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Parameter Estimates for Direct, Maternal, and Grandmaternal Genetic Effects for Birth Weight and Weaning Weight in Hereford Cattle¹

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ABSTRACT: Birth and weaning weights adjusted for age of dam from four lines of Hereford cattle were analyzed to determine the relationships among grandmaternal, maternal, and direct genetic effects. Three lines were selected for 1) weaning weight (WWL), 2) yearling weight (YWL), and 3) an index of yearling weight and muscle score (IXL). The fourth line was an unselected control line (CTL). Numbers of observations ranged from 1,699 (CTL) to 2,811 (WWL), and number of animals in the pedigree file ranged from 2,266 to 3,192. Two animal models were used to obtain estimates by REML using an average information method. Model 1 included random direct and maternal genetic, permanent maternal environmental, and residual environmental effects, and fixed sex \times year effects. Model 2 additionally included random grandmaternal genetic and permanent grandmaternal environmental effects. For birth weight, Models 1 and 2 gave almost identical estimates for direct and maternal heritability, and for the fraction of variance that was due to maternal permanent environmental effects. Estimates for grandmaternal heritability could

be obtained only for IXL (.03) and CTL (.01). For weaning weight, estimates for direct heritability were similar from both models. Estimates for maternal heritability from Model 1 were .18, .20, .13, and .20, and corresponding estimates from Model 2 were .34, .31, .13, and .34 for WWL, YWL, IXL, and CTL, respectively. For IXL, estimates for variances that were due to grandmaternal genetic and grandmaternal permanent environmental variances could not be obtained and were set to zero. Grandmaternal heritability estimates for WWL, YWL, and CTL were .05, .09, and .12. Estimates of correlations between direct and maternal genetic effects were $-.13$, $-.44$, $-.11$, and $-.26$ for WWL, YWL, IXL, and CTL. Estimates of correlations between direct and grandmaternal genetic effects were .21, .83, and .55, and those between maternal and grandmaternal genetic effects were $-.99$, $-.84$, and $-.76$ for WWL, YWL, and CTL, respectively. These results indicate that grandmaternal effects may be important for weaning weight and that maternal heritability may be underestimated if grandmaternal effects are not included in the model.

Key Words: Beef Cattle, Growth, Genetic Parameters

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Introduction

Some traits of beef cattle have long been known to be affected by maternal effects (e.g., birth and weaning weights). For these traits, a random mater-

nal effect is recommended in models for genetic evaluation (BIF, 1996). Early on, rather complex models were found necessary to fully explain these traits. Koch and Clark (1955) presented a path diagram including the maternal granddam to illustrate the correlation between offspring and dam. Willham (1963) mentioned the possible influence of a grandmaternal effect. He suggested that the maternal effect of a dam may be affected by the maternal effect of the granddam. Falconer (1965) proposed the maternal effect as a linear function of a mother's phenotypic value influenced by all maternal ancestors. An example often given for a grandmaternal effect is the so-called fatty udder syndrome. A granddam with a superior maternal ability overfeeds her daughter, and thereby development of her daughter's udder tissue is inhibited such that the maternal ability of

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Table 1. Characteristics of the data

Line ^a	Records	Sires	Dams	Granddams	Records without granddam
WWL	2,811	92	791	466	66
YWL	2,706	95	783	465	65
IXL	2,752	95	766	446	70
CTL	1,699	91	631	436	14

^aWWL = weaning wt, YWL = yearling wt, IXL = index of yearling wt and muscle score, CTL = control line.

the daughter is below average (Totusek et al., 1971). Among others, Willham (1972), Koch (1972), Baker (1980), and Cantet et al. (1988) were concerned that a negative influence of dams on their daughters' maternal ability, which is often discussed in terms of a negative dam-offspring correlation, may cause a negative bias in the covariance between direct and maternal effects. Animal models used to analyze maternally influenced traits typically include direct and maternal effects and the covariance between them, and a permanent environmental effect of the dam (e.g., Waldron et al., 1993, Robinson, 1996). Meyer (1992), who also used such a model, considered it to be suboptimal and pointed out that modeling of maternal effects in beef traits needed to be improved. Objectives of this study were to estimate grandmaternal effects for birth and weaning weights in Hereford cattle and to compare models including maternal effects with and without grandmaternal effects.

Materials and Methods

Data for this analysis were from a long-term selection experiment that began at Fort Robinson and concluded at USMARC, both in Nebraska (Koch et al., 1994). Starting with the formation of lines in 1960, three lines of Hereford cattle were selected for weaning weight (**WWL**), yearling weight (**YWL**), and an index of yearling weight and muscle score (**IXL**). Another line was established in 1969 as an unselected control line (**CTL**). Records were from 1960 through 1985. Numbers of animals with records in the selected lines ranged from 2,702 to 2,811. In CTL, there were 1,699 animals with records. Parents without records were added to the pedigree file so that the total number of animals was from 3,106 to 3,192 in the selected lines and 2,266 in the control line. Numbers of sires, dams, and granddams in each line are given in Table 1. Traits analyzed were birth weight and weaning weight, which was calculated as birth weight plus 200 times average daily gain to weaning. Records were standardized (Koch et al., 1994) and adjusted for age of dam. All animals had their birth and weaning weights recorded. Two single-trait animal models were used for this analysis. Model 1 was the same model as used by Koch et al. (1994):

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{W}_1\mathbf{p} + \mathbf{e}$$

Model 2 was based on Model 1 and was extended to include grandmaternal effects:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{Z}_3\mathbf{g} + \mathbf{W}_1\mathbf{p} + \mathbf{W}_2\mathbf{q} + \mathbf{e}$$

where \mathbf{y} is an $N \times 1$ vector of observations; \mathbf{b} is the vector of fixed effects (sex \times year); \mathbf{a} , \mathbf{m} , and \mathbf{g} are vectors of breeding values for direct genetic, maternal genetic, and grandmaternal genetic effects; \mathbf{p} and \mathbf{q} are vectors of permanent maternal environmental and permanent grandmaternal environmental effects; \mathbf{e} is the vector of random error effects; and \mathbf{X} , \mathbf{Z}_1 , \mathbf{Z}_2 , \mathbf{Z}_3 , \mathbf{W}_1 , and \mathbf{W}_2 are known incidence matrices that relate observations to their respective fixed and random effects. Matrices \mathbf{Z}_1 , \mathbf{Z}_2 , and \mathbf{Z}_3 were augmented for animals without records that were included in the relationship matrix.

For both models,

$$E[\mathbf{y}] = \mathbf{Xb}$$

The (co)variance structure of the random effects for

$$\text{Model 2 was } \mathbf{V} \begin{bmatrix} \mathbf{a} \\ \mathbf{m} \\ \mathbf{g} \\ \mathbf{p} \\ \mathbf{q} \\ \mathbf{e} \end{bmatrix} = \mathbf{B} =$$

$$\begin{bmatrix} \mathbf{A}\sigma_a^2 & \mathbf{A}\sigma_{am} & \mathbf{A}\sigma_{ag} & 0 & 0 & 0 \\ \mathbf{A}\sigma_{am} & \mathbf{A}\sigma_m^2 & \mathbf{A}\sigma_{gm} & 0 & 0 & 0 \\ \mathbf{A}\sigma_{ag} & \mathbf{A}\sigma_{gm} & \mathbf{A}\sigma_g^2 & 0 & 0 & 0 \\ 0 & 0 & 0 & \mathbf{I}_{N_d}\sigma_p^2 & 0 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{I}_{N_g}\sigma_q^2 & 0 \\ 0 & 0 & 0 & 0 & 0 & \mathbf{I}_N\sigma_e^2 \end{bmatrix}$$

where N_d and N_g are numbers of dams and granddams, respectively, and N is number of records; \mathbf{A} is the numerator relationship matrix among animals in

the pedigree file, and the \mathbf{I} matrices are identity matrices. Let $\mathbf{Z} = [\mathbf{Z}_1|\mathbf{Z}_2|\mathbf{Z}_3]$, $\mathbf{W} = [\mathbf{W}_1|\mathbf{W}_2]$, $\mathbf{u}' = [\mathbf{a}'|\mathbf{m}'|\mathbf{g}']$, $\mathbf{c}' = [\mathbf{p}'|\mathbf{q}']$, $\mathbf{V}(\mathbf{u}) = \mathbf{G}$, $\mathbf{V}(\mathbf{c}) = \mathbf{Q}$, and $\mathbf{V}(\mathbf{e}) = \mathbf{R}$ so that $\mathbf{V}(\mathbf{y}) = \mathbf{V} = \mathbf{ZGZ}' + \mathbf{WQW}' + \mathbf{R}$.

Model 2 required each animal with a record to have a granddam. Therefore, unique "dummy" granddams were used for records with the granddam unknown (Table 1). All dams were known and if unrelated as assumed at the initiation of the experiment, then the dummy granddams are unique but with a different identification than what they might have had originally.

Estimation of Covariance Components

Estimates by REML of (co)variances were obtained using an average information (\mathbf{AvI}) algorithm as proposed by Johnson and Thompson (1995). Johnson and Thompson (1995) compared AvI REML with other methods and in their example found it to reach convergence five times faster than with a derivative-free algorithm and 15 times faster than with an expectation-maximization algorithm. As with the Newton-Raphson method and Fisher's method of scoring, this algorithm is a Newton method that uses first and second derivatives to find estimates of genetic parameters that maximize the likelihood function. The logarithm of the restricted maximum likelihood function is (e.g., Graser et al., 1987)

$$L = -\frac{1}{2}[\text{constant} + \ln|\mathbf{V}| + \ln|\mathbf{X}'\mathbf{V}^{-1}\mathbf{X}| + \mathbf{y}'\mathbf{P}\mathbf{y}]$$

where

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

The Newton-Raphson method uses the matrix of second derivatives (Hessian, \mathbf{H}) to maximize the likelihood function where, at the $m + 1$ st iteration,

$$\theta^{m+1} = \theta^m - (\mathbf{H}^m)^{-1}\mathbf{k}^m$$

where θ is the vector of parameters and \mathbf{k} is the vector of first derivatives of the likelihood function (the gradient or score function) for which the i^{th} element can be written as

$$k_i = \frac{\partial L}{\partial \theta_i} = -\frac{1}{2}\left[\text{tr}\left(\mathbf{P}\frac{\partial \mathbf{V}}{\partial \theta_i}\right) - \mathbf{y}'\mathbf{P}\frac{\partial \mathbf{V}}{\partial \theta_i}\mathbf{P}\mathbf{y}\right]$$

In Fisher's method of scoring (e.g., Searle et al., 1992) \mathbf{H} is replaced by its expected value, $E[\mathbf{H}]$:

$$\theta^{m+1} = \theta^m - (E[\mathbf{H}^m])^{-1}\mathbf{k}^m$$

where $-E[\mathbf{H}]$ is also called an *information matrix*. The matrices \mathbf{H} and $E[\mathbf{H}]$ can be written (Searle et al., 1992) as

$$\mathbf{H} = \frac{\partial^2 L}{\partial \theta_i \partial \theta_j} = \frac{1}{2}\text{tr}\left(\mathbf{P}\frac{\partial \mathbf{V}}{\partial \theta_i}\mathbf{P}\frac{\partial \mathbf{V}}{\partial \theta_j}\right) - \mathbf{y}'\mathbf{P}\frac{\partial \mathbf{V}}{\partial \theta_i}\mathbf{P}\frac{\partial \mathbf{V}}{\partial \theta_j}\mathbf{P}\mathbf{y}$$

and

$$E[\mathbf{H}] = E\left[\frac{\partial^2 L}{\partial \theta_i \partial \theta_j}\right] = -\frac{1}{2}\text{tr}\left(\mathbf{P}\frac{\partial \mathbf{V}}{\partial \theta_i}\mathbf{P}\frac{\partial \mathbf{V}}{\partial \theta_j}\right)$$

Both the Hessian and its expected value include terms that are computationally demanding to calculate. Johnson and Thompson (1995) noticed that the trace parts drop out if the two expressions are averaged:

$$\mathbf{AvI} = \frac{1}{2}(\mathbf{H} + E[\mathbf{H}]) = -\frac{1}{2}\mathbf{y}'\mathbf{P}\frac{\partial \mathbf{V}}{\partial \theta_i}\mathbf{P}\frac{\partial \mathbf{V}}{\partial \theta_j}\mathbf{P}\mathbf{y}$$

Taking advantage of algebraic simplifications (Johnson and Thompson, 1995) makes the average information matrix feasible to compute in some cases. A matrix $\mathbf{F} = \{\mathbf{f}_i\}$, $i = 1, \dots, r$ of order $N \times r$ is defined, where r is the number of elements in θ , and the general vector \mathbf{f}_i is

$$\mathbf{f}_i = \frac{\partial \mathbf{V}}{\partial \theta_i}\mathbf{P}\mathbf{y} = \mathbf{Z}\frac{\partial \mathbf{G}}{\partial \theta_i}\mathbf{G}^{-1}\hat{\mathbf{u}} + \mathbf{W}\frac{\partial \mathbf{Q}}{\partial \theta_i}\mathbf{Q}^{-1}\hat{\mathbf{c}} + \frac{\partial \mathbf{R}}{\partial \theta_i}\mathbf{R}^{-1}\hat{\mathbf{e}}$$

where $\hat{\mathbf{u}}$ is the solution vector of the direct, maternal, and grandmaternal additive genetic effects, $\hat{\mathbf{c}}$ is the solution vector of the permanent maternal and grandmaternal environmental random effects, and $\hat{\mathbf{e}}$ is the solution vector of the residual effects. The average information matrix can be rewritten as

$$\mathbf{AvI} = -\mathbf{F}'\mathbf{P}\mathbf{F} = -\frac{1}{2}\left(\mathbf{F}'\mathbf{R}^{-1}\mathbf{F} - \begin{bmatrix} \hat{\mathbf{b}}_F \\ \hat{\mathbf{u}}_F \\ \hat{\mathbf{c}}_F \end{bmatrix}' \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{F} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{F} \\ \mathbf{W}'\mathbf{R}^{-1}\mathbf{F} \end{bmatrix}\right)$$

To obtain $\hat{\mathbf{b}}_F$, the solution vector for the fixed effects, $\hat{\mathbf{u}}_F$, and $\hat{\mathbf{c}}_F$ the MME are solved r times with the \mathbf{f}_i replacing \mathbf{y} , where MME are Henderson's mixed model equations (Henderson, 1975) corresponding to the mixed linear model [Model 2] and $\mathbf{V}(\mathbf{y})$.

Calculation of the first derivatives is shown for Model 2 where \mathbf{k} has 10 elements. Six of the elements in \mathbf{k} are first derivatives with respect to additive genetic (co)variances. Using expressions from Johnson and Thompson (1995) and Madsen et al. (1994), they are calculated as

$$\begin{bmatrix} \mathbf{k}_1 & 1/2\mathbf{k}_2 & 1/2\mathbf{k}_3 \\ 1/2\mathbf{k}_2 & \mathbf{k}_4 & 1/2\mathbf{k}_5 \\ 1/2\mathbf{k}_3 & 1/2\mathbf{k}_5 & \mathbf{k}_6 \end{bmatrix} = \frac{1}{2}(\mathbf{G}_0^{-1}(\mathbf{T} + \mathbf{S})\mathbf{G}_0^{-1} - N_a\mathbf{G}_0^{-1})$$

where N_a is the number of animals in the pedigree file, and \mathbf{G}_0 is the (co)variance matrix of the additive genetic effects:

$$\mathbf{G}_0 = \begin{bmatrix} \sigma_a^2 & \sigma_{am} & \sigma_{ag} \\ \sigma_{am} & \sigma_m^2 & \sigma_{mg} \\ \sigma_{ag} & \sigma_{mg} & \sigma_g^2 \end{bmatrix}$$

$$\mathbf{T} = \begin{bmatrix} \text{tr}(\mathbf{A}^{-1}\mathbf{C}^{aa}) & \text{tr}(\mathbf{A}^{-1}\mathbf{C}^{am}) & \text{tr}(\mathbf{A}^{-1}\mathbf{C}^{ag}) \\ \text{tr}(\mathbf{A}^{-1}\mathbf{C}^{am}) & \text{tr}(\mathbf{A}^{-1}\mathbf{C}^{mm}) & \text{tr}(\mathbf{A}^{-1}\mathbf{C}^{mg}) \\ \text{tr}(\mathbf{A}^{-1}\mathbf{C}^{ag}) & \text{tr}(\mathbf{A}^{-1}\mathbf{C}^{mg}) & \text{tr}(\mathbf{A}^{-1}\mathbf{C}^{gg}) \end{bmatrix}$$

and

$$\mathbf{S} = \begin{bmatrix} \hat{\mathbf{a}}'\mathbf{A}^{-1}\hat{\mathbf{a}} & \hat{\mathbf{a}}'\mathbf{A}^{-1}\hat{\mathbf{m}} & \hat{\mathbf{a}}'\mathbf{A}^{-1}\hat{\mathbf{g}} \\ \hat{\mathbf{m}}'\mathbf{A}^{-1}\hat{\mathbf{a}} & \hat{\mathbf{m}}'\mathbf{A}^{-1}\hat{\mathbf{m}} & \hat{\mathbf{m}}'\mathbf{A}^{-1}\hat{\mathbf{g}} \\ \hat{\mathbf{g}}'\mathbf{A}^{-1}\hat{\mathbf{a}} & \hat{\mathbf{g}}'\mathbf{A}^{-1}\hat{\mathbf{m}} & \hat{\mathbf{g}}'\mathbf{A}^{-1}\hat{\mathbf{g}} \end{bmatrix}$$

with $\hat{\mathbf{a}}$, $\hat{\mathbf{m}}$, and $\hat{\mathbf{g}}$ are the solution vectors for the direct, maternal, and grandmaternal additive genetic effects, and \mathbf{C}^{aa} , \mathbf{C}^{am} , \mathbf{C}^{ag} , \mathbf{C}^{mm} , and \mathbf{C}^{gg} are submatrices of the inverse of the coefficient matrix, \mathbf{C} . The FSPAK package (Perez-Enciso et al., 1992) was used to calculate this inverse. In FSPAK, an algorithm by Takahashi et al. (1973) is used to compute elements of a sparse matrix inverse corresponding to nonzero elements of the matrix.

The partial derivatives with respect to permanent environmental maternal (\mathbf{k}_7) and permanent environmental grandmaternal variances (\mathbf{k}_9) are calculated as

$$\mathbf{k}_7 = \frac{1}{2} \left[\frac{\text{tr}(\mathbf{C}^{pp}) + \hat{\mathbf{p}}'\hat{\mathbf{p}}}{\sigma_p^4} - \frac{N_d}{\sigma_p^2} \right]$$

and

$$\mathbf{k}_9 = \frac{1}{2} \left(\frac{\text{tr}(\mathbf{C}^{qq}) + \hat{\mathbf{q}}'\hat{\mathbf{q}}}{\sigma_q^4} - \frac{N_g}{\sigma_q^2} \right)$$

where $\hat{\mathbf{p}}$ and $\hat{\mathbf{q}}$ are the solution vectors of permanent environmental maternal and permanent environmental grandmaternal effects, and \mathbf{C}^{pp} and \mathbf{C}^{qq} are submatrices of the inverse of the coefficient matrix, \mathbf{C} . Because the covariance between the permanent environmental effects was assumed to be zero, $\mathbf{k}_8 = 0$.

Finally, the partial derivative with respect to the residual variance is

$$\begin{aligned} \mathbf{k}_{10} &= \frac{1}{2} \left[\frac{\hat{\mathbf{e}}'\hat{\mathbf{e}}}{\sigma_e^4} - \frac{N - \text{tr}(\mathbf{M}\mathbf{R}^{-1}\mathbf{M}\mathbf{C}^{-1})}{\sigma_e^2} \right] \\ &= \frac{1}{2} \left[\frac{\hat{\mathbf{e}}'\hat{\mathbf{e}}}{\sigma_e^4} - \frac{N - (r(\mathbf{X}) + 3N_a + N_d + N_g)}{\sigma_e^2} \right] \\ &\quad - \frac{1}{\sigma_e^2} \left(\frac{\text{tr}(\mathbf{A}^{-1}\mathbf{C}^{aa})}{\sigma_a^2} + \frac{\text{tr}(\mathbf{A}^{-1}\mathbf{C}^{mm})}{\sigma_m^2} + \frac{\text{tr}(\mathbf{A}^{-1}\mathbf{C}^{gg})}{\sigma_g^2} \right) \end{aligned}$$

$$\begin{aligned} &+ \frac{2\text{tr}(\mathbf{A}^{-1}\mathbf{C}^{am})}{\sigma_{am}} + \frac{2\text{tr}(\mathbf{A}^{-1}\mathbf{C}^{ag})}{\sigma_{ag}} + \frac{2\text{tr}(\mathbf{A}^{-1}\mathbf{C}^{mg})}{\sigma_{mg}} \\ &- \frac{1}{\sigma_e^2} \left(\frac{\text{tr}(\mathbf{C}^{pp})}{\sigma_p^2} + \frac{\text{tr}(\mathbf{C}^{qq})}{\sigma_q^2} \right) \end{aligned}$$

where $\mathbf{M} = [\mathbf{X} | \mathbf{Z} | \mathbf{W}]$, $\hat{\mathbf{e}} = \mathbf{y} - \mathbf{X}\hat{\mathbf{b}} - \mathbf{Z}\hat{\mathbf{u}} - \mathbf{W}\hat{\mathbf{c}}$, and $r(\mathbf{X}) = \text{rank of } \mathbf{X}$.

The $m + 1$ st iteration step using the average information matrix (\mathbf{AvI}) is

$$\theta^{m+1} = \theta^m + (\mathbf{AvI}^m)^{-1} \mathbf{k}^m$$

The Euclidian norm of the gradient was used as the convergence criterion. Convergence was assumed to have been reached if the norm was less than 10^{-4} .

Standard Errors of Estimated Parameters

The inverse of the negative average information matrix is an asymptotic dispersion matrix of the estimated parameters, $V(\hat{\theta}) = [-\mathbf{AvI}]^{-1}$. With a Taylor series expansion, variances of functions of random variables can be estimated (e.g., Stuart and Ord, 1994). Let $f(\hat{\theta})$ be a function of the estimated variance components (e.g., a heritability). Then a first-order Taylor series expansion to approach zero is

$$f(\hat{\theta}) \approx f(\theta) + \left\{ \frac{\partial f(\theta)}{\partial \theta'} \right\} (\hat{\theta} - \theta)$$

and the asymptotic variance of $f(\hat{\theta})$ can be estimated as

$$\begin{aligned} V(f(\hat{\theta})) &\approx V(f(\theta) + \left\{ \frac{\partial f(\theta)}{\partial \theta'} \right\} (\hat{\theta} - \theta)) \\ &\approx \left\{ \frac{\partial f(\theta)}{\partial \theta'} \right\} V(\hat{\theta}) \left\{ \frac{\partial f(\theta)}{\partial \theta} \right\} \end{aligned}$$

For example, the vector of partial derivatives of the direct heritability in Model 2 is

$$\begin{aligned} \frac{\partial h^2}{\partial \theta'} &= \\ &\left[\frac{h^2 - h^4}{\sigma_a^2} - \frac{h^4}{\sigma_a^2} - \frac{h^4}{\sigma_a^2} - \frac{h^4}{\sigma_a^2} - \frac{h^4}{\sigma_a^2} - \frac{h^4}{\sigma_a^2} - \frac{h^4}{\sigma_a^2} - \frac{h^4}{\sigma_a^2} - \frac{h^4}{\sigma_a^2} - \frac{h^4}{\sigma_a^2} \right] \mathbf{0} \end{aligned}$$

and the standard error of the estimate of h^2 is calculated as

$$SE(h^2) \approx \sqrt{\left\{ \frac{\partial h^2}{\partial \theta'} \right\} (-\mathbf{AvI})^{-1} \left\{ \frac{\partial h^2}{\partial \theta} \right\}}$$

Table 2. Parameter estimates^a and standard errors (in parentheses) for birth weight

Line ^b	Model 1							Model 2										
	-2logL	h ²	m ²	r _{am}	p ²	e ²	σ _p	-2logL	h ²	m ²	g ²	r _{am}	r _{ag}	r _{mg}	p ²	q ²	e ²	σ _p
WWL ^c	2,096.97	.45 (.068)	.10 (.033)	.15 (.182)	.01 (.020)	.40 (.048)	.98	2,096.97	.45 (.068)	.10 (.033)	—	.15 (.182)	—	—	.01 (.020)	—	.40 (.048)	.98
YWL	1,967.73	.47 (.076)	.09 (.037)	-.07 (.193)	.04 (.023)	.41 (.055)	.96	1,967.65	.47 (.076)	.09 (.037)	—	-.07 (.194)	—	—	.04 (.030)	.01 (.020)	.41 (.054)	.96
IXL	2,130.62	.38 (.066)	.14 (.041)	.15 (.174)	.02 (.023)	.43 (.047)	.99	2,127.68	.39 (.068)	.13 (.053)	.03 (.025)	.20 (.182)	-.30 (.286)	-.01 (.416)	.01 (.033)	—	.43 (.048)	.99
CTL	1,373.66	.39 (.071)	.11 (.035)	.29 (.241)	—	.45 (.054)	1.00	1,372.68	.38 (.073)	.09 (.037)	.01 (.019)	.25 (.256)	.26 (.645)	.39 (.758)	—	—	.45 (.054)	1.00

^ah² = direct heritability, m² = maternal heritability, g² = grandmaternal heritability, r_{am} = genetic correlation between direct and maternal effects, r_{ag} = genetic correlation between direct and grandmaternal effects, r_{mg} = genetic correlation between maternal and grandmaternal effects, p² = fraction of variance due to maternal permanent environmental effects, q² = fraction of variance due to grandmaternal permanent environmental effects, e² = fraction of variance due to temporary environmental effects, σ_p = phenotypic standard deviation.

^bWWL = weaning wt, YWL = yearling wt, IXL = index of yearling wt and muscle score, CTL = control line.

^cModels are identical because parameters for grandmaternal effects failed to converge in the parameter space.

A likelihood ratio test was used to compare the models (Dobson, 1990). Even though Model 2 had potentially five additional (co)variance components compared with Model 1, the difference between the -2L values was assumed to be χ^2 distributed with four degrees of freedom because the covariance between the maternal and grandmaternal permanent environmental effects was assumed to be 0. The critical values for significance are 9.49 ($P < .05$) and 13.28 ($P < .01$).

Results and Discussion

Birth Weight

Parameter estimates for birth weight from Models 1 and 2 for each of the four lines are shown in Table 2. Estimates for WWL and IXL from Model 1 agree well with those obtained by Koch et al. (1994), who analyzed data from the same experiment but from a shorter time span (1960–1982) so that the number of animals in each of the lines was less. Additive genetic heritability (h²) was greater for YWL (.47 vs .43) and for CTL (.39 vs .34) than in Koch et al. (1994), and the correlation between direct and maternal effects (r_{am}) was smaller in CTL (.29 vs .46). For CTL, the fraction of variance that was due to permanent maternal environmental effects (p²) could not be estimated for either Model 1 or 2 (i.e., during the iteration process, the estimate tended to become negative and was therefore set to zero). Meyer (1992) and Waldron et al. (1993) used the same animal model as Model 1 to analyze Hereford data from Australia and New Zealand, respectively. Even though estimates of Meyer (1992) were similar to those in Table 2, Waldron et al. (1993) found a lower direct heritability (.24) and a larger correlation between direct and maternal effects (.37). Results from earlier studies, mostly obtained from sire-maternal grandsire

models, often showed negative correlations between direct and maternal effects (for review, see Meyer (1992)).

In none of the lines could all of the effects additionally fitted in Model 2 be estimated. For WWL, neither the fraction that was due to grandmaternal genetic variance (g²) nor the fraction of variance due to permanent grandmaternal environmental effects (q²) could be estimated so that Model 2 gave the same results as Model 1. When the grandmaternal genetic variance tended to become negative during iteration, it was set to a very small positive value (10⁻⁸) in order to keep **G**₀ positive definite while the appropriate covariances were set to 0. A small q² (.01) was estimated for YWL, but, compared with Model 1, the other estimates were not affected. For IXL, an estimate of g² could be obtained (.03) but not an estimate of q². The estimate of the correlation between the direct and the grandmaternal effects (r_{ag}) was negative (-.30). The correlation (r_{mg}) between maternal and grandmaternal effects was slightly negative (-.01). Compared with Model 1, r_{am} increased from .15 to .20; h², m², and p² changed only slightly; and the fraction of variance due to residual effects (e²) did not change at all. A small g² was also estimated for CTL. The r_{ag} and r_{mg} were positive, .26 and .39, respectively. The estimate of r_{am} decreased from .29 in Model 1 to .25 in Model 2. In this line, neither p² nor q² could be estimated. Likelihood ratio tests showed that the -2L values for Model 2 were not significantly less than those for Model 1.

Results indicate that grandmaternal effects do not play an important role in birth weight. This result agrees with Koch (1972), who concluded that maternal ability of cows was not affected by their dam's maternal ability, whereas Cantet et al. (1988) obtained estimates of -.15 for the path between maternal phenotypes of dam and daughter. Koch

Table 3. Parameter estimates^a and standard errors (in parentheses) for weaning weight

Line ^b	Model 1							Model 2										
	-2logL	h ²	m ²	r _{am}	p ²	e ²	σ _p	-2logL	h ²	m ²	g ²	r _{am}	r _{ag}	r _{mg}	p ²	q ²	e ²	σ _p
WWL	2,202.96	.18 (.051)	.18 (.052)	-.22 (.169)	.24 (.039)	.44 (.038)	1.00	2,190.96 ^c	.18 (.049)	.34 (.102)	.04 (.042)	-.13 (.151)	.20 (.362)	-.99 (.309)	.07 (.068)	.07 (.037)	.43 (.038)	1.01
YWL	1,957.85	.13 (.042)	.20 (.057)	-.35 (.171)	.29 (.041)	.44 (.033)	.98	1,937.49 ^d	.14 (.039)	.31 (.094)	.09 (.051)	-.44 (.148)	.83 (.286)	-.84 (.145)	.16 (.062)	.03 (.042)	.41 (.035)	1.01
IXL ^e	2,346.76	.16 (.045)	.13 (.051)	-.11 (.224)	.29 (.039)	.44 (.035)	1.04	2,346.76	.16 (.045)	.13 (.051)	—	-.11 (.224)	—	—	.29 (.039)	—	.44 (.035)	1.04
CTL	1,273.72	.10 (.042)	.20 (.070)	-.25 (.241)	.28 (.053)	.45 (.038)	.98	1,266.61	.10 (.039)	.34 (.124)	.12 (.068)	-.26 (.221)	.55 (.400)	-.76 (.148)	.15 (.084)	—	.44 (.039)	1.00

^ah² = direct heritability, m² = maternal heritability, g² = grandmaternal heritability, r_{am} = genetic correlation between direct and maternal effects, r_{ag} = genetic correlation between direct and grandmaternal effects, r_{mg} = genetic correlation between maternal and grandmaternal effects, p² = fraction of variance due to maternal permanent environmental effects, q² = fraction of variance due to grandmaternal permanent environmental effects, e² = fraction of variance due to temporary environmental effects, σ_p = phenotypic standard deviation.

^bWWL = weaning wt, YWL = yearling wt, IXL = index of yearling wt and muscle score, CTL = control line.

^cFunction value smaller ($P < .05$) than the function value for Model 1.

^dFunction value smaller ($P < .01$) than the function value for Model 1.

^eModels are identical because parameters for grandmaternal effects failed to converge in the parameter space.

(1972) and Cantet et al. (1988) used Falconer's (1965) concept of a geometric series accounting for all female ancestors.

Weaning Weight

Shown in Table 3 are the parameter estimates for weaning weight for each of the four lines. With Model 1, estimates of h², m², r_{am}, and p² for YWL, IXL, and CTL were similar to those in Koch et al. (1994). For WWL, h² and m² were greater (.18 and .18 vs .13 and .14), and p² was less (.24 vs .29). Estimates of m² were of the same magnitude as h² for WWL and IXL, which is similar to results of Meyer (1992) and Waldron et al. (1993). For YWL and CTL, m² was larger than h² in agreement with Skaar (1985) and Koch et al. (1994) for Herefords.

With Model 2, small to moderate estimates for the variance of grandmaternal effects were estimated for WWL (.04), YWL (.09), and CTL (.12), but for IXL no estimate of g² could be obtained. For CTL, g² was greater than h² (.12 vs .10). Small estimates of q² were found for WWL (.07) and YWL (.03). Direct heritability estimates did not change from Model 1 to Model 2, but maternal heritability was considerably affected. The estimate of m² increased for WWL from .18 to .34, for YWL from .20 to .31, and for CTL from .20 to .34, which indicated that the contribution of maternal effects may be underestimated with Model 1. Correlation between direct and maternal genetic effects decreased (WWL), increased (YWL), and did not change (CTL). Correlations between direct and grandmaternal effects were moderate (.20 for WWL) to high (.83 for YWL). Large negative correlations were found between maternal and grandmaternal effects. Estimates of p² decreased by about the same amount that m² increased. For WWL, p² was of the

same magnitude as q² (.07). The decrease in p² was similar for the three lines regardless of whether an estimate of q² could be obtained. Likelihood ratio tests showed that Model 2 was a significantly better fit to the data than Model 1 for WWL ($P < .05$) and YWL ($P < .01$). For IXL, the likelihood values are identical because the grandmaternal effects became negative and were set to zero, which made Models 1 and 2 identical.

The large negative estimates for r_{mg} suggest that the negative influence of a dam's maternal ability on the maternal ability of her daughter may be even stronger than suspected in the past. Koch (1972) suggested a dam-offspring regression coefficient of -.10 to -.20 for gain from birth to weaning, and Cantet et al. (1988) found a similar value of -.25 for weaning weight. Analyses for other traits (not presented) gave results for gain from birth to weaning similar to weaning weight, and grandmaternal effects did not seem to be important for postweaning gain, final weight, muscle score, and an index of yearling weight and muscle score.

Implications

Results of this study suggest that grandmaternal effects may be important for weaning weight. Estimates of variance that is due to grandmaternal effects are moderate, and correlations with direct and maternal genetic effects are large. Maternal heritability seems to be considerably underestimated if grandmaternal effects are not included in the model but exist. Further research might be necessary to determine whether considerable reranking of animals occurs by using models that include grandmaternal effects.

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