Genetic analysis of gain from birth to weaning, milk production, and udder conformation in Line 1 Hereford cattle[1,2]

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ABSTRACT: The objective of this research was to partition phenotypic variation in calf gain from birth to weaning, and milk production measured, by the weigh-suckle-weigh method, and udder score of cows into genetic and nongenetic components. Data were from the Line 1 Hereford population maintained by USDA-ARS at Miles City, MT, and included observations of preweaning gain (n = 6,835) from 2,172 dams, milk production (n = 692) from 403 cows, and udder score (n = 1,686) from 622 cows. Data were analyzed using a Gibbs sampler for multiple-trait animal models. Results are reported as means ± SD derived from the posterior distributions of parameter estimates. Mean estimates of the phenotypic variance of preweaning gain, milk production, and udder score were 476.3 kg^2, 8.88 kg^2, and 1.89 (1 to 9 scale), respectively. Estimates of phenotypic correlations between preweaning gain and milk production, preweaning gain and udder score, and milk production and udder score were 0.37 ± 0.04, –0.07 ± 0.04, and –0.09 ± 0.05, respectively. Estimates of heritability for direct and maternal preweaning gain, milk production, and udder score were 0.13 ± 0.03, 0.25 ± 0.04, 0.25 ± 0.06, and 0.23 ± 0.05, respectively. Genetic correlations of milk production with maternal preweaning gain and udder score were estimated as 0.80 ± 0.08 and –0.36 ± 0.16, respectively. Posterior distributions of the other genetic correlations all contained 0.00 within the respective 90% probability density posterior intervals. Estimates of repeatability of maternal preweaning gain, milk production, and udder score were 0.43 ± 0.03, 0.39 ± 0.05, and 0.34 ± 0.03, respectively. Breeding value for maternal gain from birth to weaning was highly predictive of breeding value for milk production. Direct measurement of milk production to use in genetic improvement may not be justified because it is difficult to measure, and selection based on the breeding value for maternal preweaning gain may be nearly as effective in changing milk production as direct selection. A potentially undesirable consequence of selection to increase milk production is the degradation of udder quality. However, this correlation is not so strong as to preclude simultaneous improvement of milk production and udder quality using appropriate predicted breeding values for each trait.

Key words: genetic correlation, growth, heritability, maternal, udder score

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INTRODUCTION

Milk production has been positively related to beef production efficiency (Kress et al., 1969; Freking and Marshall, 1992; Miller et al., 1999). Whereas milk production has only been assessed directly in experimental settings, partitioning gain from birth to weaning into direct and maternal genetic effects facilitates indirect selection for presumed milk production. However, relatively few studies have validated this assumed relationship (Diaz et al., 1992; Meyer et al., 1994; Miller and Wilton, 1999). Previous estimates of genetic correlation between milk yield and maternal preweaning gain of 0.80 and 0.76 have been reported (Meyer et al., 1994; Miller and Wilton, 1999, respectively). Additional estimates of this correlation provide increased confidence in the utility of maternal breeding values for preweaning gain for changing milk production.

Large teats and pendulous udders adversely affect ability of a calf to nurse (Wythe, 1970; Frish, 1982). Thus, udder conformation motivates culling of beef

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cows (Rohrer et al., 1988; Arthur et al., 1992), and Vukašinović et al. (1994) found udder and teat scores (1 = worst to 5 = best) had positive genetic correlations with longevity. In dairy cattle, genetic correlations between udder type traits and milk production have been inconsistent with favorable and antagonistic relationships reported (Harris et al., 1992; Cruickshank et al., 2002). Sapp et al. (2004) found genetic correlations indicative of an antagonism between tight udders with small teats and maternal gain from birth to weaning in Gelbvieh cattle. Relationships between udder conformation and milk production in breeds with less genetic potential for milk production have not been reported.

Thus, objectives of this research were to 1) confirm the utility of breeding value for maternal gain from birth to weaning as a predictor of breeding value for milk production, and 2) evaluate the relationship between udder conformation and milk production in Hereford cattle.

MATERIALS AND METHODS

Procedures involving animals were reviewed and approved by the Fort Keogh Livestock and Range Research Laboratory Animal Care and Use Committee. Cattle used in this research came from the Line 1 Hereford population at Fort Keogh Livestock and Range Research Laboratory, Miles City, MT (Knapp et al., 1951; MacNeil et al., 1992; MacNeil et al., 2000). At this location, annual precipitation averages 34 cm, and 21 cm of precipitation occurs during March through July. Average temperatures are −9°C in January and 23°C in July. Broken badlands and plains rangelands typical of eastern Montana and the Northern Great Plains region provided annual support for a cow-calf pair on approximately 14 ha, with some supplemental feed during winter. Native vegetation has been predominantly western wheatgrass, Sandberg bluegrass, blue gramma grass, buffalo grass, needle-and-thread, green needle grass, thread leaf sedge, greasewood, and silver and big sagebrush. Annual brome grasses have been increasingly prevalent since the 1980s.

Calving commenced in mid March and continued until mid May of each year. Within 24 h of parturition, calves were weighed, and the udder of the cow was assessed subjectively and scored using a pictorial reference to a 9-point scale, as provided by the American Hereford Association (1981; Figure 1). Udder scores were recorded for all cows calving from 1995 through 2005. During that period, 622 cows were scored an average of 2.7 times each. These cows were sired by 107 bulls. Cow-calf pairs were moved to native rangeland spring pastures a few days after birth.

In early June, the cow-calf pairs were moved to breeding pastures of 222 to 549 ha. The first of 4 estimates of milk production was obtained using a weigh-suckle-weigh procedure within a few days of the movement to breeding pastures. Because of logistical constraints, it was only feasible to collect milk production data from samples of approximately 57 cows each year. Two subsequent estimates of milk production were similarly obtained from these same cows; the period between the first estimate and weaning was divided into 3 approximately equal intervals. A fourth and final estimate of milk production was obtained at weaning.

Each time milk production was recorded, cow-calf pairs were gathered from the breeding pastures to a central handling facility on the day preceding the data collection, and calves were separated from their dams from approximately 1500 to 1800 and then reunited and allowed to nurse. After nursing, the calves were again separated from their dams and remained apart until 0600 the next morning, when they were weighed, allowed to nurse until satiated or milk was no longer available, and quickly reweighed. The difference between weights was assumed to reflect milk consumed by the calf and to measure milk produced by the cow during the preceding 12 h. The 4 measurements of milk production for a cow during a year were totaled. Milk production was measured from 1994 through 2005. Milk production of 403 cows was measured, with an average of 1.7 observations per cow. These cows were sired by 91 bulls.

All calves were weighed and weaned on a single day, when their average age was approximately 180 d. Thus, preweaning gain was linearly preadjusted to a constant age at weaning of 180 d for use in the subsequent analysis. There were 6,835 observations of preweaning gain of calves from 2,172 dams and 252 sires.

Data analyses were conducted using a multiple-trait Gibbs sampler for animal models (Van Tassell and Van Vleck, 1996). The linear model for gain from birth to weaning was

$$Y_1 = \mu + CG_1 + b_{1,1}F_x + b_{1,2}F_d + a + u + c + e,$$

where Y_1 = a vector of observations of preweaning gain (kg) linearly preadjusted to a constant age at weaning of 180 d; μ = a constant applicable to all observations; CG_1 = a year-sex of calf-age of dam classification effect (n = 491) with age of dam recoded as 2, 3, 4, and 5+ yr, and that did not include breeding pasture; $b_{1,1}$ = the linear regression on inbreeding of calf (F_x = 0 to 1.0); $b_{1,2}$ = the linear regression on inbreeding of dam (F_d = 0 to 1.0); a = a direct genetic effect associated with the calf; u = a maternal genetic effect associated with the dam of the calf; c = a permanent environmental effect due to the dam; and e = temporary environmental effect associated with each phenotype. The linear model for milk production was

$$Y_2 = \mu + CG_2 + b_{2,1}F_d + b_{2,2}DP + u + c + e,$$

where Y_2 = the total of 4 observations of weigh-suckle-weigh milk production (kg) as described earlier; μ = a constant applicable to all observations; CG_2 = an age of cow classification effect (n = 72), with age of cow recoded as 2, 3, 4, 5, 6, or 7+ yr, and that did not

Score	Description
9	An ideal mammary system. Udder is held high up near the rear and is level in front. Teats are small.
8	Very good udder with level attachment in front and high attachment in the rear with desirable teats.
7	A sound and functional udder fairly level with small, good teats.
6	A very functional udder and teats. This is a problem free udder and teats, but will not have the balance of an udder scored 7, 8, or 9.
5	A functional udder and teats and labor free. Udder and teat scores of 5 or better should be "Labor Free."
4	An udder that could become a problem because of attachments and/or shape and size of teats.
3	A problem udder and teats. The udder will show tendencies of breaking down and teats are too large and balloon shaped.
2	A definite problem udder and teats. The udder is poorly attached in the front and back with weak suspension and teats are large and balloon shaped.
1	A very pendulous udder and balloon teats. These udders will cause frequent labor problems.

Figure 1. System for scoring udder conformation as implemented in the Total Performance Records program of the American Hereford Association (1981).

include breeding pasture; $b_{2,1}$ = the linear regression on inbreeding of cow; $b_{2,2}$ = the linear regression on day of the year when parturition occurred (DP = 58 to 143), to adjust for differences in stage of lactation; u = a direct genetic effect associated with the cow; c = a permanent environmental effect due to repeated observation of cows over years; and e = temporary environmental effect associated with each phenotype. The linear model for udder score was

$$Y_3 = \mu + CG_2 + b_{3,1}F_d + u + c + e,$$

where Y_3 = the udder score assigned to a cow at calving (1 to 9 scale) as described earlier; μ = a constant applicable to all observations; CG_2 = an age of cow classification effect (n = 66), with age of cow recoded as 2, 3, 4, 5, 6, or 7+ yr; $b_{3,1}$ = the linear regression on inbreeding of cow; u = a direct genetic effect associated with the cow; c = a permanent environmental effect due to repeated

Table 1. Estimates of the posterior mean of genetic variance (diagonal) and covariance components (above diagonal), heritability, and genetic correlation (below diagonal) for preweaning gain (G_d = direct, G_m = maternal), weigh-suckle-weigh milk production (M), and udder score (U)

Component	G_m	M	U	G_d	h^2
G_m	121.66	13.149	–1.89	2.94	0.25 ± 0.04
M	0.80 ± 0.08	2.25	–0.36	2.18	0.25 ± 0.06
U	–0.26 ± 0.17	–0.36 ± 0.16	0.44	–0.37	0.23 ± 0.05
G_d	0.04 ± 0.13	0.18 ± 0.17	–0.06 ± 0.20	63.67	0.13 ± 0.03

observation of cows over years; and e = temporary environmental effect associated with each phenotype.

The multiple-trait model expressed in matrix notation was

$$y = X\beta + Zu + Z_a a + Wc + e,$$

where y is a vector of phenotypes; β is the vector of systematic effects; u is a vector of animal effects associated with the cows (dams); a is a second vector of animal effects associated with the calves and affecting only preweaning gain; c is a vector of permanent environmental effects for repeated records of the phenotypes of each cow; e is a vector of temporary environmental effects; and X, Z, Z_a, and W are incidence matrices of appropriate dimensions associating the effects with the phenotypes. Inverted Wishart distributions were assumed for the (co)variances of u, a, c, and e, as shown here:

$$\mathrm{Var}\begin{bmatrix} u_1 \\ u_2 \\ u_3 \\ a_1 \\ c_1 \\ c_2 \\ c_3 \\ e_1 \\ e_2 \\ e_3 \end{bmatrix} = \begin{bmatrix} A\sigma^2_{u1} & A\sigma_{u1u2} & A\sigma_{u1u3} & A\sigma_{u1a1} & 0 & 0 & 0 & 0 & 0 & 0 \\ & A\sigma^2_{u2} & A\sigma_{u2u3} & A\sigma_{u2a1} & 0 & 0 & 0 & 0 & 0 & 0 \\ & & A\sigma^2_{u3} & A\sigma_{u3a1} & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & A\sigma^2_{a1} & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & I\sigma^2_{c1} & I\sigma_{c1c2} & I\sigma_{c1c3} & 0 & 0 & 0 \\ & & & & & I\sigma^2_{c2} & I\sigma_{c1c2} & 0 & 0 & 0 \\ & \text{symmetric} & & & & & I\sigma^2_{c3} & 0 & 0 & \\ & & & & & & & I\sigma^2_{e1} & 0 & 0 \\ & & & & & & & & I\sigma^2_{e2} & I\sigma_{e2e3} \\ & & & & & & & & & I\sigma^2_{e3} \end{bmatrix},$$

where A is the additive relationship matrix among all animals in the pedigree file (n = 8,507); and I denotes identity matrices of dimensions equal to number of calves for residual effects on preweaning gain, and to number of cows/dams for all permanent environmental effects and for residual effects on milk production and udder score.

Shape parameters (**p**) for the inverted Wishart distributions were set equal to the minimums required for proper priors; p = 6 for animal effects, p = 5 for permanent environmental effects, p = 3 for temporary environmental effects on preweaning gain, and p = 4 for temporary environmental effects on milk production and udder score. Note that the temporary environmental covariances of milk production and udder score with preweaning gain are zero because these phenotypes are measured on different animals.

An initial analysis was conducted to obtain Gibbs samples from a chain of 55,000 rounds, saving every 50th round and discarding the first 5,000 rounds as burn-in. The Gibbsit program of Raftery and Lewis (1996) was used to evaluate the chain length, length of the burn-in period, and the thinning interval needed to obtain stationary chains of independent samples required for the cumulative distribution function of the 0.025 quantile, to be estimated within ± 0.0125, with a probability of 0.95 for each (co)variance component. Based on the results of this initial analysis, a final analysis was conducted using a burn-in of 10,000 rounds, 200,000 rounds of postburn-in Gibbs sampling, and a thinning interval of 200 rounds. In summarizing the Gibbs samples, results are reported as means ± SD of the posterior samples.

RESULTS AND DISCUSSION

Unadjusted mean values for 180-d preweaning gain, total weigh-suckle-weigh milk production, and udder score were 148.6 kg, 9.5 kg, and a score of 5.4, respectively. Corresponding phenotypic variances derived from the posterior distribution were 476.2 kg^2, 8.86 kg^2, and 1.89 (1 to 9 scale), respectively. Posterior means for the genetic (co)variance components and estimates of heritability and genetic correlation derived from these (co)variances are shown in Table 1. Average estimates of direct and maternal heritability for preweaning gain from Koots et al. (1994a) are at the 34th and 62nd percentiles of the respective posterior distributions in this study. Similarly, the average estimates for preweaning gain from this study are within 1 observed

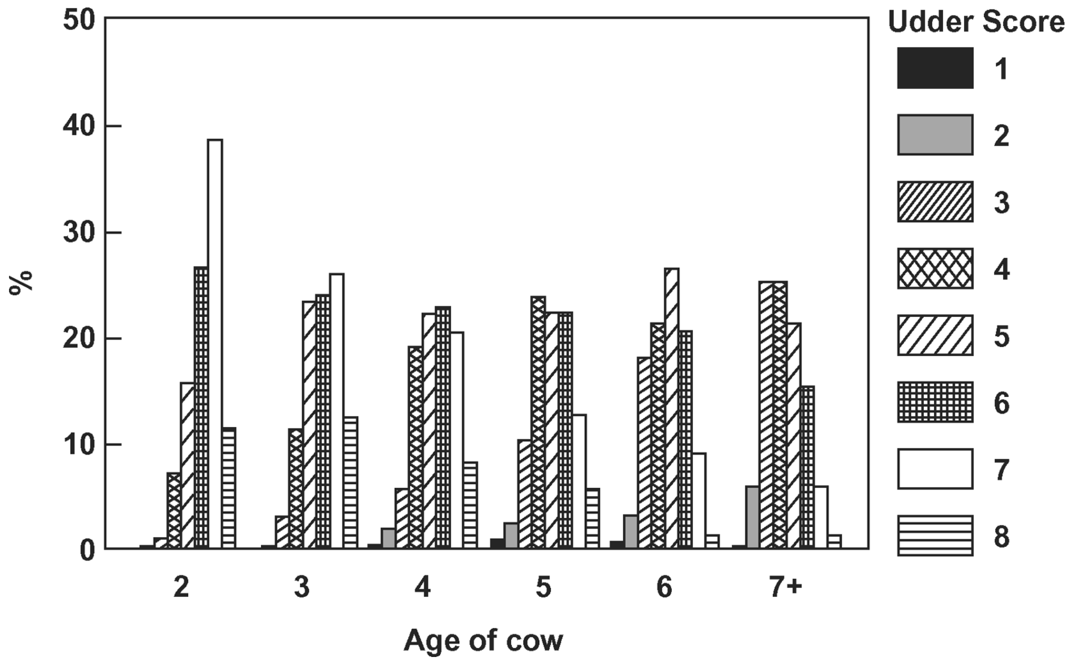

Figure 2. Percentile distributions of udder scores by age of cow.

SD of the corresponding mean of estimates summarized by Koots et al. (1994a).

The estimate of the genetic correlation between maternal effects on preweaning gain and milk production found here (0.80 ± 0.08) is consistent with similar estimates of 0.80 from Meyer et al. (1994) for Hereford and Wokalups and 0.76 from Miller and Wilton (1999) for Hereford and multibreed rotational cross cattle. The estimate of Meyer et al. (1994) was calculated from single observations of milk production per lactation obtained by the weigh-suckle-weigh method near the time of peak lactation. Miller and Wilton (1999) used 2 to 4 records from machine milking after oxytocin injection after a 6-h calf removal to estimate 200-d milk yield. Differences among studies in protocol for measuring milk production make comparisons of levels of milk production suspect. However, the consistency of estimates of the genetic correlation between milk production and maternal preweaning gain across these independent studies seems to be strong evidence to consider breeding value for maternal gain an accurate indicator of breeding value for milk production. Based on the present data, selection to change milk production using the indicator trait maternal gain from birth to weaning would be, on average, 82 ± 14% as effective as mass selection. In 11 ± 31% of samples from the posterior distribution, selection based on maternal breeding value for the indicator trait preweaning gain would be as or more efficient in altering milk production than direct selection.

The average posterior heritability of udder score estimated from these data was 0.23, in close agreement with estimates of heritability for teat and suspensory scores (0.27 and 0.22, respectively) for Gelbvieh cattle calculated by Sapp et al. (2004) using a scoring system with finer gradations than was employed here. DeNise et al. (1987) used 5-point scales in assessing the udder capacity and shape of Hereford cows and derived heritability estimates of 0.12 and 0.15, respectively, from paternal half-sib analyses. In dairy cattle, general udder conformation has been routinely described with a series of component traits. Heritability estimates for these component traits are typically of moderate magnitude, and estimates of genetic correlation among them are quite variable (e.g., Lund et al., 1994; DeGroot et al., 2002). In contrast to other investigations, here one composite score was assigned for the udder and teat conformation. Finding the genetic correlation of teat and suspensory scores to be 0.95, Sapp et al. (2004) concluded that these were practically the same trait in the Gelbvieh field data.

Genetic correlations of maternal preweaning gain and milk production with udder score (–0.26 ± 0.17 and –0.36 ± 0.16, respectively) were of similar magnitude, indicating a modest genetic antagonism with selection for increased milk production resulting in deterioration of udder quality. Sapp et al. (2004) previously observed a genetic antagonism of slightly greater magnitude. It is tempting to speculate that the difference between the correlations observed here and those found by Sapp et al. (2004) are due to the difference in level of milk production between Hereford and Gelbvieh. As udder quality decreases with age (Figure 2) and up to 10% of cows may be culled for having a poor udder (Rohrer et al., 1988; Arthur et al., 1992), selection for increased milk production may decrease length of productive life when open cows are culled (Rogers et al., 2004). However, DeNise et al. (1987) did not detect a phenotypic

Table 2. Estimates of the posterior mean of permanent environmental variance (diagonal) and covariance components (above diagonal), correlations (below diagonal), and repeatability (r_p) for preweaning gain (G), weigh-suckle-weigh milk production (M), and udder score (U)

Component	G	M	U	r_p
G	83.56	8.68	0.16	0.43 ± 0.03
M	0.87 ± 0.07	1.21	−0.12	0.39 ± 0.05
U	0.04 ± 0.17	−0.22 ± 0.21	0.21	0.34 ± 0.03

relationship between udder shape or capacity and longevity of the cow. Given the estimates of genetic parameters from this research, it should be feasible to simultaneously improve udder conformation and milk production using selection index methods.

The posterior distributions of the 3 genetic correlations with direct effects on preweaning gain contained 0.00 within the respective 90% probability density posterior intervals. There have been numerous estimates, both positive and negative, of the genetic correlation between direct and maternal effects on preweaning gain reported in the literature (e.g., Koots et al., 1994b).

Posterior estimates of variance and covariance components for permanent environmental effects due to the cows and correlations derived from them are shown in Table 2. Likewise, posterior estimates of variance and covariance components for temporary environmental effects associated with individual records and correlations derived from them are shown in Table 3. The proportions of posterior phenotypic variance due to repeated observations were 0.18 ± 0.02, 0.14 ± 0.04, and 0.11 ± 0.04 for gain from birth to weaning, weigh-suckle-weigh milk production, and udder score, respectively. Corresponding estimates of repeatability are also presented in Table 2. In contrast, DeNise et al. (1987) observed repeatability estimates of udder capacity and shape only 1 to 2% greater than the corresponding estimates of heritability. With the exception of the large positive correlation between permanent environmental effects on preweaning gain and milk production, posterior distributions of correlations among temporary environmental effects contained 0.00 within the respective 90% probability density posterior intervals. Temporary environmental effects explained the majority of phenotypic variance for all traits.

Table 3. Estimates of the posterior mean of temporary environmental variance (diagonal) and covariance components (above diagonal), and correlations (below diagonal) for preweaning gain (G), weigh-suckle-weigh milk production (M), and udder score (U)[1]

Component	G	M	U
G	204.43		
M		5.41	0.12
U		0.04 ± 0.05	1.24

[1]Covariances of G with M and U were assumed 0.00 because the phenotypes were measured on different animals.

IMPLICATIONS

The breeding value for maternal gain from birth to weaning is a useful predictor of breeding value for milk production. However, this research shows direct measurement of milk production for use in genetic improvement not to be justified because it is difficult to measure and selection based on the breeding value for maternal preweaning gain may be nearly as effective in changing milk production as direct selection. One potentially undesirable consequence of selection to increase maternal gain from birth to weaning or milk production is the degradation of udder quality, if not offset by simultaneous selection for udder conformation.

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