

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

---

Faculty Papers and Publications in Animal  
Science

Animal Science Department

---

May 1999

## Comparison of Models to Estimate Genetic Effects for Weaning Weight of Angus Cattle

J. Dodenhoff

*University of Nebraska-Lincoln*

L. Dale Van Vleck

*University of Nebraska-Lincoln, dvan-vleck1@unl.edu*

D. E. Wilson

*Iowa State University*

Follow this and additional works at: <https://digitalcommons.unl.edu/animalscifacpub>



Part of the [Animal Sciences Commons](#)

---

Dodenhoff, J.; Van Vleck, L. Dale; and Wilson, D. E., "Comparison of Models to Estimate Genetic Effects for Weaning Weight of Angus Cattle" (1999). *Faculty Papers and Publications in Animal Science*. 278.  
<https://digitalcommons.unl.edu/animalscifacpub/278>

This Article is brought to you for free and open access by the Animal Science Department at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Faculty Papers and Publications in Animal Science by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

# Comparison of Models to Estimate Genetic Effects for Weaning Weight of Angus Cattle<sup>1</sup>

J. Dodenhoff<sup>\*,2</sup>, L. D. Van Vleck<sup>†,3</sup>, and D. E. Wilson<sup>\*</sup>

<sup>\*</sup>Department of Animal Science, Iowa State University, Ames 50011 and <sup>†</sup>ARS, USDA, Roman L. Hruska U.S. Meat Animal Research Center, Lincoln, NE 68583-0908

**ABSTRACT:** Weaning weights from nine sets of Angus field data from three regions of the United States were analyzed. Six animal models were used to compare two approaches to account for an environmental dam-offspring covariance and to investigate the effects of sire  $\times$  herd-year interaction on the genetic parameters. Model 1 included random direct and maternal genetic, maternal permanent environmental, and residual effects. Age at weaning was a covariate. Other fixed effects were age of dam and a herd-year-management-sex combination. Possible influence of a dam's phenotype on her daughter's maternal ability was modeled by including a regression on maternal phenotype ( $f_m$ ) (Model 3) or by fitting grandmaternal genetic and grandmaternal permanent environmental effects (Model 5). Models 2, 4, and 6 were based on Models 1, 3, and 5, respectively,

and additionally included sire  $\times$  herd-year (SH) interaction effects. With Model 3, estimates of  $f_m$  ranged from  $-.003$  to  $.014$ , and (co)variance estimates were similar to those from Model 1. With Model 5, grandmaternal heritability estimates ranged from  $.02$  to  $.07$ . Estimates of maternal heritability and direct-maternal correlation ( $r_{am}$ ) increased compared with Model 1. With models including SH, estimates of the fraction of phenotypic variance due to SH interaction effects were from  $.02$  to  $.10$ . Estimates of direct and maternal heritability were smaller and estimates of  $r_{am}$  were greater than with models without SH interaction effects. Likelihood values showed that SH interaction effects were more important than  $f_m$  and grandmaternal effects. The comparisons of models suggest that  $r_{am}$  may be biased downward if SH interaction and/or grandmaternal effects are not included in models for weaning weight.

Key Words: Beef Cattle, Growth, Genetic Parameters

©1999 American Society of Animal Science. All rights reserved.

J. Anim. Sci. 1999. 77:3176–3184

## Introduction

Based on Willham's (1963) model, (co)variance components typically estimated for maternally influenced traits are direct and maternal genetic variances, direct-maternal genetic covariance, variance due to permanent environmental effects of the dam, and residual variance (e.g., Meyer, 1992b; Waldron et al., 1993; Robinson, 1996a). However, the environmental dam-offspring covariance generally is assumed to be zero, making it a "reduced" model (Koerhuis and Thompson, 1997). Problems arising when trying to estimate all

(co)variance components in Willham's model and advantages of the "reduced" model are described by Thompson (1976), Meyer (1992a), and Koerhuis and Thompson (1997). A consequence of neglecting the possible influence of a dam's phenotype on her daughter's maternal ability may be a downward bias in the estimate of the direct-maternal genetic correlation ( $r_{am}$ ) because this influence is suspected to be negative. Falconer (1965) included the dam's phenotype as a linear covariate in his model for litter size in mice. Over-feeding of beef cattle may cause a negative environmental dam-offspring covariance (e.g., Koch, 1972; Willham, 1972; Baker, 1980).

In simulation studies, ignoring additional variance among sires that results from importing new genetic material and sire  $\times$  herd or sire  $\times$  year interaction effects can lead to biased estimates of  $r_{am}$  (Robinson, 1996b; Lee and Pollak, 1997). Meyer (1997a) has reported estimates from beef cattle data using the "reduced" Willham model and models that included a regression on maternal phenotype and sire  $\times$  herd-year interaction effects.

Thus, our objective was to determine how estimates of genetic parameters for weaning weight in beef cattle

<sup>1</sup>Journal paper no. 18220 of the Iowa Agric. and Home Econ. Exp. Sta., Ames. Project no. 3436. The authors gratefully acknowledge the use of data provided by the American Angus Association.

<sup>2</sup>Current address: Bayerische Landesanstalt fuer Tierzucht, 85586 Grub, Germany.

<sup>3</sup>To whom correspondence should be addressed: A218 Animal Sciences, University of Nebraska, Lincoln 68583-0908 (phone: 402/472-6010; fax: 402/472-6362; E-mail: ansc418@unlvm.unl.edu).

Received December 17, 1998.

Accepted May 19, 1999.

are affected if the influence of a dam’s phenotype on her daughter’s maternal ability is accounted for either by regression on maternal phenotype or by grandmaternal effects. Following Lee and Pollak (1997) and Meyer (1997b), the effect on other variance components from fitting sire × herd-year interaction effects was also investigated.

**Materials and Methods**

The American Angus Association provided the data. Weaning weight records from three states (Iowa, Montana, and Nebraska) with more than 150,000 observations each were extracted. Within each of the states, three data sets were created by randomly selecting several complete herds with a minimum of 10 and a maximum of 2,000 records. For each animal in these nine statistically independent data sets, two additional generations of pedigree information, if available, were added. Characteristics of the samples, which included weaning weight records from 1972 through 1996, are given in Table 1.

Each data set was analyzed separately with six single-trait animal models. Age at weaning was fitted as a linear covariate, and age of dam and contemporary group, defined as a combination of herd, year, management, and sex, were fitted as fixed effects. Model 1 was the “reduced” model with the environmental dam-offspring covariance assumed to be zero:

$$y = Xb + Z_1a + Z_2m + W_1p + e$$

where

- y** is a  $N \times 1$  vector of observations;
- b** is the vector of fixed effects;
- a** and **m** are vectors of breeding values for random direct and maternal genetic effects;
- p** is the vector of maternal permanent environmental effects;
- e** is the vector of random error effects; and
- X**, **Z**<sub>1</sub>, **Z**<sub>2</sub>, and **W**<sub>1</sub> are known incidence matrices, with **Z**<sub>1</sub> and **Z**<sub>2</sub> augmented for animals without records that were included in the relationship matrix.

For the model:

$$E[y] = Xb,$$

and the (co)variance structure of the random effects was as follows:

$$V \begin{bmatrix} a \\ m \\ p \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & A\sigma_{am} & 0 & 0 \\ A\sigma_{am} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I_{N_d}\sigma_p^2 & 0 \\ 0 & 0 & 0 & I_N\sigma_e^2 \end{bmatrix}$$

where  $N_d$  is the number of dams,  $N$  is the number of records; **A** is Wright’s numerator relationship matrix among animals in the pedigree file, and the **I** matrices are identity matrices.

Falconer’s model does not include a maternal genetic effect, and Willham’s model cannot account for cycles of maternal effects (Lande and Kirkpatrick, 1990). Koerhuis and Thompson (1997) proposed an “integrated Falconer-Willham” model. Model 3 in this analysis was such an “integrated Falconer-Willham” model (Koerhuis and Thompson, 1997):

$$y = Xb + f_m(y_P - X_P b) + Z_1a + Z_2m + W_1p + e$$

where  $f_m$  is the coefficient of regression on maternal phenotype (“Falconer parameter”),  $y_P$  is a vector of observations on the dams, and  $X_P$  is a known incidence matrix relating these observations to the respective fixed effects. Koerhuis and Thompson (1997) provide details on the variance of **y** and how to deal with missing observations on dams.

To account for the influence of the phenotypic value of the dam on her daughter’s maternal ability, Willham (1972) extended his basic model to include grandmaternal effects, but this model does not include all females in the maternal pathway, although the most important pathway (granddam-dam-daughter) probably is included. Dodenhoff et al. (1999) used such a “grandmaternal” model to estimate genetic parameters in beef

Table 1. Characteristics of the sample data sets from three states

Sample	Herds	Weaning weight, kg		Records	Sires	Dams	Granddams	Assigned granddams <sup>a</sup>	Pedigree animals	Sire × herd-year effects
		Mean	SD							
IA-1	26	231.9	48.0	8,964	555	3,767	2,608	8	16,197	961
IA-2	34	234.3	55.9	11,675	754	4,303	2,955	53	20,464	1,438
IA-3	54	237.6	50.4	8,813	694	4,017	3,005	24	18,677	1,328
MT-1	20	246.0	43.1	9,302	502	3,272	2,076	31	14,986	1,066
MT-2	25	254.0	41.2	10,318	573	3,230	2,113	27	15,847	1,246
MT-3	36	268.4	40.1	9,349	522	2,991	2,142	2	15,713	1,236
NE-1	43	240.5	42.3	11,532	951	5,067	3,850	12	23,837	1,899
NE-2	18	233.7	39.4	9,764	611	3,892	2,735	1	16,437	1,184
NE-3	13	230.6	43.6	8,128	518	2,490	1,630	3	12,668	985

<sup>a</sup>Unique granddam identification assigned when granddam identification was not known.

Table 2. Parameters estimated with the six models<sup>a</sup>

Model	Parameter										
	$f_m$	$\sigma_a^2$	$\sigma_m^2$	$\sigma_g^2$	$\sigma_{am}$	$\sigma_{ag}$	$\sigma_{mg}$	$\sigma_p^2$	$\sigma_q^2$	$\sigma_{sh}^2$	$\sigma_e^2$
1		X	X		X			X			X
2		X	X		X			X		X	X
3	X	X	X		X			X			X
4	X	X	X		X			X		X	X
5		X	X	X	X	X	X	X	X		X
6		X	X	X	X	X	X	X	X	X	X

<sup>a</sup> $f_m$  = coefficient of regression on maternal phenotype,  $\sigma_a^2$  = direct genetic variance,  $\sigma_m^2$  = maternal genetic variance,  $\sigma_g^2$  = grandmaternal genetic variance,  $\sigma_{am}$  = direct-maternal genetic covariance,  $\sigma_{ag}$  = direct-grandmaternal genetic covariance,  $\sigma_{mg}$  = maternal-grandmaternal genetic covariance,  $\sigma_p^2$  = variance due to permanent maternal environmental effects,  $\sigma_q^2$  = variance due to permanent grandmaternal environmental effects,  $\sigma_{sh}^2$  = variance due to sire  $\times$  herd-year interaction effects,  $\sigma_e^2$  = residual variance.

cattle. Model 5 in this study was the “grandmaternal” model (Willham, 1972):

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

where  $\mathbf{g}$  is a vector of grandmaternal genetic effects,  $\mathbf{q}$  is a vector of grandmaternal permanent environmental effects, and  $\mathbf{Z}_1$ ,  $\mathbf{Z}_2$ , and  $\mathbf{Z}_3$  are known incidence matrices with the  $\mathbf{Z}_1$ ,  $\mathbf{Z}_2$ , and  $\mathbf{Z}_3$  augmented for animals without records that were included in  $\mathbf{A}$ . The covariance structure for this model additionally included a grandmaternal genetic variance ( $\sigma_g^2$ ), covariances between direct and grandmaternal genetic effects ( $\sigma_{ag}$ ) and between maternal and grandmaternal genetic effects ( $\sigma_{mg}$ ), and grandmaternal permanent environmental variance ( $\sigma_q^2$ ). Covariances between maternal and grandmaternal permanent environmental effects as well as covariances between permanent environmental and residual effects were assumed to be zero. A model with grandmaternal effects requires each animal with a record to have a known granddam. Van Vleck (1990) described how to deal with unidentified dams in models with maternal effects. Unidentified granddams were assigned a fictitious identification and were assumed to be related only to their daughters and their descendants. In the nine data sets, from 1 to 53 granddams were unidentified (Table 1).

Models 2, 4, and 6 were based on Models 1, 3, and 5, respectively, with a sire  $\times$  herd-year interaction fitted as an additional uncorrelated random effect. The respective  $\mathbf{V}$  matrices were augmented to include  $\mathbf{I}\sigma_{sh}^2$ . Table 2 shows which parameters were estimated with the six models.

Variance and covariance components and the coefficient of regression on maternal phenotype were estimated using REML. Models 1, 2, 5, and 6 were analyzed using an average information algorithm (AI REML) (Johnson and Thompson, 1995). This quasi-Newton algorithm uses first derivatives of the logarithm of the likelihood ( $\mathbf{L}$ ) and an average of observed and expected second derivatives (“average information” matrix) to

find estimates of genetic parameters that maximize  $\mathbf{L}$ . The inverse of the coefficient matrix needed to calculate first derivatives of the likelihood was obtained using sparse matrix algorithms described by Takahashi et al. (1973) and implemented in FSPAK (Perez-Enciso et al., 1992). Convergence was assumed to have been reached if the Euclidian norm of the vector of first derivatives was less than  $10^{-4}$ . When  $f_m$  was fitted (Models 3 and 4), estimates were obtained with the DFREML 2.1 package (Meyer, 1997a). Variance component estimation using a derivative-free algorithm when a regression on maternal phenotype is included in the model is described by Meyer (1997a). The likelihood was maximized using the Simplex algorithm (Nelder and Mead, 1965), with convergence assumed to have been reached if the variance of function values ( $-2\log L$ ) in the simplex was less than  $10^{-8}$ .

For these analyses, different estimation algorithms were used because DFREML did not allow for a third random genetic effect (grandmaternal genetic effects), and  $f_m$  could not be fitted in the AI REML algorithm. The different convergence criteria were not assumed to affect the likelihood values when comparing the models because likelihoods were identical by all methods for Model 1.

## Results and Discussion

### Estimation of (Co)variance Components

Parameter estimates for weaning weight for the three states with the six models are presented in Tables 3 to 5. Estimates with Model 1 were relatively similar for the three data sets within each region, but they were slightly different across regions. Particularly for Iowa, estimates of direct heritability ( $h^2$ ) were larger, and negative estimates of direct-maternal correlation had a larger absolute value than for Montana and Nebraska.

The coefficient of regression on maternal phenotype (Model 3) indicated a small influence of the dam’s phenotype, with estimates of  $f_m$  ranging from  $-0.006$  to  $.014$ . Compared to Model 1, the log likelihoods for Model 3

for Iowa and Nebraska increased very little, and estimates of maternal heritability ( $m^2$ ) and proportion of variance due to maternal permanent environmental effects ( $p^2$ ) were not affected. For Montana, estimates of  $f_m$  were positive, and estimates of  $r_{am}$  decreased slightly for Model 3 compared with Model 1. This pattern agrees with Robinson (1996b) and Koerhuis and Thompson (1997), who simulated a negative  $f_m$  and found that in a “reduced” model the negative  $f_m$  was accounted for partially as a negative direct-maternal genetic covariance and partially as a permanent maternal environmental variance. Koch (1972) suggested a  $f_m$  of  $-.2$  for weaning weight, and Cantet et al. (1988) estimated the regression coefficient to be  $-.25$ . Meyer (1997b) confirmed estimates of this magnitude for Australian Herefords, but estimates were nearer to zero ( $-.03$  to  $-.09$ ) for weaning weights of Angus from Australia and New Zealand.

To obtain permissible estimates of all (co)variance components with the “grandmaternal” model (Model 5) proved difficult. A full set of permissible solutions was obtained only for two data sets. Solutions for some variance components for the other seven data sets became negative during iteration. When this happened to the grandmaternal permanent environmental variance (for six data sets), that component was set to zero. When the grandmaternal genetic variance became negative

(for two data sets), it was set to a small positive value ( $10^{-8}$ ) in order to keep the matrix of genetic (co)variances positive definite while the corresponding covariances were set to zero. Algorithms for Newton methods that keep the estimates in the parameter space or that, after reparameterization, do not yield negative estimates have been described (see, e.g., Harville, 1977; Johnson and Thompson, 1995; Meyer and Smith, 1996), but they were not available in software used for these analyses. For sample 1 from Iowa, estimates of grandmaternal components were not permissible, so estimates with Models 1 and 5 were basically identical. For the other data sets, estimates of grandmaternal heritability ( $g^2$ ) were from .02 to .05. Although estimates of direct heritability ( $h^2$ ) did not change compared to Model 1, estimates of  $p^2$  decreased with grandmaternal effects in the model (Model 5). In most cases, estimates of  $m^2$  increased, and estimates of  $r_{am}$  were less negative. Solutions for the fraction of variance due to grandmaternal permanent environmental effects ( $q^2$ ), if permissible, were small (.01 to .03). Large negative estimates were found for the maternal-grandmaternal correlation ( $r_{mg}$ ). Any relationship of the estimates of the direct-grandmaternal correlation ( $r_{ag}$ ), which ranged from  $-.36$  to  $.37$ , with any of the other parameters was not obvious. Estimates with Model 5 generally agreed with previous studies in which a model

Table 3. Estimates of parameters<sup>a</sup> for weaning weight by model for Iowa

Sample and model	Parameter											
	$f_m$ , kg/kg	$h^2$	$m^2$	$g^2$	$r_{am}$	$r_{ag}$	$r_{mg}$	$p^2$	$q^2$	$s^2$	$\sigma_p^2$	2logL
IA-1												
1		.41	.16		-.55			.10			613.7	.00
2		.21	.11		-.27			.10		.08	615.4	65.97
3	-.003	.41	.16		-.54			.10			614.4	.37
4	-.003	.21	.11		-.26			.10		.08	616.2	66.50
5		.41	.16	— <sup>b</sup>	-.55	— <sup>b</sup>	— <sup>b</sup>	.10	— <sup>b</sup>		613.7	.00 <sup>c</sup>
6		.21	.11	— <sup>b</sup>	-.27	— <sup>b</sup>	— <sup>b</sup>	.10	— <sup>b</sup>	.08	615.4	65.97 <sup>d</sup>
IA-2												
1		.48	.14		-.57			.12			618.3	0.00
2		.31	.09		-.32			.12		.07	620.5	60.15
3	.004	.48	.15		-.58			.13			617.4	.93
4	.003	.31	.09		-.32			.13		.07	619.9	60.64
5		.48	.18	.03	-.57	.37	-.62	.09	— <sup>b</sup>		636.8	6.50
6		.32	.13	.03	-.35	.30	-.63	.10	— <sup>b</sup>	.06	633.5	65.67
IA-3												
1		.50	.16		-.57			.08			572.6	.00
2		.20	.08		-.11			.09		.10	572.0	55.34
3	-.006	.50	.16		-.55			.08			573.2	1.49
4	-.006	.20	.08		-.08			.09		.10	573.6	56.98
5		.49	.21	.04	-.51	.12	-.56	.04	— <sup>b</sup>		579.0	6.79
6		.20	.11	.04	-.10	.12	-.63	.05	.00	.10	575.7	61.24

<sup>a</sup> $f_m$  = coefficient of regression on maternal phenotype,  $h^2$  = direct heritability,  $m^2$  = maternal heritability,  $g^2$  = 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,  $p^2$  = fraction of variance due to maternal permanent environmental effects,  $q^2$  = fraction of variance due to grandmaternal permanent environmental effects,  $s^2$  = fraction of variance due to sire × herd-year interaction effects,  $\sigma_p^2$  = phenotypic variance ( $kg^2$ ), 2logL = 2log likelihood as deviation from Model 1.

<sup>b</sup>Estimate set to zero during iteration.

<sup>c</sup>Models 1 and 5 identical after grandmaternal components set to zero.

<sup>d</sup>Models 2 and 6 identical after grandmaternal components set to zero.



Table 4. Estimates of parameters<sup>a</sup> for weaning weight by model for Montana

Sample and model	Parameter											
	$f_m$ , kg/kg	$h^2$	$m^2$	$g^2$	$r_{am}$	$r_{ag}$	$r_{mg}$	$p^2$	$q^2$	$s^2$	$\sigma_p^2$	2logL
MT-1												
1		.25	.16		-.25			.17			479.0	.00
2		.18	.13		-.07			.17		.04	480.6	21.72
3	.013	.25	.16		-.30			.18			476.1	5.84
4	.013	.18	.13		-.12			.17		.04	477.5	27.20
5		.25	.27	.05	-.09	-.36	-.69	.07	.03		474.0	19.86
6		.18	.24	.05	.06	-.38	-.74	.07	.03	.04	476.7	41.34
MT-2												
1		.26	.14		-.32			.17			516.8	.00
2		.17	.12		-.14			.17		.04	515.4	40.90
3	.009	.26	.14		-.36			.18			514.4	3.80
4	.009	.16	.12		-.18			.17		.04	512.9	44.64
5		.26	.21	.05	-.24	.05	-.68	.11	— <sup>b</sup>		520.9	12.98
6		.17	.19	.04	-.08	.06	-.72	.11	— <sup>b</sup>	.04	519.5	53.12
MT-3												
1		.24	.17		-.07			.11			476.7	.00
2		.20	.16		.02			.11		.02	475.9	11.98
3	.014	.24	.17		-.12			.12			471.4	9.37
4	.014	.19	.15		.00			.12		.02	470.3	21.75
5		.24	.23	.05	-.05	.25	-.68	.05	— <sup>b</sup>		486.2	11.05
6		.20	.22	.05	.03	.25	-.66	.05	— <sup>b</sup>	.02	484.9	22.18

<sup>a</sup> $f_m$  = coefficient of regression on maternal phenotype,  $h^2$  = direct heritability,  $m^2$  = maternal heritability,  $g^2$  = 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,  $p^2$  = fraction of variance due to maternal permanent environmental effects,  $q^2$  = fraction of variance due to grandmaternal permanent environmental effects,  $s^2$  = fraction of variance due to sire  $\times$  herd-year interaction effects,  $\sigma_p^2$  = phenotypic variance (kg<sup>2</sup>), 2logL = 2log likelihood as deviation from Model 1.

<sup>b</sup>Estimate set to zero during iteration.

with grandmaternal effects was applied (Dodenhoff et al., 1998, 1999). Given a negative influence of the granddam's phenotype on the dam's maternal ability, Willham (1972) expected  $r_{mg}$  to be negative, but he doubted that a nonzero covariance between direct and grandmaternal genetic effects existed. With both  $r_{am}$  and  $r_{mg}$  negative and a possible granddam-dam-daughter cycle,  $r_{ag}$  might be expected to be positive.

Differences in the log likelihoods for Models 1, 3, and 5 indicate that including grandmaternal effects fitted the data slightly better than fitting a regression on maternal phenotype. Small estimates of  $f_m$  suggested little influence of dam's phenotype on her calf's performance, and estimates of  $r_{am}$  with Model 1 did not seem to be reduced relative to Model 3. However, negative estimates of  $r_{mg}$  and smaller estimates of  $r_{am}$  with the "grandmaternal" model support suggestions and results by Koch (1972), Willham (1972), Baker (1980), Cantet et al. (1988), and Meyer (1997b) that such a negative influence exists. Increased estimates of  $m^2$  with Model 5 may be related to the large negative estimates of  $r_{mg}$ . With Model 1, maternal genetic variance was possibly underestimated because maternal genetic effects were "overshadowed" by grandmaternal genetic effects, which were accounted for in Model 5. The disadvantage of the "grandmaternal" model is that it is computationally demanding because a third random genetic effect is fitted. Koerhuis and Thompson (1997)

fitted a direct-maternal environmental covariance ( $\sigma_{ec}$ ), but the model did not perform better than the "integrated Falconer-Willham" model. Meyer (1997b) expected computational problems with large field data sets when fitting  $\sigma_{ec}$  and turned to the "integrated Falconer-Willham" model. Quintanilla et al. (1998) proposed a model that includes a covariance between permanent maternal environmental effects of all dams in line of descent to account for nongenetic covariance between direct and maternal effects.

With Model 2, estimates of the proportion of variance due to sire  $\times$  herd-year interaction effects ( $s^2$ ) were from .02 to .10. Notter et al. (1992), Robinson (1996a), and Meyer (1997b) reported similar estimates for Australian Angus. Differences existed across regions; estimates for Iowa were larger than those for Montana. Likelihood values increased considerably over Model 1 for Iowa and Nebraska, and to a lesser extent, for Montana. Fitting a SH interaction resulted in smaller estimates of  $h^2$  and  $m^2$  and in less negative or even small positive estimates of  $r_{am}$ , particularly for Iowa, but  $p^2$  was not affected.

Similar changes in estimates of  $h^2$ ,  $m^2$ , and  $r_{am}$  were observed with Models 4 and 6, when the interaction was fitted in addition to a covariate or grandmaternal effects compared with Models 3 and 5, respectively. Estimates of  $f_m$  with Models 3 and 4 were almost identical. Although estimates of  $h^2$  and  $m^2$  were smaller with

Model 6 than with Model 5, estimates of  $g^2$  did not decrease, and  $r_{ag}$  and  $r_{mg}$  changed less than  $r_{am}$ . The differences in log likelihoods for the six models also indicate that effects of SH interaction and effects accounting for the influence of dam's phenotype on daughter's maternal ability were independent.

The log likelihoods indicate that Model 6 fitted the data best, and most of the improvement over Model 1 was due to including SH interaction effects rather than to including grandmaternal effects. Fitting the SH interaction resulted in lower estimates of  $h^2$ , whereas fitting grandmaternal effects resulted in smaller estimates of  $p^2$ . Both factors had an impact on estimates of  $m^2$ , but in opposite directions, resulting in estimates that were either greater or lower than with Model 1. The greatest effect was on the direct-maternal correlation, because both SH interaction effects and grandmaternal effects resulted in greater estimates of  $r_{am}$ , most significantly so for Nebraska data, for which estimates ranged from  $-.31$  to  $-.41$  with Model 1 and from  $-.14$  to  $.13$  with Model 6.

These results suggest that estimates of  $r_{am}$  from a "reduced" model, where SH interaction effects and(or) grandmaternal effects were not accounted for, may be biased downward. Biased estimates were found for simulated data (Robinson, 1996b; Lee and Pollak, 1997) and for field data (Lee and Pollak, 1997; Meyer, 1997b) if the SH interaction was not fitted. Lee and Pollak

(1997) speculated that a sire  $\times$  year interaction was either a true effect due to different environmental factors associated with different years, or that unidentified sources of variation created a covariance between progeny records in the same year. Meyer (1997b) suggested that a covariance between paternal sibs in a contemporary group caused by management groups or by other unidentified sources of variation might be one possible reason for bias in estimating the direct-maternal covariance. According to Bertrand et al. (1985), nonrandom mating practices or preferential treatment could contribute to an increased correlation among sire progeny in some herds. These factors may help to explain the differences in the magnitude of the SH interaction observed in this study, because nonrandom mating or preferential treatment are more likely to occur in herds with relatively small contemporary groups. The average contemporary group size was 12.4 for Iowa, 22.6 for Montana, and 17.4 for Nebraska herds. However, the average contemporary group sizes of samples within region were not uniform. Results from this study indicate that fitting SH interaction effects not only improved the likelihood in general but also removed most of the differences in the estimates of  $h^2$ ,  $m^2$ , and  $r_{am}$  across regions that were obtained with Model 1.

*Sampling Correlations and Standard Errors*

Sampling correlations among estimates of (co)variances for Models 1 and 5 were derived from the inverse

Table 5. Estimates of parameters<sup>a</sup> for weaning weight by model for Nebraska

Sample and model	Parameter											
	$f_m$ , kg/kg	$h^2$	$m^2$	$g^2$	$r_{am}$	$r_{ag}$	$r_{mg}$	$p^2$	$q^2$	$s^2$	$\sigma_p^2$	2logL
NE-1												
1		.30	.15		-.41			.13			525.1	.00
2		.17	.11		-.14			.13		.07	528.6	68.81
3	.003	.30	.15		-.42			.13			524.7	.49
4	.002	.17	.11		-.14			.13		.07	528.8	68.99
5		.30	.15	— <sup>b</sup>	-.41	— <sup>b</sup>	— <sup>b</sup>	.11	.02		525.3	1.25
6		.17	.11	— <sup>b</sup>	-.14	— <sup>b</sup>	— <sup>b</sup>	.11	.01	.07	528.6	69.46
NE-2												
1		.26	.11		-.31			.13			451.4	.00
2		.19	.10		-.18			.13		.03	450.2	16.61
3	-.003	.26	.11		-.31			.13			451.8	.33
4	-.003	.19	.10		-.17			.13		.03	450.6	17.01
5		.27	.16	.02	-.17	-.30	-.75	.09	.01		448.3	10.17
6		.20	.14	.02	-.04	-.41	-.77	.10	.01	.03	446.5	26.05
NE-3												
1		.33	.17		-.40			.17			487.8	.00
2		.21	.14		-.22			.17		.04	483.3	27.93
3	-.000	.34	.17		-.39			.17			488.0	.01
4	-.001	.21	.14		-.22			.17		.04	483.5	27.98
5		.34	.21	.03	-.30	-.31	-.33	.14	— <sup>b</sup>		481.4	5.43
6		.21	.18	.03	.13	-.31	-.40	.14	— <sup>b</sup>	.04	478.4	33.43

<sup>a</sup> $f_m$  = coefficient of regression on maternal phenotype,  $h^2$  = direct heritability,  $m^2$  = maternal heritability,  $g^2$  = 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,  $p^2$  = fraction of variance due to maternal permanent environmental effects,  $q^2$  = fraction of variance due to grandmaternal permanent environmental effects,  $s^2$  = fraction of variance due to sire  $\times$  herd-year interaction effects,  $\sigma_p^2$  = phenotypic variance (kg<sup>2</sup>), 2logL = 2log likelihood as deviation from Model 1.

<sup>b</sup>Estimate set to zero during iteration.

Table 6. Means of sampling correlations derived from the inverse of the negative of the average information matrix for nine samples between estimates of (co)variances<sup>a</sup> for Model 1 (above diagonal) and for Model 5 (below diagonal)<sup>b</sup>

Parameter	Parameter								
	$\sigma_a^2$	$\sigma_m^2$	$\sigma_g^2$	$\sigma_{am}$	$\sigma_{ag}$	$\sigma_{mg}$	$\sigma_p^2$	$\sigma_q^2$	$\sigma_e^2$
$\sigma_a^2$		.20		-.62			.02		-.89
$\sigma_m^2$	.13			-.65			-.50		-.20
$\sigma_g^2$	.00	.25							
$\sigma_{am}$	-.57	-.39	.06				.00		.55
$\sigma_{ag}$	.02	.12	-.04	-.33					
$\sigma_{mg}$	-.01	-.64	-.61	.04	-.30				
$\sigma_p^2$	.02	-.69	-.45	-.08	.04	.60			-.13
$\sigma_q^2$	.00	.03	-.43	.02	.01	.07	-.35		
$\sigma_e^2$	-.89	-.14	-.00	.52	-.03	.01	-.09	-.00	

<sup>a</sup> $\sigma_a^2$  = direct genetic variance,  $\sigma_m^2$  = maternal genetic variance,  $\sigma_g^2$  = grandmaternal genetic variance,  $\sigma_{am}$  = direct-maternal genetic covariance,  $\sigma_{ag}$  = direct-grandmaternal genetic covariance,  $\sigma_{mg}$  = maternal-grandmaternal genetic covariance,  $\sigma_p^2$  = variance due to permanent maternal environmental effects,  $\sigma_q^2$  = variance due to permanent grandmaternal environmental effects,  $\sigma_{sh}^2$  = variance due to sire  $\times$  herd-year interaction effects,  $\sigma_e^2$  = residual variance.

<sup>b</sup>Sampling correlations for regions 13.1 and 25.1 were not included because estimates of grandmaternal genetic effects could not be obtained.

of the negative of the average information matrix. Even though the estimates varied somewhat across the data sets (see Tables 3 to 5), the patterns of the sampling correlations were similar. Therefore, means of sampling correlations are presented in Table 6. Sampling correlations for Model 1 generally agreed with expected sampling correlations obtained by Meyer (1992a) for a data structure that provided a relatively large amount of information to separate components. For Models 1 and 5, the largest negative mean sampling correlation was

between estimates of direct genetic and error variances. The mean sampling correlation between estimates of maternal genetic variance and direct-maternal genetic covariance was smaller for Model 5 than for Model 1. Estimates of (co)variance components involving grandmaternal effects were not highly negatively correlated, indicating that the data structure was sufficient to apply a “grandmaternal” model. Not clear, however, is why for two data sets (IA-1, NE-1), for which the data structure can be assumed to be similar to the other

Table 7. Means of standard errors of estimates for nine samples of (co)variances and parameters<sup>a</sup> for Models 1 and 5<sup>b</sup> derived from the inverse of the negative of the average information matrix

Model	Estimates of (co)variances								
	$\sigma_a^2$	$\sigma_m^2$	$\sigma_g^2$	$\sigma_{am}$	$\sigma_{ag}$	$\sigma_{mg}$	$\sigma_p^2$	$\sigma_q^2$	$\sigma_e^2$
1	121.4	80.3		77.2			47.3		69.7
5	119.5	116.4	49.4	80.9	68.6	62.9	69.0	36.3	68.3
Model	Parameter estimates								
	$h^2$	$m^2$	$g^2$	$r_{am}$	$r_{ag}$	$r_{mg}$	$p^2$	$q^2$	$s^2$
1	.043	.031		.093			.019		.031
5	.043	.045	.020	.101	.256	.202	.028	.016	.032

<sup>a</sup> $\sigma_a^2$  = direct genetic variance,  $\sigma_m^2$  = maternal genetic variance,  $\sigma_g^2$  = grandmaternal genetic variance,  $\sigma_{am}$  = direct-maternal genetic covariance,  $\sigma_{ag}$  = direct-grandmaternal genetic covariance,  $\sigma_{mg}$  = maternal-grandmaternal genetic covariance,  $\sigma_p^2$  = variance due to permanent maternal environmental effects,  $\sigma_q^2$  = variance due to permanent grandmaternal environmental effects,  $\sigma_e^2$  = residual variance,  $h^2$  = direct heritability,  $m^2$  = maternal heritability,  $g^2$  = 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,  $p^2$  = fraction of variance due to maternal permanent environmental effects,  $q^2$  = fraction of variance due to grandmaternal permanent environmental effects,  $s^2$  = fraction of variance due to sire  $\times$  herd-year interaction effect.

<sup>b</sup>Estimates for regions IA-1 and MT-1 were not included because no estimates of grandmaternal genetic effects could be obtained.



Table 8. Product-moment and rank correlations between estimated breeding values for direct weaning weight and between estimated breeding values for maternal weaning weight with Model 1 with the other five models

Model	Direct						Maternal					
	Product-moment			Rank			Product-moment			Rank		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
2	.976	.941	.993	.970	.922	.992	.921	.715	.996	.906	.671	.995
3	.999	.999	.999	.999	.998	.999	.999	.997	.999	.999	.997	.999
4	.976	.939	.993	.970	.920	.992	.919	.699	.993	.903	.655	.991
5	.996 <sup>a</sup>	.991	.999	.994 <sup>a</sup>	.988	.998	.961 <sup>a</sup>	.943	.978	.954 <sup>a</sup>	.942	.973
6	.974 <sup>a</sup>	.934	.990	.967 <sup>a</sup>	.915	.987	.880 <sup>a</sup>	.667	.957	.863 <sup>a</sup>	.624	.952

<sup>a</sup>Correlations for IA-1 and NE-1 not included because estimates of components of variance due to grandmaternal genetic effects were not permissible.

data sets, estimates of variances due to grandmaternal genetic effects could not be obtained. Sampling correlations for variance of SH interaction with the other (co)-variance components for Model 6 were small, ranging from  $-.36$  with direct genetic variance to  $.28$  with direct-maternal covariance, thus confirming that the information to separate SH interaction and grandmaternal effects was sufficient.

Mean standard errors of estimated parameters are shown in Table 7. Including grandmaternal effects in the model did not affect standard errors of  $h^2$  and of the fraction of variance due to residual effects ( $e^2$ ). With Model 5, the mean standard error of estimates of  $m^2$  was greater than with Model 1, as were the estimates of  $m^2$  (Tables 3 to 5). The mean standard error of estimates of  $p^2$  was greater with Model 5, even though the estimates of  $p^2$  were smaller than with Model 1. Large mean standard errors were obtained for estimates of genetic correlations, particularly for the correlations involving grandmaternal genetic effects,  $r_{ag}$  and  $r_{mg}$ .

#### Correlations Between Estimated Breeding Values

Product-moment and rank correlations between estimated breeding values are given in Table 8. Presented are mean, minimum, and maximum correlations for Model 1 with the other five models. Correlations were not calculated between Models 1 and 5 or between Models 1 and 6 if estimates of parameters associated with grandmaternal genetic effects were set to zero. Correlations between estimated breeding values for direct weaning weight were large. Including SH interaction effects in the model resulted in slightly smaller correlations, indicating that fitting these effects had more impact than fitting a covariate for maternal phenotype or including grandmaternal effects. Fitting the covariate also had only little impact on the estimated breeding values for maternal weaning weight, as shown by the correlations between Models 1 and 3. Correlations were somewhat less when grandmaternal effects were included in the model. Clearly, fitting SH interaction effects had the greatest effect. The magnitude of the correlations between Models 1 and 2 was directly related to

the magnitude of the estimates of  $s^2$ ; the lowest correlations between estimated breeding values were for Iowa, which had relatively high estimates of  $s^2$ . Lee and Polak (1997) found an estimate of  $s^2$  of  $.03$  for Simmental data, with correlations between expected progeny differences of  $.978$  (direct genetic effects) and  $.967$  (maternal genetic effects). The smallest correlations in the present study were between Models 1 and 6. Model 6, with both the SH interaction and grandmaternal effects included, also had the largest log likelihoods.

#### Implications

Direct and maternal heritabilities may be overestimated, and the direct-maternal correlation may be biased downward if sire  $\times$  herd-year interaction is not included in models to estimate genetic parameters for weaning weight of Angus cattle. Thus, models with sire  $\times$  herd-year interaction as an uncorrelated random effect are recommended for routine genetic evaluation. Genetic evaluations with this interaction might result in considerable re-ranking for estimated breeding values for maternal weaning weight. A negative relationship between a dam's phenotype and her daughter's maternal ability was confirmed with estimates of parameters when grandmaternal effects were included in the model. Maternal heritability may be underestimated, and the direct-maternal genetic correlation may be biased downward if grandmaternal effects are not accounted for in the model. Inclusion of grandmaternal effects in models for routine genetic evaluation may not be feasible because adding a third genetic effect would be computationally demanding.

#### Literature Cited

- Baker, R. L. 1980. The role of maternal effects on the efficiency of selection in beef cattle: A review. In: Proc. N.Z. Soc. Anim. Prod. 40:285-303.
- Bertrand, J. K., P. J. Berger, and R. L. Willham. 1985. Sire  $\times$  environment interactions in beef cattle weaning weight field data. J. Anim. Sci. 60:1396-1402.
- Cantet, R.J.C., D. D. Kress, D. C. Anderson, D. E. Doornbos, P. J. Burfening, and R. L. Blackwell. 1988. Direct and maternal vari-

- ances and covariances and maternal phenotypic effects on pre-weaning growth of beef cattle. *J. Anim. Sci.* 66:648–660.
- Dodenhoff, J., L. D. Van Vleck, and K. E. Gregory. 1999. Estimation of direct, maternal, and grandmaternal genetic effects for weaning weight in several breeds of beef cattle. *J. Anim. Sci.* 77:840–845.
- Dodenhoff, J., L. D. Van Vleck, S. D. Kachman, and R. M. Koch. 1998. Parameter estimates for direct, maternal, and grandmaternal genetic effects for birth weight and weaning weight in Hereford cattle. *J. Anim. Sci.* 76:2521–2527.
- Falconer, D. S. 1965. Maternal effects and selection response. In: *Genetics Today. Proc. XI Int. Congr. Genet.* Vol 3. p 763. The Hague, The Netherlands.
- Harville, D. A. 1977. Maximum likelihood approaches to variance component estimation and related problems. *J. Am. Stat. Assoc.* 72:320–338.
- Johnson, D. L., and R. Thompson. 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.
- 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 R. Thompson. 1997. Models to estimate maternal effects for juvenile body weight in broiler chickens. *Genet. Sel. Evol.* 29:225–249.
- Lande, R., and M. Kirkpatrick. 1990. Selection response in traits with maternal inheritance. *Genet. Res.* 55:189–197.
- Lee, C., and E. J. Pollak. 1997. Relationship between sire  $\times$  year interactions and direct-maternal genetic correlation for weaning weight of Simmental cattle. *J. Anim. Sci.* 75:68–75.
- Meyer, K. 1992a. Bias and sampling covariances of estimates of variance components due to maternal effects. *Genet. Sel. Evol.* 24:487–509.
- Meyer, K. 1992b. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. *Livest. Prod. Sci.* 31:179–203.
- Meyer, K. 1997a. DFREML Version 2.1 $\alpha$ —Programs to Estimate Variance Components by Restricted Maximum Likelihood Using a Derivative-Free Algorithm. User Notes. AGBU, University of New England, Armidale NSW (Mimeo).
- Meyer, K. 1997b. Estimates of genetic parameters for weaning weight of beef cattle accounting for direct-maternal environmental covariances. *Livest. Prod. Sci.* 52:187–199.
- Meyer, K., and S. P. Smith. 1996. Restricted maximum likelihood estimation for animal models using derivatives of the likelihood. *Genet. Sel. Evol.* 28:23–49.
- Nelder, J. A., and R. Mead. 1965. A simplex method for function minimization. *Comput. J.* 7:147–151.
- Notter, D. R., B. Tier, and K. Meyer. 1992. Sire  $\times$  herd interactions for weaning weight in beef cattle. *J. Anim. Sci.* 70:2359–2365.
- Perez-Enciso, M., I. Misztal, and M. A. Elzo. 1992. FSPAK—An interface for public domain sparse matrix subroutines. *Proc. 5th World Congr. Genet. Appl. Livest. Prod.* 22:77–78.
- Quintanilla, R., L. Varona, M. R. Pujol, and J. Piedrafitra. 1998. Maternal animal model with correlation between maternal permanent environmental effects in beef breeding. *Proc. 6th World Congr. Genet. Appl. Livest. Prod.* 23:259–262.
- Robinson, D. L. 1996a. Estimation and interpretation of direct and maternal genetic parameters for weights of Australian Angus cattle. *Livest. Prod. Sci.* 45:1–11.
- Robinson, D. L. 1996b. Models which might explain negative correlations between direct and maternal genetic effects. *Livest. Prod. Sci.* 45:111–122.
- Takahashi, K., J. Fagan, and M. S. Chin. 1973. Formation of a sparse bus impedance matrix and its application to short circuit study. In: *Proc. 8th Inst. PICA Conf.*, Minneapolis, MN. p 63.
- Thompson, R. 1976. The estimation of maternal genetic variances. *Biometrics* 32:903–917.
- Van Vleck, L. D. 1990. Breeding value prediction with maternal genetic groups. *J. Anim. Sci.* 68:3998–4013.
- Waldron, D. F., C. A. Morris, R. L. Baker, and D. L. Johnson. 1993. Maternal effects for growth traits in beef cattle. *Livest. Prod. Sci.* 34:57–69.
- Willham, R. L. 1963. The covariance between relatives for characters composed of components contributed by related individuals. *Biometrics* 19:18–27.
- Willham, R. L. 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. *J. Anim. Sci.* 35:1288–1293.