Reducing bias in maintenance energy expected progeny difference by accounting for selection on weaning and yearling weights
J. L. Williams, D. J. Garrick and S. E. Speidel

The online version of this article, along with updated information and services, is located on
the World Wide Web at:
http://www.journalofanimalscience.org/content/87/5/1628

American Society of Animal Science

www.asas.org

Reducing bias in maintenance energy expected progeny difference by accounting for selection on weaning and yearling weights[1]

J. L. Williams,* D. J. Garrick,*†‡[2] and S. E. Speidel*

*Department of Animal Sciences, Colorado State University, Fort Collins 80523-1171;
†Institute of Veterinary, Animal and Biomedical Sciences, Massey University, Palmerston North, New Zealand;
and ‡Department of Animal Science, Iowa State University, Ames 50011

ABSTRACT: Maintenance energy requirements of cattle can be predicted from published equations utilizing metabolic BW and milk production potential. Metabolic BW is a function of BW at a constant fat percentage or BCS. Pedigree and performance records can be used in random regression models to predict genetic merit for metabolic BW and milk production potentials. The purpose of this study was to present a methodology for predicting mature cow maintenance energy EPD using mature cow BW and BCS and accounting for prior selection of replacement females at weaning and yearling ages. Variance components were obtained for direct and maternal effects on weaning weight, direct effects on postweaning BW gain, and direct coefficients for random regression on mature weights (MW) adjusted for BCS. These BW were transformed into metabolic BW by taking BW to the power of 0.75, variance components were estimated for metabolic BW, and were then used to predict breeding values from which cow maintenance energy EPD could be derived. Data used in this analysis were obtained from the Red Angus Association of America and limited to herds with MW and corresponding BCS observations. The data set included 52,338 BW records on 21,103 individuals. Weaning and yearling contemporaries to those with MW observations, but with no MW records themselves, were included to account for selection occurring before maturity. Heritability estimates for weaning weight direct, weaning weight maternal, and postweaning BW gain were 0.18 ± 0.02, 0.16 ± 0.02, and 0.18 ± 0.02, respectively. Mature BW observed at 2, 3, 4, 5, and 6 yr of age had heritability estimates of 0.45 ± 0.03, 0.44 ± 0.03, 0.49 ± 0.03, 0.66 ± 0.04, and 0.62 ± 0.05, respectively. Correlations between weaning weight direct and MW ranged from 0.65 ± 0.07 to 0.82 ± 0.04, and correlations between MW at different ages ranged from 0.95 ± 0.03 to 0.99 ± 0.01. The genetic correlations between postweaning BW gain and MW ranged from 0.48 ± 0.06 to 0.59 ± 0.06. The 15-yr genetic increase in metabolic BW was 3.6 $\text{kg}^{0.75}$, greater than the value of $0.23 \text{ kg}^{0.75}$ obtained from the same data ignoring weaning and yearling contemporaries with unobserved MW, the approach currently used in the derivation of cow maintenance EPD published by the Red Angus Association of America.

Key words: beef cattle, maintenance energy, mature body weight, random regression

INTRODUCTION

Production of economically efficient cattle is a major focus of commercial cow-calf enterprises. Rising costs of feed and other inputs along with low market prices are driving producers to look for cattle that use available feedstuffs more efficiently. It has been reported that feed accounts for 54 to 75% of annual costs on a per cow basis (Myers et al., 1999); therefore, an efficient cow herd is vital to the profitability of a producer. Selection for improved efficiency should account for production, reproduction, longevity, and feed costs (Golden et al., 2000). Breed associations have provided EPD for production traits for several decades, but feed intake is expensive to measure and problematic in grazing circumstances. Feed intake can be predicted by summing requirements for production, maintenance, gestation, and lactation. The Red Angus Association of America (**RAAA**) published the first mature cow ME EPD in the spring of 2004. It is predicted from mature weight (**MW**) of the cow adjusted for BCS and from milk production (Enns et al., 2003) because these traits affect maintenance requirements (Montano-Bermudez et al., 1990; MacNeil et al., 1991).

Table 1. Body weight adjustments (kg) for observed mature BW to constant BCS[1]

Item	BCS								
	1[2]	2	3	4	5	6	7	8	9[2]
Adjustment[3]	+116	+93	+66	+15	0	−25	−47	−67	−90

[1]Adjustments for BCS 2 to 8 from Tennant et al. (2002).

[2]BCS 1 and 9 were extrapolated.

[3]Adjustments refer to the amount of BW an animal would need to gain (+) or lose (−) to reach a BCS of 5.

Weaning (**WW**) and yearling weight (**YW**) have moderate to high genetic correlations with MW (Brinks et al., 1964; Northcutt and Wilson, 1993), indicating uninformed selection for immature growth will result in heavier BW in the mature cow herd. The effects of such selection are not taken into account in the RAAA calculations. The objectives of this study were to estimate variance components and EPD from a prototype analysis that extended the current procedure to account for selection at weaning and yearling ages and to compare genetic trends to quantify bias in the published ME EPD.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because data were acquired from an existing database.

Predicting Maintenance Energy Requirements

The equation currently being used by RAAA and used in this study to predict ME EPD was developed by Evans (2001) from NRC (1996) equations for ME for maintenance and a modified Wood's lactation function (Wood, 1969). Wood's lactation function was modified to allow for the inclusion of the genetic prediction for milk of an animal obtained from analysis of WW to be used to predict the ME requirements of the animal (MacNeil and Mott, 2000). The ME requirements (expressed in RAAA publications as MCal of ME/mo) are obtained from predicting daughter phenotypic milk production and metabolic BW at 5 yr of age and BCS 5. The prediction equation is based on summing the maintenance requirement in ME derived from EPD for metabolic BW plus 0.1 times the metabolic energy requirement for lactation, predicted from the EPD for the maternal effect of WW (**WWM**). The relevant coefficient to predict maintenance energy from metabolic BW is 3.85, and the product of the 0.1 multiplier with the coefficients to predict ME requirements from lactation yield of milk and to predict lactation yield of milk from WWM results in the ME prediction equation as a function of EPD:

$$\text{MEm} = 3.85\text{metMW}_5 + 0.13\text{WWM},$$

where MEm is the EPD for ME requirement at maintenance (as published in Mcal/mo), metMW_5 is the metabolic BW ($\text{BW}^{0.75}$) EPD (in $\text{kg}^{0.75}$) at 5 yr of age after adjustment to BCS 5, and WWM is the EPD (in kg) obtained from the RAAA national cattle evaluation.

This approach adopted by RAAA converts observed MW adjusted for BCS to estimates of metabolic BW by raising to the 3/4 power for fitting in mixed model analyses. Resultant EPD are then used in the linear function with WWM from a separate growth analysis to predict MEm. Evans (2001) described an alternative approach, whereby observed BW were used in mixed model analyses to derive EPD that were then converted to a metabolic scale and used to predict their contribution to MEm. The latter approach is problematic in terms of estimating accuracies associated with maintenance EPD.

MW Data

Body weights and pedigree information were obtained from RAAA. A total of 103,009 cow BW and 83,944 BCS collected at calf weaning were available from measurement years 1981 to 2005.

Cow age in years was calculated based on Beef Improvement Federation guidelines for age of dam (BIF, 2002). Duplicate MW records; individuals with unknown sires, unknown dams, or both; cows with less than 50% Red Angus breeding; records missing an associated BCS; observations collected on cows less than 2 or greater than 6 yr of age; as well as contemporary groups lacking variation were discarded.

Cow body composition at weaning was taken into account by adjusting MW to BCS 5. Adjustments for BCS were from Tennant et al. (2002) extrapolated for BCS of 1 and 9 (Table 1).

Contemporary groups for MW were based on the time at which MW and BCS were recorded and included percent Red Angus of the cow and weaning contemporary group of her calf. Animals that were 50 to 87.5% Red Angus were classified separately from those greater than 87.5% Red Angus to account for heterosis. This definition takes no account of the prior cohort classifications of the cow and may therefore cluster together cows that were in different contemporary groups at earlier stages of life such as when the cows themselves were yearlings and bred for the first time.

Table 2. Summary of BW observations, means, contemporary group (CG) levels, and pedigree information by age at weighing

Trait[1]	Age,[2] yr	No. of observations	Mean BW, kg	No. of CG[3]	Sires	Dams
WW	0.6	21,103	241.9	1,684	2,309	15,919
YW	1	17,796	345.7	1,724	2,199	13,599
MW	2	4,355	461.5	599	896	3,792
	3	3,113	509.5	533	748	2,755
	4	2,567	547.4	492	714	2,351
	5	2,022	563.5	415	615	1,875
	6	1,382	572.2	301	491	1,302

[1]WW = weaning weight; YW = yearling weight; and MW = mature weight.
[2]Age 0.6 = adjusted 205-d weight.
[3]CG for ages 0.6 and 1 is sex, work group (herd-yr), weight date, and management code and for ages 2 to 6 is weaning CG of the offspring in that year and percentage Red Angus of the individual (cow).

WW and YW Data

Weaning and yearling weights of cows with MW observations and their unselected contemporaries at weaning and yearling ages (with no MW observations themselves) were included in the analysis to account for weaning and yearling selection. Weaning and yearling weights were adjusted according to BIF guidelines (BIF, 2002) to 205 and 365 d, respectively. Weaning contemporary groups were formed according to RAAA guidelines based on sex, weaning work group, weigh date, and management code. Yearling contemporary groups were formed similarly with the addition of yearling work group. Animals with MW observations were required to have a WW observation to remain in the data set. Postweaning BW gain (**PWG**) was obtained by subtracting adjusted WW from adjusted YW.

Weaning and yearling contemporary groups lacking variation were removed. The final data set contained 52,338 records on 21,103 individuals. A total of 13,439 of these records were MW observations, 21,103 were weaning observations, and 17,796 were PWG observations.

A 2-generation pedigree consisting of animals in the data set, their parents, and their grandparents was compiled from the animals included in the final datafile to estimate variance components and consisted of 46,229 animals. There was an average of 9.1 progeny per sire with a minimum of 1 and a maximum of 243. The average number of progeny per dam was 1.3 with a minimum of 1 and a maximum of 6. Twenty-one percent (1,793) of the 8,533 individuals with MW observations were also dams of animals with MW measurements. A summary of the BW observations by age category in the final datafile and corresponding pedigree file can be found in Table 2.

Estimation of Variance Components

Variance components from multivariate models including random regressions for MW were estimated from BW data, or separately from transformed metabolic BW. The metabolic data were obtained from WW, YW, and MW adjusted for BCS, each raised to the power of 0.75. Metabolic PWG was obtained by subtracting metabolic WW from metabolic YW.

Fixed effects in the model included weaning, yearling, and MW contemporary groups, as well as linear regressions of age for weaning, yearling, and each mature age. Linear regressions of age at WW and YW were fitted despite the fact that WW and YW had been preadjusted to 205 and 365 d respectively. Random effects included WWM and direct effects for WW (**WWD**), PWG, and a slope (**b1**) and intercept (**b0**) for random regression of MW on age in years (2 to 6). Correlated residual effects were fitted for WW, PWG, and MW at each age.

In matrix notation using WW, PWG and MW from 2 to 6 yr adjusted for BCS,

$$
\begin{bmatrix} \mathbf{y_{WW}} \\ \mathbf{y_{PWG}} \\ \mathbf{y_{MW2}} \\ \vdots \\ \mathbf{y_{MW6}} \end{bmatrix} = \mathbf{X\beta} +
$$

$$
\begin{bmatrix} \mathbf{Z_{WWD}} & \mathbf{Z_{WWM}} & \mathbf{Z_{PWG}} & \mathbf{Z_{b0}} & \mathbf{Z_{b1}} \end{bmatrix} \begin{bmatrix} \mathbf{u_{WWD}} \\ \mathbf{u_{WWM}} \\ \mathbf{u_{PWG}} \\ \mathbf{u_{b0}} \\ \mathbf{u_{b1}} \end{bmatrix} + \begin{bmatrix} \mathbf{e_{WW}} \\ \mathbf{e_{PWG}} \\ \mathbf{e_{MW2}} \\ \vdots \\ \mathbf{e_{MW6}} \end{bmatrix},
$$

where $\mathbf{y_i}$ is a vector of observations on trait i; $\mathbf{X}$ is a known incidence matrix relating observations to the fixed effects in $\mathbf{\beta}$ (contemporary groups, age covariates); $\mathbf{Z_{WWD}}$ is a known incidence matrix relating WW observations in $\mathbf{y_{WW}}$ to random direct animal effects in $\mathbf{u_{WWD}}$; $\mathbf{Z_{WWM}}$ is a known incidence matrix relating WW observations to random maternal effects in $\mathbf{u_{WWM}}$; $\mathbf{Z_{PWG}}$ is a known incidence matrix relating PWG observations in $\mathbf{y_{PWG}}$ to random animal effects in $\mathbf{u_{PWG}}$; $\mathbf{Z_{b0}}$ is a column containing 1 corresponding to MW observations (regardless of age) to identify random MW intercept coefficients in $\mathbf{u_{b0}}$; $\mathbf{Z_{b1}}$ is a known incidence matrix of covariates relating MW observations to the additive genetic linear (or slope) regression coefficients

in $\mathbf{u_{b1}}$; and $\mathbf{e}$ is a vector of random residual effects corresponding to animals with records. The immature BW, WW and PWG, were fitted as correlated traits to MW, rather than including these in the random regression, because only WW had a maternal effect and previous experience had shown that convergence could not be achieved when attributing WW and YW (or PWG) to the same intercept and slope as MW.

Variances and covariances for this multivariate random regression model are represented as

$$
\text{var}\begin{bmatrix}
\mathbf{u_{WWD}} \\
\mathbf{u_{WWM}} \\
\mathbf{u_{PWG}} \\
\mathbf{u_{bo}} \\
\mathbf{u_{b1}} \\
\mathbf{e}
\end{bmatrix} =
$$

$$
\begin{bmatrix}
\mathbf{A}\sigma^2_{WWD} \\
\mathbf{A}\sigma_{WWD, WWM} & \mathbf{A}\sigma^2_{WWM} & & & \text{Symmetric} \\
\mathbf{A}\sigma_{WWD, PWG} & \mathbf{A}\sigma_{WWM, PWG} & \mathbf{A}\sigma^2_{PWG} \\
\mathbf{A}\sigma_{WWD, b0} & \mathbf{A}\sigma_{WWM, b0} & \mathbf{A}\sigma_{PWG, b0} & \mathbf{A}\sigma^2_{b0} \\
\mathbf{A}\sigma_{WWD, b1} & \mathbf{A}\sigma_{WWM, b1} & \mathbf{A}\sigma_{PWG, b1} & \mathbf{A}\sigma_{b0, b1} & \mathbf{A}\sigma^2_{b1} \\
0 & 0 & 0 & 0 & 0 & \mathbf{R}
\end{bmatrix},
$$
[1]

where $\mathbf{A}$ is Wright's numerator relationship matrix, $\mathbf{R}$ is the residual (co)variance matrix between BW and would be $\mathbf{I}$ (order 21,103) $\otimes$ $\mathbf{R_0}$ (order 7) if all animals had a record for each trait (WW, PWG, and MW from 2 to 6 yr of age), and $\otimes$ is the Kronecker product between 2 matrices. This study included missing observations for some traits due to sequential selection; therefore, $\mathbf{R}$ from [1] represents $\mathbf{I} \otimes R_0$ with rows and columns corresponding to missing BW observations being deleted.

The formation of the incidence matrix for MW involved ages being first standardized (Kirkpatrick et al., 1990) to values between -1 and 1 to reduce rounding errors

$$
s_i = -1 + 2\left(\frac{x_i + x_{min}}{x_{max} - x_{min}}\right),
$$
[2]

where s_i is the standardized age for age i, x_i is the age from 2 to 6 yr, x_{min} is the minimum (2), and x_{max} is the maximum (6) mature age in the analysis.

Variance components were estimated using the statistical package ASREML (Gilmour et al., 2002), which uses REML methodology to fit linear mixed models. Convergence of the parameters was assumed when simplex variances were less than or equal to 1×10^{-9}. No more than 10 rounds were required before convergence was reached. The genetic (co)variance structure

estimated by ASREML under the random regression model was back transformed to calculate heritability of MW at 2 to 6 yr of age, as well as genetic correlations between each combination of ages.

The analysis of metabolic BW (i.e., power transformed BW) used the same model equation and other assumptions, but with metabolic BW and effects denoted by the prefix (**met**) providing the abbreviations **metWW, metWWD**, **metWWM**, **metPWG**, **metMW**, **metb0**, and **metb1**, respectively.

Estimation of variance components using a 3-generation pedigree was too large for ASREML, so a separate BLUP evaluation using the larger pedigree was undertaken using the ASREML estimates of parameters for metabolic BW from the 2-generation pedigree. Henderson's mixed model equations (Henderson, 1984) were used to predict breeding values for each trait:

$$
\begin{bmatrix}
\mathbf{X'R^{-1}X} & \mathbf{X'R^{-1}Z} \\
\mathbf{Z'R^{-1}X} & \mathbf{Z'R^{-1}Z + G^{-1} \otimes A^{-1}}
\end{bmatrix}
\begin{bmatrix}
\hat{\boldsymbol{\beta}} \\
\hat{\mathbf{u}}
\end{bmatrix} =
\begin{bmatrix}
\mathbf{X'R^{-1}y} \\
\mathbf{Z'R^{-1}y}
\end{bmatrix},
$$

with the mixed model equations being assembled and solved using the animal breeder's tool kit (**ABTK**; Golden et al., 1992). The ABTK is designed to deal with large sparse matrices, enabling it to handle more substantial pedigrees than ASREML.

The metb0 and metb1 EBV coefficients for metMW were used to calculate EBV for metMW at age i (in yr) using standardized age from [2] in the equation:

$$
\text{EBV}_i = u_{metb0} + s_i u_{metb1}.
$$

In this manner, an EBV for metMW5 was calculated to estimate ME EPD. Correlations calculated with the rank command in ABTK were used to compare EPD calculated for ME in this study with those from the RAAA, the latter being obtained without inclusion of weaning or BW gain data in the metabolic BW analysis. Genetic trends set to a common base year of 1988 for MW5 and ME were produced by plotting average EPD by birth year of animals in the data set.

RESULTS AND DISCUSSION

Heritabilities and Variance Parameters

Estimates of heritability and genetic correlations among untransformed BW for WWD, WWM, PWG, and backtransformed from random regression to MW at 2 to 6 yr of age are in Table 3. The corresponding estimates of residual variances and covariances are in Table 4. The estimate for WWM is close to the value of 0.15 used by RAAA in their genetic evaluation, but the WWD estimate is less than the 0.27 assumed by RAAA. Estimates for WWD and WWM are in agreement with those found in the literature. Dodenhoff et al. (1999) investigated WWD and WWM in several different breeds of beef cattle. They looked at 2

Table 3. Multivariate estimates of heritability $\pm$ SE (top number on the diagonal), genetic correlations $\pm$ SE (below diagonal), and genetic variances ($\hat{\sigma}_a^2$) for weaning weight (WW), postweaning BW gain (PWG), and mature weights (MW) adjusted to BCS 5 observed at 2 to 6 yr of age, estimated from a random regression model for MW[1]

Item	WWD	WWM	PWG	MW2	MW3	MW4	MW5	MW6
WWD	0.18 ± 0.02							
WWM	0.07 ± 0.09	0.16 ± 0.02						
PWG	0.17 ± 0.09	-0.28 ± 0.07	0.18 ± 0.02					
MW2	0.82 ± 0.04	0.06 ± 0.06	0.48 ± 0.06	0.45 ± 0.03				
MW3	0.77 ± 0.05	0.03 ± 0.06	0.52 ± 0.05	0.99 ± 0.00	0.44 ± 0.03			
MW4	0.72 ± 0.05	0.01 ± 0.06	0.55 ± 0.05	0.98 ± 0.01	0.99 ± 0.00	0.49 ± 0.03		
MW5	0.68 ± 0.06	-0.01 ± 0.06	0.57 ± 0.06	0.97 ± 0.02	0.99 ± 0.01	0.99 ± 0.00	0.66 ± 0.04	
MW6	0.65 ± 0.07	-0.03 ± 0.06	0.59 ± 0.06	0.95 ± 0.03	0.98 ± 0.01	0.99 ± 0.00	0.99 ± 0.00	0.62 ± 0.05
$\hat{\sigma}_a^2$	97	88	117	716	906	1,136	1,406	1,716

[1]D = direct; M = maternal; and MW 2 (MW2) to 6 (MW6) yr of age.

models, one including grandmaternal effects and the other excluding these effects, and reported heritability estimates of 0.25 and 0.22 for WWD and 0.11 for WWM in Angus cattle. These estimates were very close to those calculated in this study (0.18 ± 0.02 and 0.16 ± 0.02 for WWD and WWM, respectively) for Red Angus cattle. Slightly decreased estimates of 0.14 and 0.17 for WWD and WWM, respectively, were reported in a study looking at growth of Nelore cattle (Eler et al., 1995). The slightly decreased estimates could be attributed to the use of a multivariate model analyzing birth weight, WW, and YW, whereas the present study used a random regression model that included MW. Winder et al. (1990), analyzing growth rate in Red Angus cattle, reported a slightly greater estimate for WWD (0.39). They mention this could be due to the use of a nested model, which results in slight overestimation of variance parameters.

The moderate heritability estimate for PWG agreed with estimates in the literature, but was a little less than the value of 0.28 assumed by RAAA in their genetic evaluation. An estimate of 0.21 was obtained in a multiple trait mixed model analysis by Sapp et al. (2004) when including teat scores in first-parity Gelbvieh cows. A Red Angus data set yielded an estimate of 0.36, which, although slightly greater than the estimate in this study, is still considered moderate in magnitude (Winder et al., 1990). A comparable estimate, also

from Red Angus data, of 0.31 was reported by Evans et al. (2000). Their study involved analysis of MW as a repeated measure in which a uniform (co)variance structure is assumed, unlike the present study, which allowed this structure to change from one MW measure to the next.

Literature estimates for heritability of MW range from 0.21 (Brown et al., 1972; Roughsedge et al., 2005) to 0.84 (Choy et al., 2002), suggesting selection for or against MW would be effective. The heritability of MW in this study was estimated to range from 0.44 to 0.66 for BW taken at 2 to 6 yr of age. The smallest estimate of heritability came from 3 yr of age and the greatest came from 5 yr of age, in agreement with previous findings that heritability increases with age (Evans, 2001). The increasing trend in heritability might reflect differences in rates of maturing that disappear as cows approach their mature age or erosion of unaccounted for environmental effects from the period before first calving.

Evans (2001) applied random regression with a linear term to both the additive genetic and residual effects in a data set representing a subset of that used in this study. Using a model consisting of fixed contemporary group effects and a linear covariate of age, heritability was 0.47, 0.57, and 0.69 for BW at 2, 4, and 6 yr of age, respectively. The smallest estimated residual covariance was between WW and PWG, whereas the

Table 4. Multivariate residual variances (on the diagonal; kg[2]), residual covariances (above diagonal; kg), and phenotypic ($\hat{\sigma}_p^2$) variances (kg[2]) for weaning weight (WW), postweaning BW gain (PWG), and mature weights (MW) adjusted to BCS 5 observed at 2 to 6 yr of age (MW2 to MW6)

Item	WW	PWG	MW2	MW3	MW4	MW5	MW6
WW	355	-61	242	272	276	277	289
PWG		523	227	173	117	107	69
MW2			869	533	507	513	520
MW3				1,173	757	700	619
MW4					1,172	715	690
MW5						1,067	614
MW6							1,047
$\hat{\sigma}_p^2$	546	640	1,585	2,079	2,308	2,121	2,763

Table 5. Random regression estimates of genetic correlations $\pm$ SE (below diagonal) and genetic variances ($\hat{\sigma}_a^2$) for metabolic weaning weight (metWW), metabolic postweaning BW gain (metPWG), metabolic mature BW intercept (metb0), and metabolic mature weight slope (metb1)[1]

Item	metWWD	metWWM	metPWG	metb0	metb1
metWWD					
metWWM	0.12 ± 0.09				
metPWG	0.04 ± 0.09	-0.36 ± 0.07			
metb0	0.71 ± 0.05	0.01 ± 0.06	0.47 ± 0.05		
metb1	0.21 ± 0.17	-0.19 ± 0.14	0.60 ± 0.15	0.79 ± 0.10	
$\hat{\sigma}_a^2$	3.51	2.80	3.62	26.45	1.55

[1]D = direct; M = maternal.

greatest was between MW at 3 and 4 yr of age. The negative relationship between WW and PWG could be due to compensatory BW gain often seen in cattle with low WW.

Nobre et al. (2003) used random regression models to analyze BW observed from birth to 733 d of age in Nelore cattle. Using a cubic polynomial, those researchers found genetic and residual variances that tended to increase with age in a similar fashion as estimates from the present study. In the study by Meyer (1999), cubic random regression was used to model MW observed at 2 to 10 yr of age in Hereford and composite cows. Meyer (1999) reported that residual variances were greatest for records at 3 yr of age and least for records at 2 yr of age. A similar tendency was observed in the current study with the greatest residual variances being observed at 3 and 4 yr of age.

Genetic variance-covariance estimates for the analysis of metMW are in Table 5. The genetic variance increased from weaning to yearling age, as did the results obtained for untransformed BW.

Metabolic (Table 6) and untransformed BW (Table 3) heritabilities are in agreement overall. Heritability estimates for metWW and metMW observed at 2, 3, 5, and 6 yr of age are slightly less in comparison with the untransformed BW estimates, although the trend of increasing with age is still apparent. Both untransformed and metabolic BW additive genetic variances tended to

increase with age (Tables 3 and 6), and this trend was comparable with that observed by Evans (2001). Residual variances for MW (Table 4) and metMW (Table 7) at 5 and 6 yr of age tended to decrease from those at 3 and 4 yr of age; however, this could be due to the reduced number of observations associated with the 2 categories of greatest age in this study. As was observed for untransformed BW, the residual covariance for metabolic BW between MW at 3 and 4 yr of age was greatest, whereas that between WW and PWG was least.

Genetic Correlations

Genetic correlations among untransformed or metabolic BW were similar and are in Tables 3 and 6, respectively. Because literature estimates for metabolic BW were not available, comparisons involved only untransformed BW. The low correlation (0.07) between WWD and WWM indicates that selection to improve the direct component has little effect on the maternal component (Table 3). The estimate is close to the zero value assumed by RAAA in their genetic evaluation and similar to several studies that found this correlation to be low, but negative (Koots et al., 1994; Bennett and Gregory, 1996; Mwansa et al., 2002; MacNeil, 2005). Recently, Speidel et al. (2007) analyzed WW inheritance based on the nutritional environment provided by

Table 6. Multivariate estimates of heritability $\pm$ SE (top number on the diagonal), genetic correlations $\pm$ SE (below diagonal) and genetic variances ($\hat{\sigma}_a^2$) for metabolic weaning weight (metWW), metabolic postweaning BW gain (metPWG), and metabolic mature BW (metMW) adjusted to BCS 5 observed at 2 to 6 yr of age, estimated from Table 5 results from a random regression model for mature BW[1]

Item	metWWD	metWWM	metPWG	metMW2	metMW3	metMW4	metMW5	metMW6
metWWD	0.18 ± 0.02							
metWWM	0.12 ± 0.09	0.14 ± 0.02						
metPWG	0.04 ± 0.08	-0.36 ± 0.07	0.18 ± 0.02					
metMW2	0.81 ± 0.04	0.07 ± 0.06	0.39 ± 0.06	0.44 ± 0.03				
metMW3	0.76 ± 0.05	0.04 ± 0.06	0.44 ± 0.06	0.99 ± 0.00	0.43 ± 0.03			
metMW4	0.71 ± 0.05	0.01 ± 0.06	0.47 ± 0.05	0.98 ± 0.01	0.99 ± 0.00	0.49 ± 0.03		
metMW5	0.67 ± 0.06	-0.01 ± 0.06	0.49 ± 0.06	0.97 ± 0.02	0.99 ± 0.01	0.99 ± 0.00	0.65 ± 0.04	
metMW6	0.64 ± 0.07	-0.03 ± 0.06	0.51 ± 0.06	0.95 ± 0.03	0.98 ± 0.01	0.99 ± 0.00	0.99 ± 0.00	0.60 ± 0.05
$\hat{\sigma}_a^2$	3.51	2.80	3.62	17.87	21.77	26.45	31.90	38.13

[1]D = direct; M = maternal; and MW 2 (MW2) to 6 (MW6) yr of age.

Table 7. Multivariate residual variances [on the diagonal $(kg^{0.75})^2$], residual covariances (above diagonal; $kg^{0.75}$), and phenotypic $(\hat{\sigma}_p^2)$ variances $[(kg^{0.75})^2]$ for metabolic weaning weight (metWW), metabolic postweaning BW gain (metPWG), and metabolic mature weights (metMW) adjusted to BCS 5 observed at 2 to 6 yr of age (metMW2 to metMW6)

Item	metWW	metPWG	metMW2	metMW3	metMW4	metMW5	metMW6
metWW	13.20	−3.30	7.50	8.17	8.17	8.13	8.54
metPWG		16.02	5.60	3.89	2.40	2.17	1.10
metMW2			22.77	13.32	12.33	12.47	12.78
metMW3				28.95	18.20	16.71	14.81
metMW4					28.07	16.90	16.30
metMW5						25.38	14.70
metMW6							25.09
$\hat{\sigma}_p^2$	16.71	19.64	40.63	50.73	54.52	48.80	63.22

the dam and reported genetic correlation estimates of −0.47 and −0.20 between WWM and WWD for good and poor environments, respectively. These estimates are less than that reported in this study (0.07); however, the current study did not analyze WW in the same manner. An estimate of similar magnitude in the opposite direction (−0.09) to the one from the present study was found by Evans et al. (2000) with a multiple trait analysis that included MW observed at 3 yr of age, as well as WW. This negative correlation has been attributed to a dam with superior milking ability producing more milk than her calf requires, leading to excess fat and a decrease in growth rate (Willham, 1972).

Weaning weight direct was found to have a moderate positive correlation with PWG (0.17), which indicates selection for WWD will increase gain from 205 to 365 d of age. Winder et al. (1990) reported a similar estimate (0.18) of the genetic correlation between WWD and PWG in Red Angus cattle, although Brinks et al. (1964) obtained a much smaller estimate of −0.20. The extremely low correlation reported by Brinks et al. (1964) may be due to the severe Montana winter experienced by the cattle in that study. Few estimates of correlations between PWG and WWM could be located in the literature. Garrick et al. (1989) obtained estimates of 0.22 or −0.02 in sire-maternal grandsire analyses of Simmental-cross or ≥75% Simmental calves, respectively. Bennett and Gregory (1996), using a multiple trait model, obtained estimates of 0.29 and 0.18 between 200-d WWM and 168-d gain for purebred and composite beef cattle, respectively, though this study found a much smaller estimate of −0.28.

Correlations between WWM and MW at various ages were near zero and ranged from −0.03 to 0.06. Estimates from the literature range from −0.45 (Kaps et al., 1999) to 0.01 (Evans et al., 2000) and encompass those in the current study. More research should be conducted to determine this relationship.

Numerous estimates of the correlation between WWD and MW have been reported in the literature. Former estimates have ranged from 0.51 (Brinks et al., 1964) to 0.85 (Brown et al., 1972), whereas more recently values of 0.49 (Meyer et al., 2004) to 0.90 (Meyer, 1995) have been reported. The greatest correlation in the current

study was that with MW at 2 yr of age (0.82). This high positive relationship indicates selection for an increase in WW will likely lead to correlated response in MW. Cattle with heavier MW have been shown to require more feed to maintain their BW (Montano-Bermudez et al., 1990); therefore, greater WW typically rewarded by the market is leading to greater feed costs to the cow-calf producer in the long run. Profit made from cattle at weaning may be going back into maintaining the cow herd.

Postweaning BW gain and MW were discovered to have a high, positive relationship of 0.48 to 0.59. Evans et al. (2000) reported an average estimate of 0.68 between MW observed at 2 to 9 yr of age and PWG. Although their estimate is slightly greater than the estimates in this study, the current study looked only at MW observed at 2 to 6 yr of age. Other estimates include 0.76 (Bullock et al., 1993) and 0.35 (Brinks et al., 1964) and are similar in magnitude to those reported here. This relationship suggests that bulls that sire offspring with a greater rate of BW gain will likely have heavier MW as adults. Fitzhugh and Taylor (1971) deduced that an increase in maturity at any age should increase growth rate before 12 mo of age and is reflected in the positive relationship exhibited in this study.

The genetic correlations between different MW age categories were estimated to be high and positive, indicating that selection on MW at an early age will have a correlated response on MW at an older age. Correlations were greater between ages that were closer together than those farther apart. The greatest genetic correlation calculated was 0.99, suggesting that the 2 measurements were essentially the same trait. Exploring MW at 2 to 10 yr of age in Red Angus cows with a similar data set to that used in this study, Evans (2001) arrived at genetic correlation estimates of 0.95 to 0.96 between BW at 2 to 4 yr of age. Not surprisingly, these same correlations calculated in the current study are very similar and in agreement.

The genetic correlations among metabolic BW are in Table 5. Estimates ranged from −0.19 to 0.79 with the greatest correlation calculated between the b0 and b1 coefficients. The metWWM and the metb1 were negatively correlated, which is expected because un-
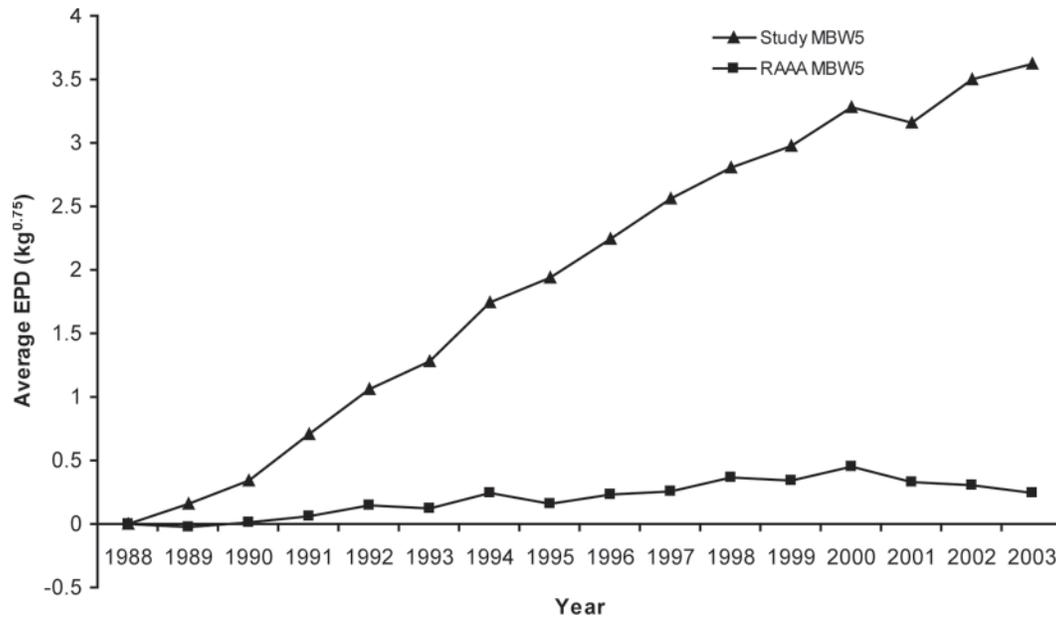
Figure 1. Average EPD for metabolic BW ($kg^{0.75}$) at constant BCS, and 5 yr of age (metBW5) by birth year for the Red Angus Association of America (RAAA, 2006) and for the current study accounting for selection on immature weights of Red Angus cattle born from 1988 to 2003.

transformed MW and WWM were also negatively correlated.

A similar random regression model with the addition of a quadratic term for MW was attempted in this study because growth has been suggested to follow a sigmoidal curve (Brody, 1945); however, convergence could not be reached by ASREML. Therefore, no results from that model were presented.

The correlations and heritabilities reported in this study agree with the literature. The authors are unaware of any previous studies in the literature that have attempted to fit immature BW together with MW into a random regression model in which regression coefficients are fitted only for MW. This study has provided a simple alternative method that can be implemented to analyze immature and MW together using random regression.

Maintenance Energy Requirements

Genetic trends for metMW5 reported by the RAAA and those estimated in this study with the year 1988 set as the base are in Figure 1. Although the magnitude of the trends is different, they both show a constant increase in mature metabolic BW from 1988 to 2000 and are reflective of the preferences of producers for cattle with heavier WW and YW that are associated with correlated increases in MW. The trend produced from the EPD generated in this study shows a continued increase in MW from 2000 to 2003, whereas the RAAA trend shows a slight decrease. Presumably, cattle producers are selecting for animals with heavier immature BW; however, the consequence is heavier MW in the cow herd and the current RAAA analysis is not properly accounting for this prior selection.

The current study shows an increase from 1988 to 2003 in metabolic BW of 3.6 $kg^{0.75}$, whereas that from the RAAA for the same period was a 0.23 $kg^{0.75}$ increase. These resulting EPD differences indicate that adding metWW and metPWG to the analysis of metMW accounts for some selection bias in the current analysis. It may be that sires with poorer growing offspring had only their heaviest daughters kept as replacements, reducing the apparent genetic trend for MW when the preselection of replacements was ignored in the analysis. In not accounting for the performance of the culled animals, the current analysis portrays these sires with inflated EPD for metMW compared with sires with a greater proportion of progeny having MW observations (Bourdon, 2000).

A similar trend to that for metabolic BW can be seen in the resulting ME EPD (Figure 2). The current analysis used by RAAA is not accounting for the selection that is taking place on animals at weaning or 1 yr of age, and this is leading to bias in the MW and ME EPD. This method is failing to reward those bulls producing offspring with heavy WW and low ME requirements. To account for the selection of animals with heavier immature BW such as WW, the MW analysis should include these younger observations.

The rank correlation calculated between the 2 sets of EPD was 0.63, indicating significant reranking of sires due to the inclusion of metWW and metPWG observations. Sires currently appearing to have superior genetic merit for ME encounter a change in status once immature BW are accounted for in the MW analysis. Therefore, the currently reported EPD could be very misleading to producers trying to decrease maintenance requirements in their cow herd.

In conclusion, MW is an economically relevant trait. Genetic correlations between immature weights and BW
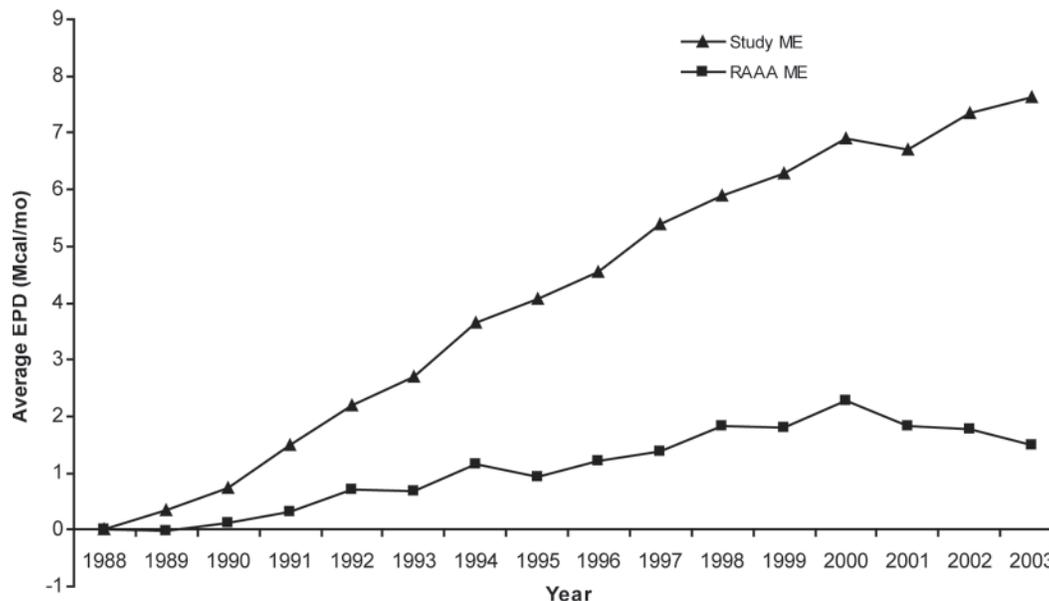
Figure 2. Average EPD for mature cow ME (Mcal/mo) by birth year for the current study and for the Red Angus Association of America (RAAA, 2006) for all Red Angus cattle born from 1988 to 2003.

observed at maturity suggest selection to increase BW at young ages will result in a corresponding response in weights at older ages. Mature cow BW is moderately to highly heritable, indicating selection to decrease BW of the cow herd would be effective. The results from this study show that the inclusion of immature weights in the MW analysis leads to reranking of sires, as well as an increase in the genetic trend currently being reported. Collectively, these results support the inclusion of metabolic immature BW in the current MW analysis as a means of removing bias due to selection that is occurring at younger ages.

LITERATURE CITED

Bennett, G. L., and K. E. Gregory. 1996. Genetic (co)variances among birth weight, 200-day weight, and postweaning gain in composites and parental breeds of beef cattle. J. Anim. Sci. 74:2598–2611.

BIF. 2002. Guidelines for uniform beef improvement programs. Beef Improv. Fed., Univ. Georgia, Athens.

Bourdon, R. 2000. Understanding Animal Breeding. 2nd ed. Prentice-Hall, Upper Saddle River, NJ.

Brinks, J. S., R. T. Clark, N. M. Kieffer, and J. J. Urick. 1964. Estimates of genetic, environmental and phenotypic parameters in range Hereford females. J. Anim. Sci. 23:711–716.

Brody, S. 1945. Bioenergetics and Growth. Reinhold Publ. Corp., New York, NY.

Brown, J. E., C. J. Brown, and W. T. Butts. 1972. A discussion of the genetic aspects of weight, mature weight and rate of maturing in Hereford and Angus cattle. J. Anim. Sci. 34:525–537.

Bullock, K. D., J. K. Bertrand, and L. L. Benyshek. 1993. Genetic and environmental parameters for mature weight and other growth measures in Polled Hereford cattle. J. Anim. Sci. 71:1737–1741.

Choy, Y. H., J. S. Brinks, and R. M. Bourdon. 2002. Repeated-measure animal models to estimate genetic components of mature weight, hip height, and body condition score. J. Anim. Sci. 80:2071–2077.

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.

Eler, J. P., L. D. Van Vleck, J. B. S. Ferraz, and R. B. Lobo. 1995. Estimation of variances due to direct and maternal effects for growth traits of Nelore cattle. J. Anim. Sci. 73:3253–3258.

Enns, R. M., D. J. Garrick, and S. E. Speidel. 2003. Maintenance Energy Requirements The Technical Details Explained. Red Angus Association of America. www.redangus.org/index.php Accessed May 11, 2007.

Evans, J. L. 2001. Genetic prediction of mature weight and mature cow maintenance energy requirements in Red Angus cattle. PhD Diss. Colorado State Univ., Fort Collins.

Evans, J. L., B. L. Golden, R. M. Bourdon, and R. L. Hough. 2000. Genetic parameter estimates for mature weight, weaning weight, and postweaning gain in Red Angus cattle. Proc. West. Sec. Am. Soc. Anim. Sci., Davis, CA. Vol. 51.

Fitzhugh, H. A. Jr., and St. C. S. Taylor. 1971. Genetic analysis of degree of maturity. J. Anim. Sci. 33:717–725.

Garrick, D. J., E. J. Pollak, R. L. Quaas, and L. D. Van Vleck. 1989. Variance heterogeneity in direct and maternal weight traits by sex and percent purebred for Simmental-sired calves. J. Anim. Sci. 67:2515–2528.

Gilmour, A. R., B. J. Gogel, B. R. Cullis, S. J. Welham, and R. Thompson. 2002. ASReml User Guide Release 1.0 VSN Int. Ltd., Hemel Hempstead, UK.

Golden, B. L., D. J. Garrick, S. Newman, and R. M. Enns. 2000. Economically Relevant Traits A Framework for the Next Generation of EPD. Proc. Beef Improv. Fed. 32:2–13.

Golden, B. L., W. M. Snelling, and C. H. Mallinckrodt. 1992. Animal breeder's tool kit user guide and reference manual. Colorado State Univ., Fort Collins.

Henderson, C. R. 1984. Applications of Linear Models in Animal Breeding. Univ. Guelph Press, Guelph, Canada.

Kaps, M., W. O. Herring, and W. R. Lamberson. 1999. Genetic and environmental parameters for mature weight in Angus cattle. J. Anim. Sci. 77:569–574.

Kirkpatrick, M., D. Lofsvold, and M. Bulmer. 1990. Analysis of the inheritance, selection and evolution of growth trajectories. Genetics 124:979–993.

Koots, K. R., J. P. Gibson, and J. W. Wilton. 1994. Analyses of published genetic parameter estimates for beef production traits.

2. Phenotypic and genetic correlations. Anim. Breed. Abstr. 62:825–853.

MacNeil, M. D. 2005. Genetic evaluation of the ratio of calf weaning weight to cow weight. J. Anim. Sci. 83:794–802.

MacNeil, M. D., D. R. C. Bailey, J. J. Urick, R. P. Gilbert, and W. L. Reynolds. 1991. Heritabilities and genetic correlations for postweaning growth and feed intake of beef bulls and steers. J. Anim. Sci. 69:3183–3189.

MacNeil, M. D., and T. B. Mott. 2000. Using genetic evaluations for growth and maternal gain from birth to weaning to predict energy requirements of Line 1 Hereford beef cows. J. Anim. Sci. 78:2299–2304.

Meyer, K. 1995. Estimates of genetic parameters for mature weight of Australian beef cows and its relationship to early growth and skeletal measures. Livest. Prod. Sci. 44:125–137.

Meyer, K. 1999. Estimates of genetic and phenotypic covariance functions for postweaning growth and mature weight of beef cows. J. Anim. Breed. Genet. 116:181–205.

Meyer, K., D. J. Johnston, and H. Graser. 2004. Estimates of the complete genetic covariance matrix for traits in multi-trait genetic evaluation of Australian Hereford cattle. Aust. J. Agric. Res. 55:195–210.

Montano-Bermudez, M., M. K. Nielsen, and G. H. Deutscher. 1990. Energy requirements for maintenance of crossbred beef cattle with different genetic potential for milk. J. Anim. Sci. 68:2279–2288.

Mwansa, P. B., D. H. Crews Jr., J. W. Wilton, and R. A. Kemp. 2002. Multiple trait selection for maternal productivity in beef cattle. J. Anim. Breed. Genet. 199:391–399.

Myers, S. E., D. B. Faulkner, F. A. Ireland, L. L. Berger, and D. F. Parrett. 1999. Production systems comparing early weaning to normal weaning with or without creep feeding for beef steers. J. Anim. Sci. 77:300–310.

Nobre, P. R. C., I. Misztal, S. Tsuruta, J. K. Bertrand, L. O. C. Silva, and P. S. Lopes. 2003. Analyses of growth curves of Nellore cattle by multiple-trait and random regression models. J. Anim. Sci. 81:918–926.

Northcutt, S. L., and D. E. Wilson. 1993. Genetic parameter estimates and expected progeny differences for mature size in Angus cattle. J. Anim. Sci. 71:1148–1153.

NRC. 1996. Nutrient Requirements of Beef Cattle. 7th ed. Natl. Acad. Press, Washington, DC.

RAAA. 2006. Rancher's guide to EPD: Cows eat money. Red Angus Assoc. Am., Denton, TX. http://redangus.org/index.php Accessed May 15, 2006.

Roughsedge, T., P. R. Am, R. Thompson, and G. Simm. 2005. Genetic parameters for a maternal breeding goal in beef production. J. Anim. Sci. 83:2319–2329.

Sapp, R. L., R. Rekaya, and J. K. Bertrand. 2004. Teat scores in first-parity Gelbvieh cows: Relationship with suspensory score and calf growth traits. J. Anim. Sci. 82:2277–2284.

Speidel, S. E., R. M. Enns, and D. J. Garrick. 2007. Weaning weight inheritance in environments classified by maternal body weight change. J. Anim. Sci. 85:610–617.

Tennant, C. J., J. C. Spitzer, W. C. Bridges Jr., and J. H. Hampton. 2002. Weight necessary to change body condition scores in Angus cows. J. Anim. Sci. 80:2031–2035.

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.

Winder, J. A., J. S. Brinks, R. M. Bourdon, and B. L. Golden. 1990. Genetic analysis of absolute growth measurements, relative growth rate and restricted selection indices in Red Angus cattle. J. Anim. Sci. 68:330–336.

Wood, P. D. P. 1969. Factors affecting the shape of the lactation curve in cattle. Anim. Prod. 11:307–316.

References

This article cites 31 articles, 24 of which you can access for free at:
http://www.journalofanimalscience.org/content/87/5/1628#BIBL