

# Progeny Testing Sires Selected by Independent Culling Levels for Below-Average Birth Weight and High Yearling Weight or by Mass Selection for High Yearling Weight<sup>1,2</sup>

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**ABSTRACT:** Breeding values of sires resulting from selection either for reduced birth weight and increased yearling weight (YB, n = 8) or for increased yearling weight alone (YW, n = 9) were compared with each other and with sires representative of the population before selection began (BS, n = 12) using progeny testing. Reference sires (n = 6) connected these Line 1 sires with the Hereford international genetic evaluation. Thirty-five sires produced 525 progeny that were evaluated through weaning. After weaning, 225 steer progeny were individually fed, slaughtered, and carcass data collected. Data were analyzed using restricted maximum likelihood procedures for multiple traits to estimate breeding values for traits measured on the top-cross progeny while simultaneously accounting for selection of the sires. Results of the progeny test substantiate within-line

results for traits upon which sires were selected. Breeding values for gestation length were greater in YB sires than in YW sires and were unchanged relative to BS sires. Breeding values for growth rate and feed intake for the YB and YW sires were greater than for BS sires. Predicted breeding values for indicators of fat deposition tended to be greater in YB sires and less in YW sires relative to BS sires, although YB and YW sires had similar breeding values for marbling score. Selection based on easily and routinely measured growth traits, although achieving the intended direct responses, may not favorably affect all components of production efficiency. Further, divergence of selection lines may not be easily anticipated from preexisting parameter estimates, particularly when selection is based on more than one trait.

Key Words: Beef Cattle, Selection Responses, Progeny Testing, Growth, Carcasses

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## Introduction

Net effects of selection on efficiency of beef production depend on a large number of interacting effects within the production system (Cartwright, 1974). Selection for reduced birth weight and increased yearling weight could improve production efficiency

with only minor effects on body composition (Dickerson et al., 1974). MacNeil et al. (1998) demonstrated the divergence of two sublines of Line 1 Hereford cattle, one selected by independent culling levels for below-average birth weight and high yearling weight (**YB**) and the other selected by mass selection for high yearling weight (**YW**). Frozen semen from sires of different generations may be used to produce contemporary progenies for measuring direct and correlated responses from selection (Dickerson, 1969). Primary objectives of this research were to compare breeding values for growth, feed consumption, and carcass characteristics of top-cross progeny of sires from each subline relative to the base population and to further compare the diverged sublines. A secondary objective was to characterize Line 1 relative to other Hereford germ plasm.

## Materials and Methods

Semen was collected from bulls used in Line 1 before the sublines were established (**BS**, n = 12) and

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from bulls with generation numbers between three and four of the YB ( $n = 8$ ) and YW ( $n = 9$ ) surnines. Bulls designated for semen collection were sampled from those used in the primary selection experiment (MacNeil et al., 1998), without further regard for their genetic merit. Total numbers of sires in BS, YB, and YW were 54, 11, and 14, respectively. Additive genetic relationships of sires that were progeny tested with contemporary sires that were not progeny tested were .53, .63, and .64 for BS, YB, and YW, respectively.

Matings to crossbred cows were made at random using AI to produce top-cross progenies of BS, YB, and YW sires in each of 3 yr. The cows were various crosses of predominantly Angus, Simmental, Red Angus, Charolais, and Tarentaise breeding. Numerous other breeds contributed to the genetic makeup of a small number of the cows. In addition to these Line 1 sires, semen from largely unrelated sires<sup>4</sup> (**RF**,  $n = 6$ ) was used to benchmark Line 1 relative to other Hereford germ plasm. Calves ( $n = 525$ ) were weighed at birth and reared by their dams, without creep, until weaning at approximately 180 d of age. Contemporary groups for the preweaning analysis were defined by year, sex of calf, and age of dam.

After weaning, male calves ( $n = 225$ ) were acclimated to a Calan-Broadbent feeding system (American Calan, Northwood, NH) and individually fed a backgrounding diet formulated to result in an approximate gain of 1 kg/d with intake at 2.17% of body weight until they reached 386 kg. For those traits measured during the backgrounding phase, contemporary groups were synonymous with years.

As each calf reached 386 kg, it was switched to a finishing diet formulated to result in an approximate gain of 1.4 kg/d with intake at 2.30% of body weight. All calves born in 1993 were fed the finishing diet for 100 d. Calves born in 1994 and 1995 were randomly assigned to a finishing period of either 90 or 132 d. Contemporary groups for analyses of traits expressed during the finishing period and for carcass traits were defined by year and number of days fed the finishing diet. Based on preliminary analyses of the data, age of dam effects on postweaning performance after acclimation to the individual feeding system were assumed negligible.

Upon completion of the finishing period, the steers were held without feed overnight, weighed, transported to a local abattoir, and humanely slaughtered. The liver was weighed immediately after evisceration. Following slaughter, carcasses were cooled and held at 2 to 3°C for 40 to 48 h, at which time they were graded

and fabricated into wholesale cuts (Anonymous, 1997). Excess fat was removed from the external surfaces of the wholesale cuts to a depth of approximately .5 cm, and the wholesale cuts were weighed individually.

A 2.5-cm thick steak was removed from the loin end of the wholesale rib at fabrication, vacuum-packed, and frozen at -20°C without additional aging. Subsequently, steaks were thawed for 48 h at 2 to 5°C for determination of shear force. The rack of a Faberware "Open-Hearth" electric broiler (Walter Kidde Co., Bronx, NY) was positioned 4 cm above the heating element and the broiler preheated for 10 min. Steaks were placed on the broiler with a continuously recording temperature probe (Omega Engineering, Inc., Stamford, CT) in the approximate geometric center of the steak. They were cooked on the initial side until reaching an internal temperature of 40°C, turned, and further broiled until reaching 70°C. After removal from the broiler, the steaks were allowed to cool to room temperature (minimum of 2 h). Six, 1.2-cm diameter cylindrical cores, free of connective tissue and fat globules, were obtained from the longissimus muscle of each steak and sheared using a Warner-Bratzler shear device (G-R Electrical Manufacturing Co., Manhattan, KS).

Multiple-trait mixed model methodology was used to reduce or eliminate bias in prediction of breeding values from selection of sires based on birth weight and yearling weight (Pollak et al., 1984). The model was:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \\ \mathbf{y}_3 \end{bmatrix} = \begin{bmatrix} \mathbf{x}_1\beta_1 + \mathbf{z}_1\mathbf{u}_1 \\ \mathbf{x}_2\beta_2 + \mathbf{z}_2\mathbf{u}_2 + \mathbf{z}_2\mathbf{m}_2 \\ \mathbf{x}_3\beta_3 + \mathbf{z}_3\mathbf{u}_3 + \mathbf{z}_3\mathbf{m}_3 + \mathbf{Cd} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \mathbf{e}_3 \end{bmatrix},$$

where:  $\mathbf{y}_1$  represents the phenotype of the trait of interest (Table 1) expressed by the top-cross calves and affected by fixed contemporary group effects ( $\beta_1$ ), random direct additive genetic effects ( $\mathbf{u}_1$ ), and random residual effects ( $\mathbf{e}_1$ );  $\mathbf{y}_2$  represents birth weights for Line 1 Hereford calves affected by fixed effects ( $\beta_2$ ), random direct ( $\mathbf{u}_2$ ) and maternal ( $\mathbf{m}_2$ ) genetic effects, and random residual effects ( $\mathbf{e}_2$ ); and  $\mathbf{y}_3$  represents 365-d weights for Line 1 Hereford calves affected by fixed effects ( $\beta_3$ ), random direct ( $\mathbf{u}_3$ ) and maternal ( $\mathbf{m}_3$ ) genetic effects, permanent environmental effects due to dams ( $\mathbf{d}$ ), and random residual effects ( $\mathbf{e}_3$ ). Fixed effects applicable to birth weight ( $\beta_2$ ) were contemporary groups composed of year-sex-age-of-dam subclasses, linear and quadratic regressions on Gregorian date of birth, and linear regressions on inbreeding of calf and dam. Fixed effects applicable to 365-d weight ( $\beta_3$ ) were contemporary groups composed of year-sex-age-of-dam subclasses and linear regressions on inbreeding of calf and dam. Expectations of  $\mathbf{y}_i$  are  $\mathbf{x}_i\beta_i$  and the variance covariance structure of random effects were assumed to be:

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Table 2. Average breeding values for growth traits based on top-cross progeny of four genetic groups of Hereford sires: reference sires (RF), sires from Generation 0 (BS), and sires from Generations 3 and 4 of selection by either independent culling levels for below-average birth weight and high yearling weight (YB) or by mass selection for high yearling weight (YW). The BS, YB, and YW sires collectively represent Line 1 (L1); RF sires have little pedigree relationship with L1

Trait	Genetic group				Probability			
	RF	BS	YB	YW	BS = YB	BS = YW	YB = YW	RF = L1
Birth to weaning								
Birth weight, kg	-.24	-.31	-2.10	.40	.01	.27	<.01	.57
Gestation length, d	-.84	1.35	2.99	.96	.04	.60	.01	<.01
180-d weight, kg	2.96	2.73	4.80	10.67	.52	.01	.08	.40
Backgrounding								
Daily gain, g/d	2.86	27.1	47.1	41.8	<.01	.03	.44	<.01
Time on feed, d	-.1	7.3	10.9	8.9	.04	.32	.26	<.01
ME intake, Mcal/d	-.09	.43	.68	.60	.01	.02	.32	<.01
Feed conversion, Mcal/kg	-.09	-.09	-.55	.12	<.01	.12	<.01	.57
Finishing								
Daily gain g/d	17.6	-1.03	24.0	28.5	.25	.16	.84	.98
ME intake, Mcal/d	-.02	1.84	2.54	2.06	.07	.54	.22	<.01
Feed conversion, Mcal/kg	-.07	.11	-.66	.69	<.01	.01	<.01	.66

being mitigated by harvested feedstuffs after weaning. For the carcass data, 83% of the steers sired by Line 1 Hereford bulls had carcass weights between 249 and 386 kg, Choice minus or better Quality Grade, and Yield Grade 3 or lower, simultaneously. Of the remaining 17%, 2% were underweight, 3% were Yield Grade 4 or 5, and 12% were of Select or Standard Quality Grade.

**Breeding Values for Growth and Feed Intake.** As anticipated, average breeding values for birth weight, based on top-cross progeny, of YB sires were significantly less than for YW sires (Table 2). It was expected that selection for lower birth weight and higher yearling weight would shorten gestation length and, thus, permit higher prenatal growth rate without adverse effects on calving difficulty (Dickerson et al., 1974). However, average breeding value of YB sires for gestation length was significantly greater than for YW sires (Table 2). Note that the foregoing results with respect to birth weight and gestation length were not affected by including linear and quadratic partial regressions on day born in  $\beta_2$ . Further, this unexpected result is consistent with differences in gestation length observed during 1991 and 1992 determined using chin-ball harnesses to record breeding dates in natural service and actual calving dates of YB and YW cows. In the North American Limousin population, the reciprocal relationship has been observed with the genetic trend for birth weight increasing while the genetic trend for gestation length was decreasing (Anonymous, 1998). Consistent with the usual positive genetic correlation between birth weight and gestation length (Cundiff et al., 1986), within-subline genetic and phenotypic relationships between birth weight and gestation length were positive in both YB and YW.

The preceding and seemingly conflicting results may be reconciled. Growth of the fetus occurs continu-

ously (MacNeil and Koong, 1983), although at a reduced rate in YB relative to YW, due to the reduced genetic potential for growth resulting from the selection. Maturation of the fetal pituitary-adrenal system and ACTH-mediated secretion of cortisol provides the physiological basis for initiation of parturition (Thorburn et al., 1977; Bazer and First, 1983). The involvement of these hormones in response to other stresses suggests that fetal initiation of parturition may be a response to stress (Liggins et al., 1979). This stress is presumably positively correlated with fetal weight. Thus, at a given gestational age, the YB-sired fetus would weigh less than the YW-sired fetus, and imposition of stress triggering parturition might occur later in YB than in YW. The mathematical interplay of these effects results in 1) substantial positive correlations of gestation length and birth weight within the YB and YW sire lines; 2) lighter birth weight in YB- than in YW-sired calves; and 3) longer gestation length for YB-sired calves as opposed to YW-sired calves.

The conclusion that birth weight will increase as a correlated response to selection for increased yearling weight (Olthoff et al., 1990; Morris et al., 1992; Koch et al., 1994) seems unequivocal. Most of this correlated response originates from direct effects, as shown either by the within-line results (MacNeil et al., 1998) or line-cross results (Koch et al., 1995). However, Mrode et al. (1990b) failed to detect significant correlated response in birth weight to selection for either rate or efficiency of lean gain in Hereford cattle. This result may arise from the short duration (8 yr) and relative small size of their experiment, because estimated genetic correlations of birth weight with selection criteria were positive and of moderate magnitude. Arnold et al. (1990) estimated direct effects of selection for low birth weight and high yearling weight using sires previously

evaluated in the Angus national cattle evaluation. Progeny of bulls with average birth and yearling weight EPD of 3.3 and 25.5 kg were compared with progeny of bulls with average birth and yearling weight EPD of .4 and 19.1 kg, respectively. Differences in birth weight and yearling weight between sire groups were consistent with prior predictions of the breeding values. Gestation length was similar for both groups.

Predicted breeding values indicative of genetic potentials for growth and feed conversion are presented in Table 2. Breeding values for 180-d weight were greater in YW than in either YB or BS, which were similar. Both YW and YB diverged from BS for daily gain during the backgrounding phase. Differences among genetic groups in breeding values for daily gain during the finishing phase were similar to those observed during the backgrounding phase. However, increased additive genetic variation observed during the finishing phase precluded detection of significant differences ( $P > .10$ ).

The postweaning feeding strategy used in this experiment was intended to bulk-limit feed intake during the backgrounding period and then energetically limit intake during the finishing phase. By incorporating a weight-constant point for switching from backgrounding to finishing, this strategy reduces the opportunity for expression of differences in carcass traits correlated with live weight relative to strategies incorporating time-constant endpoints. This strategy also obviates the usefulness of time-constant measurements, such as yearling weight, to describe postweaning growth. However, this strategy has the distinct advantage of routinely finishing Hereford-sired steers to an end point at which their carcasses are consistent with current market demands. It also facilitates evaluation of growth and feed intake in two distinct nutritional environments.

In the present experiment, the backgrounding phase was of variable length and ended when each calf reached 386 kg. In contrast, the finishing phase was over a time-constant interval. Thus, during backgrounding, faster growing steers would potentially have improved feed conversion relative to slower growing contemporaries as a result of being maintained on feed for fewer days. However, similar results are not necessarily anticipated during the time-constant finishing phase. Breeding values for feed intake during the backgrounding phase increased similarly in both YB and YW over BS. The tendency for YB to have greater genetic potential for feed intake than BS remained through the finishing phase. The YB subline had a consistent genetic advantage in feed conversion over both YW and BS during both the backgrounding and finishing periods. During the finishing period only, genetic potential of YW for feed conversion was compromised relative to BS.

Koch et al. (1982) found that selection of Hereford cattle for weaning weight, final weight, or an index of

final weight and muscle score improved postweaning feed conversion over an interval of 227 to 408 kg relative to cattle from a randomly selected control line. Much of this effect was attributed to the increased growth rate of the selection lines resulting in less time on feed being required to reach the prescribed final weight, rather than to any alteration of live weight gain per megacalorie of ME intake. Herd et al. (1991) compared feed requirements for Angus steers that had resulted from four generations of selection for either fast or slow yearling growth rate. Divergent selection for growth rate produced different-sized animals without altering efficiency of feed use for either maintenance or gain per unit of metabolic size.

In selecting Hereford cattle for either lean growth rate or the ratio of feed intake to lean gain, Mrode et al. (1990a) observed similar improvement of feed conversion in both lines. Relative to the control line, feed intake and lean growth rate were increased and feed conversion improved in the lean growth rate line. However, in the lean-feed conversion selected line, lean growth rate was little changed relative to the control line, with most of the improvement in feed conversion resulting from reduced feed intake.

*Breeding Values for Carcass Characteristics.* Predicted breeding values for carcass traits are shown in Table 3. The primary source of divergence among sublimes stems from the apparent increase in breeding values for fat depth and KPH fat of YB sires and a corresponding reduction in YW sires relative to BS sires. The greater genetic potential for fat deposition of YB sires was also manifest in marbling. However, breeding values for marbling of YW and BS sires were similar.

Selection for increased body weight is expected to result in larger and faster growing animals that would also be less mature at a given age (Fitzhugh, 1976). In contrast, selection for low birth weight and high yearling weight may result in less correlated increase in mature size without reducing response in yearling weight very much (Dickerson et al., 1974), and, hence, increase degree of maturity at 12 mo of age. In the context of the present experiment, one may hypothesize that at slaughter, YW-sired calves were less mature than BS-sired calves, and BS-sired calves were less mature than YB-sired calves. This hypothesis is supported by the observed changes in indicators of fat deposition, given that fatness increases with increasing degree of maturity (Taylor, 1982).

Despite the apparent increase in genetic potential for fat deposition of YB sires, breeding values for yield grade were similar in all three genetic groups. Consistent with the similarity of yield grades is the tendency for breeding values for ribeye area to be increased in YB, but not YW, sires. Even though some fat was trimmed from the external surfaces of the primal cuts, breeding values for percent primal cuts were consistent with YB sires having greater genetic potential for fat deposition than BS sires. Likewise,

Table 3. Average breeding values for carcass traits based on top-cross progeny of four genetic groups of Hereford sires: reference sires (RF), sires from Generation 0 (BS), and sires from Generations 3 and 4 of selection by either independent culling levels for below-average birth weight and high yearling weight (YB) or by mass selection for high yearling weight (YW). The BS, YB, and YW sires collectively represent Line 1 (L1); RF sires have little pedigree relationship with L1

Trait	Genetic group				Probability			
	RF	BS	YB	YW	BS = YB	BS = YW	YB = YW	RF = L1
Dressing percentage	.04	.05	-.07	.10	.17	.61	.07	.89
Carcass weight, kg	1.81	-1.78	.45	-2.68	.27	.66	.13	.18
Ribeye depth, cm <sup>2</sup>	-.22	.73	1.33	.76	.09	.93	.11	<.01
Fat depth, mm	.00	.41	1.13	.02	<.01	.04	<.01	.01
KPH fat <sup>a</sup> , %	-.00	.03	.12	-.03	<.01	<.01	<.01	.03
Yield grade	.00	.06	.06	.04	.89	.60	.72	.25
Primal cut wt, kg	.66	-1.14	-.20	-1.69	.19	.42	.05	.04
Percent primal cuts	.04	-.06	.30	-.27	<.01	.09	<.01	.70
Marbling score <sup>b</sup>	-.21	1.93	2.78	1.83	.01	.76	.01	<.01
Shear force, decagram	3.77	-9.72	-16.49	-7.92	.08	.62	.03	<.01
Liver wt, decagram	.09	-1.98	-2.22	-4.09	.82	.05	.09	.02

<sup>a</sup>Kidney, pelvic, and heart.

<sup>b</sup>One unit represents the difference between adjacent degrees of marbling, with higher scores indicating more marbling; i.e., the change between slight<sup>0</sup> and small<sup>0</sup> is +1.

the breeding values for percent primal cuts reflected YW sires' lower breeding values for external fat deposition relative to BS sires.

In the present experiment, YB sires had breeding values for shear force indicative of greater tenderness relative to the BS and YW sires. This correlated response in tenderness paralleled that of marbling score. However, it is presumptuous to ascribe cause and effect, as the genetic correlation of marbling with tenderness is only moderate (Wheeler et al., 1996).

Before beginning the selection experiment that gave rise to the sires' progeny tested here, Dickerson et al. (1974) theorized that selection for increased yearling weight and reduced birth weight would more effectively improve efficiency of beef production than selection for yearling weight alone. The gains in efficiency were proposed to result from a 10% reduction in weaning and yearling weights being offset by birth weight increasing only 44% as much with no change in backfat. Most changes in breeding values for growth observed in the present experiment seem consistent with these predictions. However, the increased breeding values for fat deposition seen here, resulting from selection of sires by independent culling levels for below-average birth weight and high yearling weight, are greater than previously anticipated.

Estimates of genetic trends for carcass traits of beef cattle are rare. Following 10 yr of selection for weight, Morris et al. (1992) observed no significant correlated response in dressing percentage, ribeye area, or fat depth. Wheeler et al. (1996) found that carcass composition and meat tenderness of steer progeny from Hereford and Angus sires born in 1982 to 1984 were not much different relative to steer progeny of Hereford and Angus sires born 1963 to 1970, despite

considerable positive genetic trend for growth in both breeds. In laboratory animals, correlated responses in percentage of body fat that result from selection for growth traits are variable, but protein content has been remarkably stable (Eisen, 1976).

*Comparison with Reference Sires.* Line 1 and other Hereford germ plasm were compared by contrasting breeding values of RF sires with the average breeding values of BS, YB, and YW sires. The RF sires had lower breeding values for gestation length than Line 1 sires, perhaps as a consequence of the delayed maturation of inbred stocks (Nelson and Lush, 1950; Dinkel et al., 1972) and natural selection against immaturity at birth (Monteiro, 1969). The RF sires had breeding values for 180-d weight similar to Line 1 sires and had lower breeding values for daily gain during the backgrounding phase. The anomalous result of RF sires also having lower breeding values than Line 1 sires for time on feed seems to result from their progeny having phenotypically greater weaning weights due to nongenetic effects that resulted in the progeny also reaching the end of the backgrounding phase with less time on feed. In separate analyses of numerous phenotypes recorded on relatively few individuals, consistent partitionings of genetic and environmental effects cannot be assured. Several analyses of time on feed and backgrounding daily gain with alternative sets of fixed effects consistently produced similar results, except when 180-d weight was included as a covariate. In this latter analysis, RF sires had breeding values for time on feed greater than Line 1 sires, but the model is not consistent with observed genetic differences between sublimes within Line 1. Also, RF sires had lower breeding values for ME intake and indicators of fat deposition. Similar to the interrelationship of breeding values for fat deposi-

tion and shear force observed among BS, YB, and YW sires, breeding values for shear force of RF sires were greater than those of Line 1 sires.

For a more limited suite of traits, similar comparisons can be made using the American Hereford Association (1998) international cattle evaluation. For birth weight, direct weaning weight, yearling weight, scrotal circumference, and maternal weaning weight, average expected progeny differences (EPD) of RF sires were .95 kg, 12.9 kg, 23.1 kg, .3 cm, and 5.1 kg and of Line 1 sires were .18 kg, 9.6 kg, 18.2 kg, .3 cm, and -1.5 kg, respectively. For the same traits, average EPD of all 1996 and 1997 Hereford calves born in 1996 and 1997 were 1.68 kg, 14.1 kg, 23.6 kg, .4 cm, and 4.1 kg, respectively. It is noteworthy that the Hereford breed is a mixture of Line 1 and other germ plasm. Variation between Line 1 and other germ plasm provides opportunities for conventional breed improvement programs and for identification of quantitative trait loci segregating within Hereford.

### Implications

Selection is an effective means for changing characteristics of populations. Basing selection on easily and routinely measured growth traits, while achieving the intended direct responses, may not favorably impact all components of production efficiency. Correlated increases in fatness resulting from selection on increased yearling weight and reduced birth weight provide one such example. In addition, not all consequences of selection may be easily anticipated from preexisting parameter estimates, as illustrated by the increase in breeding value for gestation length of sires selected for increased yearling weight and reduced birth weight.

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