meyer *et al.*, 1993) and age at weighing and age of dam were taken into account by fitting each as a linear and quadratic covariable. In addition, analyses under models 6, 7, 7a and 8 were carried out not fitting year-paddock subclasses as fixed effects.

Results

Wokalup selection experiment

Estimates from analyses for the two experimental data sets are summarised in Table 3. Not fitting maternal genetic effects (Models 2 and 2^{β}) clearly did not describe the data adequately.

Fitting year × paddock subclasses as fixed effects, estimates of the direct-maternal genetic covariance (Model 6) were close to zero and did not increase likelihoods significantly for both breeds. This had led Meyer *et al.* (1993) to surmise that there were no problems with environmental dam-offspring covariances not taken into account in these data sets.

Indeed, for Polled Herefords, all estimates of β were close to zero and did not increase log $\mathcal{L}$ markedly. For Wokalups, estimates of the regression on maternal phenotype were positive, ranging from 0.07 to 0.1, and, except for Model 5, likelihoods were significantly higher than for $\beta = 0$. This indicates the presence of a small, positive environmental covariance, possibly management induced, between cows and their calves. Whether this is specific to the synthetic breed or whether it might be present in the Polled Hereford herd as well, but ‘counteracted’ by a negative, “fatty udder” type covariance which we might expect to find in this breed, can only be speculated upon. For both breeds, estimates of the other genetic parameters, however, differed little between models allowing for and ignoring a regression on maternal phenotype.

An inexplicable, substantial negative estimate of the direct-maternal genetic covariance has mostly been observed in field data while it has by and large been absent in corresponding experimental data sets. This has been attributed to factors like more uniform management and lack of preferential treatment. Alternatively, it might reflect better identification of contemporary (CG) or management groups. In beef cattle, these are generally equivalent to paddocks. If CG are defined too large, for instance due to missing identification of the appropriate management group or paddock, related calves from the same paddock might be more similar to each other than expected from their degree of relationship. This would yield an overestimate of the additive genetic variance and, due to high sampling correlations between parameters, corresponding biases in the other (co)variance components.

For the purpose of argument, assume that we were estimating variance components by equating covariances between relatives to their expectations, and consider the case where we have the covariance between paternal half sibs, and the covariances between sires and dams and their offspring as sources of information. If the covariance between paternal half sibs were inflated by σ^2_{SH} due to systematic environmental effects not taken into account, estimates of σ^2_A, σ^2_M and σ_{AM} would be biased by $+4\sigma^2_{SH}$, $+16\sigma^2_{SH}$ and $-8\sigma^2_{SH}$, respectively. Most studies concerned with large, negative estimates of σ_{AM} reported a marked increase in estimates of σ^2_A and σ^2_M over those obtained assuming σ_{AM} was zero, i.e. a change in estimates consistent with the hypothesis of an inflated covariance between sibs.

As shown in Table 3, omitting a fixed paddock (× year) effect from the model of analysis did indeed generate a substantial, negative estimate for σ_{AM} (or c_{AM}), accompanied by greatly inflated estimates of the direct and maternal genetic components (h^2 and m^2; Model 6). For Polled Herefords, accounting for a negative regression on maternal phenotype (Model 6^β) somewhat tempered the effects of ignoring paddocks. In field data, paddocks generally coincide with mating groups. If this is the case, missing management group codes can be approximated to some extent by a sire × (herd-) year effect. Even though the experimental regimen involved re-randomisation of cows over paddocks between mating and calving each year, fitting such effect (Model 7) resulted in markedly less negative estimates of σ_{AM} accompanied by estimates of h^2 (and m^2 for Wokalups) similar or less than those obtained when fitting (fixed) paddock × year effects, and a marked increase in likelihood.

Fitting a random paddock × year effect (Model 7a) instead gave a substantially higher increase in likelihood, i.e. as expected the sire × year effect was not a good approximation of the paddock × year effect for these data. For Polled Herefords, estimates of σ_{AM} were less negative and for both breeds estimates of h^2 were higher than under Model 7. Analyses under Model 8 identified a significant sire × year effect, amounting to about 3% of the phenotypic variation, over and above the variation explained by paddocks × years.

Contrasting results from Models 7, 7a and 8 indicated that the sire × year interaction might have removed some genetic variation between animals and thus yielded estimates of h^2 biased downwards. This was confirmed by fitting a sire × year effect in addition to fixed paddock × year subclasses (not shown). This produced similar estimates of the variance due to sires × years and reduced estimates of h^2 to 0.15 and 0.20 for Polled Herefords and Wokalups, respectively, while the remaining parameters were little affected.

Field data

Estimates from analyses of the other 5 data sets are given in Table 4. In all cases, the most parameterised model (7^β) fitted best, but there were distinct differences in the relative importance of genetic and environmental correlations between dams and offspring.

Results for both Polled Herefords and Herefords followed the same pattern. Estimates of the regression on maternal phenotype were negative, amounting up to 20%. This and the estimate of -0.13 for Polled Herefords in the Wokalup selection experiment agreed with Koch (1972) who thought that β was of the order of -0.1 to -0.2 for gain of beef calves from birth to weaning. Ignoring β but allowing for a direct-maternal genetic covariance (Model 6) resulted in substantial, negative estimates for σ_{AM}. Results indicate that most of the direct-maternal covariance in Herefords is environmental rather than genetic. This substantiates earlier, more speculative explanations for a large negative estimate for σ_{AM} observed repeatedly for field data. This is confirmed by results from fitting Model 6^β : Estimates of β were only slightly reduced (in absolute value) compared to those under Model 5^β, while estimates of σ_{AM} though negative, amounted to only 5 to 8% of the phenotypic variance, resulting in estimates of the direct-maternal genetic correlation (r_{AM}) of -0.36 to -0.24.

Allowing for a direct-maternal covariance (either kind), increased estimates of both the direct (h^2) and maternal (m^2) heritability (Models 5^β, 6 and 6^β compared to Model 5), while fitting a regression on maternal phenotype tended to reduce the estimate of the permanent environmental, maternal variance. As shown above (7), estimates of the phenotypic variance depend on β, i.e. are not directly comparable across models as they were for models not fitting β. Estimates for Polled Herefords were similar to those obtained earlier under Models 5 and 6 considering a subset of the data utilised here and carrying out analyses for 1–3 herds at a time (Meyer, 1993).

Fitting a sire × herd-year 'interaction' as an additional random effect (Model 7 and 7^β) resulted in a substantial increase in likelihood, accompanied by a reduction in estimates of the direct and, to a lesser extent, also maternal heritabilities compared to Models 6 and 6^β as well as the magnitude (absolute value) of σ_{AM}. In contrast, estimates of the permanent environmental maternal effects (c^2) and the regression on maternal phenotype were virtually unchanged. Estimates of the sire × herd-year effects (s^2) amounted to about 4% of the phenotypic variance.

For Angus and Limousin, maternal phenotypes proved to be considerably less important than for (Polled) Herefords. There was a substantially larger increase in log $\mathcal{L}$ due to adding an extra parameter from Model 5^β to 6^β than from 6 to 6^β, suggesting that Model 6 fitted the data better than Model 5^β. As observed for the Hereford data sets, there was some cross-substitution between parameters, i.e fitting β only (Model 5^β) resulted in sizable, negative estimates for β. Fitting β over and above σ_{AM} though (Model 6^β versus Model 6), resulted in slightly reduced estimates (absolute value) of σ_{AM} only for Angus which were accompanied by small, negative estimates for β (-0.03 to -0.04). For Limousins, the corresponding reduction in magnitude of σ_{AM} was somewhat larger with an estimate of β close to -0.1. This gave moderately strong, negative estimates of r_{AM} under Model 6^{β} of -0.56, -0.45 and -0.51, for Australian Angus, New Zealand Angus and Limousins, respectively. Again, allowing for σ_{AM} resulted in a marked increase in estimates for h^2 and m^2, while c^2 was little affected.

Augmenting the model of analysis by a sire × herd-year effect resulted in a dramatic increase in $\log \mathcal{L}$ for these data sets, substantially more than due to allowing for a non-zero σ_{AM} or β. Estimates of s^2 were 7%, 4% and 9 % for Australian Angus, New Zealand Angus and Limousin, respectively. Notter *et al.* (1992) reported estimates of a sire × herd interaction for weaning weight of Australian Angus of 3.3% to 6.2%. Considering a subset of only 5 herds of the data used here (Australian Angus) and omitting a maternal permanent environmental effect, Robinson (1996) obtained estimates of h^2, m^2, s^2 and r_{AM} for weaning weight of 0.11, 0.25, 0.11 and 0.014, respectively, compared to estimates of 0.29 (h^2), 0.14 (m^2) and -0.52 (r_{AM}) under Model 6.

Table 5 summarises estimates of regression coefficients on age of dam and age at weighing together with estimates for the "heifer factor" for the Hereford and Angus data sets. Overall, differences between estimates under different models of analyses were small. Allowing for a direct-maternal covariance (either σ_{AM} or β) tended to reduce the magnitude of the regression coefficients, both linear and quadratic, on age of dam somewhat as well as reducing the estimate of the "heifer factor" slightly.

Discussion

As in previous studies, results identify clear breed differences in the relative importance of genetic and environmental maternal effects on weaning weight in beef cattle. In particular, for Herefords there appears to be a substantial direct-maternal environmental covariance resulting in estimates of the regression on maternal phenotype between -0.1 and -0.2.

Fitting the regression on maternal phenotype alleviated the problem of inexplicably large (absolute value), negative estimates of σ_{AM} to a large extent in (Polled) Herefords. However, it had comparatively little effect in the Angus and Limousin data sets. Fitting a sire × herd-year interaction as an additional effect resulted in a dramatic increase in likelihood in all cases. This was accompanied by reduction in magnitude of estimates of σ_{AM} (absolute value) as well as of h^2 and m^2. This suggests that inflated estimates of σ_{AM} might have been caused, to some extent at least, by unaccounted sources of variation, such as paddocks or management groups, inflating the covariance between paternal sibs in a contemporary group.

Other factors contributing to an apparent sire × herd-year interaction might be heterogeneous variances. In dairy cattle, Meyer (1987) demonstrated a considerable reduction in estimates of s^2 when standardising data. Notter *et al.* (1992) found a similar effect on estimates of a sire × herd variance for weaning weight in Australian Angus. Alternatively, σ^2_{SH} might reflect variation between sires due to different genetic origins (Robinson, 1996), e.g. due to importation of bulls or semen. For Australian Angus in particular, there has been considerable import of genetic material from New Zealand and North America (c.f. Meyer, 1995).

Analyses of experimental data ignoring paddock effects clearly illustrate the effects of missing information or erroneous models on estimates of genetic parameters for maternal effects. With very high sampling correlations between parameters, even slight biases of some covariances between relatives can affect estimates dramatically.

Acknowledgments

This work was supported by grant UNE35 of the Australian Meat Research Corporation (MRC).

References

Baker, R.L 1980. The role of maternal effects on the efficiency of selection in beef cattle : a review. *Proc. N.Z. Soc. Anim. Prod.* **40** : 285–303.

Cundiff, L.V. 1972. The role of maternal effects in animal breeding : VIII. Comparative aspects of maternal effects. *J. Anim. Sci.* **35** : 1335–1337.

Falconer, D.S 1965. Maternal effects and selection response. Genetics Today, S.J. Geerts (ed.), Pergamon Press, New York.

Foulley, J.L. and Lefort, G. 1978. Méthodes d'estimation des effects directs et maternels en sélection animale. *Ann. Génét. Sél. Anim.* **10** : 475–496.

Graser, H.-U., Smith, S.P. and Tier, B. 1987. A derivative-free approach for estimating variance components in animal models by Restricted Maximum Likelihood. *J. Anim. Sci.* **64** : 1362–1370.

Johnson, D.L. and Thompson, R. 1995. Restricted Maximum Likelihood estimation of variance components for univariate animal models using sparse matrix techniques and average information. *J. Dairy Sci.* **78** : 449–456.

Johnsson, I.D. and Morant, S.V. 1984. Evidence of a negative relationship between heifer growth and first calf weaning weight in commercial beef herds. *J. Aust. Exp. Agric. Anim. Husb.* **24** : 10–14.

Henderson, C.R. 1976. A simple method for computing the inverse of a numerator relationship matrix used in prediction of breeding values. *Biometrics* **32** : 69–83.

Koch, R.M. 1972. The role of maternal effects in animal breeding : VI. Maternal effects in beef cattle. *J. Anim. Sci.* **35** : 1316–1323.

Koerhuis, A.N.M. and Thompson, R. 1997. Models to estimate maternal effects for juvenile body weight in broiler chickens. *Genet. Select. Evol.* **29** : 225–249.

Meyer, K 1987. Estimates of variances due to sire x herd interactions and environmental covariances between paternal half-sibs for first lactation dairy production. *Livest. Prod. Sci.* **17** : 95–115.

Meyer, K. 1989. Restricted Maximum Likelihood to estimate variance components for animal models with several random effects using a derivative-free algorithm. *Genet. Select. Evol.* **21** : 317–340.

Meyer, K. 1992. Bias and sampling covariances of estimates of variance components due to maternal effects. *Genet. Select. Evol.* **24** : 487–509.

Meyer, K. 1993. Estimating covariance matrices for growth traits of Australian Polled Hereford cattle using field data. *Anim. Prod.* **57** : 37–45.

Meyer, K. 1995. Estimates of genetic parameters and breeding values for New Zealand and Australian Angus cattle. *Aust. J. Agric. Res.* **46** : 1219–1229.

Meyer, K., Carrick, M.J. and Donnelly, B.J.P. 1993. Genetic parameters for growth traits of Australian beef cattle from a multi-breed selection experiment. *J. Anim. Sci.* **71** : 2614–2622.

Nelder, J.A. and Mead, R. 1965. A simplex method for function minimization. *Computer J.* **7** : 147–151.

Notter, D.R., Tier, B. and Meyer, K. 1992. Sire X herd interactions for weaning weight in beef cattle. *J. Anim. Sci.* **70** : 2359–2365.

Powell, M.J.D. 1965. An efficient method for finding the minimum of a function of several variables without calculating derivatives. *Computer J.* **7** : 155–162.

Robinson, D.L. 1996. Estimation and interpretation of direct and maternal genetic parameters for weights of Australian Angus cattle. *Livest. Prod. Sci.* **45** : 1–11.

Thompson, R. 1976. The estimation of maternal genetic variance. *Biometrics* **32** : 903–917.

Willham, R.L. 1963. The covariance between relatives for characters composed of components contributed by related individuals. *Biometrics* **19** : 18–27.

Willham, R.L. 1980. Problems in estimating maternal effects. *Livest. Prod. Sci.* **7** : 405–418.

Table 3 : Estimates of genetic parameters[a], residual (σ^2_E) and phenotypic (σ^2_P) variance for weaning weight of calves in the Wokalup selection experiment.

Model[b]	β	h^2	m^2	c_{AM}	r_{AM}	c^2	s^2	p^2	σ^2_E	σ^2_P	log $\mathcal{L}$[c]
	Polled Herefords										
	Fitting year × paddock as fixed effect										
2		0.223				0.316			352.8	764.9	-7.21
2^{β}	0.021	0.218				0.320			355.5	761.9	-7.10
5		0.195	0.143			0.193			362.2	772.7	-1.03
5^{β}	-0.048	0.199	0.165			0.168			354.8	790.0	-0.39
6		0.213	0.176	-0.048	-0.248	0.195			355.5	765.5	-0.15
6^{β}	-0.030	0.212	0.181	-0.036	-0.184	0.179			252.7	776.2	0
	Omitting year × paddock										
6		0.389	0.373	-0.295	-0.774	0.165			294.8	800.5	-1.99
6^{β}	-0.133	0.357	0.331	-0.188	-0.547	0.110			289.2	841.8	0
7		0.202	0.257	-0.159	-0.698	0.179	0.090		346.4	803.3	14.32
7^{β}	-0.129	0.186	0.231	-0.074	-0.357	0.122	0.090		338.6	845.6	17.61
7a		0.222	0.240	-0.135	-0.585	0.167		0.159	288.1	828.9	109.76
$7a^{\beta}$	-0.132	0.206	0.214	-0.061	-0.291	0.118		0.155	278.7	876.7	114.77
8		0.169	0.217	-0.104	-0.543	0.171	0.025	0.152	304.4	824.1	112.07
8^{β}	-0.135	0.150	0.192	-0.031	-0.183	0.122	0.024	0.151	297.2	873.5	117.26
	Wokalups										
	Fitting year × paddock as fixed effect										
2		0.316				0.150			425.7	793.3	-6.35
2^{β}	0.085	0.286				0.157			444.8	772.5	-3.79
5		0.294	0.071			0.096			430.1	797.3	-2.61
5^{β}	0.068	0.277	0.062			0.107			444.9	777.4	-0.90
6		0.307	0.075	-0.016	-0.105	0.099			425.2	795.4	-2.52
6^{β}	0.095	0.313	0.080	-0.057	-0.360	0.121			431.3	771.4	0
	Omitting year × paddock										
6		0.361	0.122	-0.087	-0.415	0.110			374.3	757.0	-0.88
6^{β}	0.086	0.372	0.141	-0.149	-0.651	0.131			377.4	740.3	0
7		0.194	0.055	0.022	0.213	0.101	0.093		411.9	769.0	20.40
7^{β}	0.034	0.189	0.058	0.003	0.029	0.111	0.094		418.1	756.6	20.59
7a		0.242	0.056	0.016	0.137	0.101		0.133	360.6	795.9	73.43
$7a^{\beta}$	0.025	0.241	0.056	0.004	0.034	0.107		0.134	360.6	795.9	73.56
8		0.186	0.047	0.046	0.492	0.096	0.030	0.121	375.3	792.1	77.07
8^{β}	0.019	0.182	0.046	0.039	0.426	0.102	0.030	0.122	379.5	784.3	77.13

[a] h^2: direct heritability, m^2: maternal heritability, c_{AM}: direct-maternal genetic covariance as proportion of the phenotypic variance, c^2: permanent environmental maternal variance as proportion of the phenotypic variance, s^2: variance due to sire × year effect as proportion of the phenotypic variance, p^2: variance due to paddock × year effect as proportion of the phenotypic variance, and β : regression on maternal phenotype

[b] of analysis, see text for explanation

[c] log likelihood, expressed as deviation from log $\mathcal{L}$ under Model 6^{β}

Table 4 : Estimates of genetic parameters[a], residual (σ_E^2) and phenotypic (σ_P^2) variance for weaning weight of (Polled) Hereford, Angus and Limousin calves (field data).

Model[b]	β	h^2	m^2	c_{AM}	r_{AM}	c^2	s^2	σ_E^2	σ_P^2	log $\mathcal{L}$[c]
Polled Herefords										
5		0.155	0.112			0.266		327.6	701.8	-360.41
5^β	-0.171	0.192	0.142			0.218		270.2	736.8	-196.22
6		0.251	0.225	-0.153	-0.642	0.263		291.4	703.7	-247.43
6^β	-0.157	0.240	0.193	-0.077	-0.357	0.223		262.7	728.5	-155.85
7		0.163	0.190	-0.102	-0.582	0.265	0.040	311.9	701.1	-92.89
7^β	-0.155	0.162	0.168	-0.038	-0.230	0.224	0.038	281.9	725.8	0
Herefords										
5		0.165	0.105			0.232		358.0	718.2	-564.66
5^β	-0.195	0.228	0.138			0.170		279.6	772.8	-268.39
6		0.283	0.210	-0.159	-0.650	0.231		313.0	720.0	-419.95
6^β	-0.186	0.272	0.168	-0.051	-0.241	0.173		268.8	767.6	-249.04
7		0.176	0.170	-0.098	-0.564	0.233	0.045	338.2	717.2	-182.79
7^β	-0.188	0.172	0.138	-0.003	-0.022	0.175	0.045	294.3	763.8	0
Angus - Australia										
5		0.239	0.092			0.148		272.5	523.1	-673.31
5^β	-0.089	0.272	0.102			0.125		250.4	543.2	-598.30
6		0.387	0.181	-0.165	-0.625	0.154		232.8	525.5	-496.52
6^β	-0.035	0.384	0.171	-0.144	-0.562	0.146		230.5	529.9	-490.18
7		0.220	0.130	-0.077	-0.456	0.156	0.071	262.2	523.7	-7.83
7^β	-0.037	0.222	0.123	-0.059	-0.359	0.147	0.070	258.6	528.7	0
Angus - New Zealand										
5		0.180	0.082			0.144		333.9	561.9	-168.48
5^β	-0.076	0.207	0.095			0.125		315.1	577.6	-139.51
6		0.256	0.145	-0.100	-0.519	0.147		311.1	563.2	-114.25
6^β	-0.032	0.256	0.138	-0.084	-0.445	0.139		308.5	567.2	-111.57
7		0.144	0.111	-0.042	-0.329	0.150	0.038	335.7	560.3	-3.23
7^β	-0.033	0.147	0.109	-0.029	-0.230	0.140	0.037	332.5	564.6	0
Limousin										
5		0.252	0.117			0.159		290.7	615.5	-74.53
5^β	-0.130	0.286	0.131			0.132		243.3	635.4	-57.57
6		0.400	0.264	-0.210	-0.647	0.160		241.4	624.1	-47.72
6^β	-0.093	0.392	0.231	-0.153	-0.509	0.141		226.9	632.5	-43.19
7		0.225	0.201	-0.113	-0.532	0.159	0.086	280.2	632.6	-5.07
7^β	-0.099	0.224	0.172	-0.060	-0.304	0.137	0.085	262.3	642.7	0

[a] h^2: direct heritability, m^2: maternal heritability, c_{AM}: direct-maternal genetic covariance as proportion of the phenotypic variance, c^2: permanent environmental maternal variance as proportion of the phenotypic variance, s^2: variance due to sire × year effects as proportion of the phenotypic variance, and β : regression on maternal phenotype

[b] of analysis; see text for explanation

[c] log likelihood, as deviation from model 7^β

Table 5 : Estimates of regression coefficients on dam age (in kg/year and kg/year^2, respectively) and age at weighing within sex (in kg/day), and the estimated difference in weight of calves of cows over that of calves of heifers ("heifer factor"; in kg) for weaning weight of Hereford and Angus calves.

Model[a]	Dam age		Age at weaning			Heifer
	linear	quadratic	heifers	bulls	steers	factor
			Polled Herefords			
5	3.5068	-0.8128	0.7424	0.8054	0.7579	8.24
5^{β}	3.3944	-0.7994	0.7437	0.8039	0.7561	7.84
6	3.3057	-0.7895	0.7420	0.8027	0.7563	7.67
6^{β}	3.2900	-0.7874	0.7432	0.8029	0.7552	7.60
7	3.2391	-0.7767	0.7420	0.8043	0.7515	7.37
7^{β}	3.2191	-0.7735	0.7433	0.8047	0.7509	7.24
			Herefords			
5	4.5877	-0.7943	0.6660	0.7605	0.5596	10.73
5^{β}	4.4765	-0.7865	0.6682	0.7590	0.5522	10.48
6	4.3594	-0.7749	0.6646	0.7586	0.5514	10.43
6^{β}	4.4092	-0.7800	0.6676	0.7586	0.5501	10.40
7	4.2703	-0.7660	0.6657	0.7558	0.5514	10.36
7^{β}	4.3048	-0.7630	0.6881	0.7556	0.5501	10.29
			Angus (Australia)			
5	3.3850	-0.5882	0.7626	0.8497	0.7314	10.37
5^{β}	3.3537	-0.5880	0.7619	0.8496	0.7297	10.29
6	3.1834	-0.5739	0.7595	0.8464	0.7278	10.07
6^{β}	3.1933	-0.5750	0.7595	0.8465	0.7276	10.08
7	3.0342	-0.5519	0.7582	0.8430	0.7251	10.00
7^{β}	3.0442	-0.5529	0.7582	0.8432	0.7250	9.99
			Angus (New Zealand)			
5	2.6714	-0.5473	0.8312	0.8914	0.5614	9.04
5^{β}	2.6385	-0.5471	0.8331	0.8923	0.5713	9.07
6	2.5646	-0.5390	0.8311	0.8910	0.5642	8.97
6^{β}	2.5664	-0.5398	0.8318	0.8913	0.5670	9.00
7	2.5240	-0.5316	0.8324	0.8938	0.5663	9.14
7^{β}	2.5272	-0.5324	0.830	0.8942	0.5701	9.17

[a] of analysis; see text for explanation