Characteristics of Line 1 Hereford females resulting from selection by independent culling levels for below-average birth weight and high yearling weight or by mass selection for high yearling weight^{1,2}

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ABSTRACT: Simultaneous selection for low birth weight and high yearling weight has been advocated to improve efficiency of beef production. Two sublines of Line 1 Hereford cattle were established by selection either for below-average birth weight and high yearling weight (YB) or for high yearling weight alone (YW). Direct effects on birth weight and yearling weight diverged between sublines with approximately four generations of selection. The objective of this study was to estimate genetic trends for traits of the cows. A threeparameter growth curve $[W_t = A(1 - b_0e^{-kt})]$ was fitted to age (t, d)-weight (W, kg) data for cows surviving past 4.5 yr of age (n = 738). The resulting parameter estimates were analyzed simultaneously with birth weight and yearling weight using multiple-trait restricted maximum likelihood methods. To estimate maternal additive effects on calf gain from birth to weaning (MILK) the two-trait model previously used to analyze birth weight and yearling weight was transformed to the equivalent three-trait model with birth weight, gain from birth to weaning, and gain from weaning to yearling as dependent variables. Heritability estimates were 0.32, 0.27, 0.10, and 0.20 for A, b₀, k, and MILK, respectively. Genetic correlations with direct effects on birth weight were 0.34, -0.11, and 0.55 and with direct effects on yearling weight were 0.65, -0.17, and 0.11 for A, b₀, and k, respectively. Genetic trends for YB and YW, respectively, were as follows: A (kg/generation), 8.0 ± 0.2 and 10.1 ± 0.2 ; $b_0 \times 1,000$, -1.34 ± 0.07 and -1.16 ± 0.07 ; k (× 1,000), -14.3 ± 0.1 and 4.3 ± 0.1 ; and MILK (kg), 1.25 ± 0.05 and 1.89 ± 0.05 . Beef cows resulting from simultaneous selection for below-average birth weight and increased yearling weight had different growth curves and reduced genetic trend in maternal gain from birth to weaning relative to cows resulting from selection for increased yearling weight.

Key Words: Feed Intake, Genetic Parameters, Growth Curve, Maternal Effects

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Introduction

Net effects of selection for improved efficiency of beef production depend on a large number of interacting effects within the production system (Cartwright, 1974). The cow herd consumes approximately two-thirds to three-fourths of the feed energy used in beef production systems (Gregory, 1972; Heitschmidt et al.,

Received October 1, 1999. Accepted April 12, 2000. It has been suggested that selection for reduced birth weight and increased yearling weight could improve production efficiency, primarily through improvements in net reproduction (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). The objective of the present research was

1996). Body weight, growth rate, and milk production are commonly used indicators of energy requirements

(NRC, 1996). However, a plethora of weights measured

at numerous ages do not lend themselves to straight-

forward assessment of impacts on energy require-

ments or production systems. Nonlinear growth func-

tions provide a convenient approach to reducing a

large number of weights measured over the lifetime of each animal to a few biologically interpretable pa-

rameter estimates (Brown et al., 1976).

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to characterize genetic changes in age-weight relationships of females resulting from these selection strategies. Parameter estimates for the Brody (1945) growth function, maternal effects on growth from birth to weaning, and predicted annual energy requirements were estimated.

Materials and Methods

Cattle used in this research came from the Line 1 Hereford population at USDA, ARS, Fort Keogh Livestock and Range Research Laboratory, Miles City, MT. At this location annual precipitation averages 34 cm, with 21 cm occurring from 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 support a cow on approximately 14 ha with some supplemental feed during winter. Native vegetation is predominantly western wheatgrass, Sandberg bluegrass, blue grama grass, buffalo grass, needleand-thread, green needle grass, thread leaf sedge, greasewood, and silver and big sagebrush. Annual brome grasses were increasingly prevalent in the 1980s and early 1990s.

Management and Data Recording. Management of the Line 1 population at Fort Keogh Livestock and Range Research Laboratory from 1935 to 1989 has been chronicled by MacNeil et al. (1992). Management of the cattle through the conclusion of this experiment was similar to the protocol in place in 1989.

In late February, cows were weighed before calving. Calving commenced in late March and continued until late May of each year. The weight of each calf was recorded within 24 h of birth. Cow-calf pairs were moved to native range spring pasture a few days after parturition. In early June, cow-calf pairs were weighed and moved to smaller breeding pastures of 222 to 549 ha. A 45-d breeding season commenced approximately June 15. After the breeding season, cows were weighed and cow-calf pairs were moved to rangeland summer pasture, where they remained until weaning in mid-October when cows and calves were both weighed again.

After weaning, calves were allowed 2 to 4 wk of recovery from weaning and adaptation to their new nutritional regimen. Until 1987, weaned heifer calves were wintered on pasture and supplemented as needed to gain approximately 454 g/d. Subsequently, heifer calves were wintered in a feedlot and fed a corn silage-based diet sufficient to gain approximately 568 g/d. Yearling weights were recorded when the average age of the heifers was approximately 1 yr. The actual weights measured at weaning and yearling ages were used without adjustment in fitting the growth curves. With the onset of green grass in the spring, heifers were turned out on crested wheatgrass pasture, where they remained until they were moved to breeding pastures. Heifers were bred to the same bulls and in the

same pastures as cows. Thereafter, heifers were managed similarly to cows and all data recording was concurrent for both heifers and cows. In the fall, nonpregnant and unsound heifers were culled. Thereafter, selected females remained in the herd until they failed to conceive twice, became unsound, or reached 10 yr of age.

Formation of Selection Lines. In 1977, all females in the Line 1 Hereford herd were randomly divided into two sublines. Sires for YB were selected for belowaverage birth weight and high yearling weight phenotypes. Sires YW were selected for high yearling weight phenotype alone. Sires used in both lines to produce calves in 1978 and 1979 were born from 1973 to 1977 and were identified based on their own performance, and in some cases on progeny performance, to meet the intent of the respective selection lines. This selection of sires from the base population contributes to a founder effect, resulting in genetic divergence between lines at the start of the experiment. Generation 0 of this experiment was composed of the parents of calves born in the project in 1978 or thereafter that themselves were born before 1978 and their herd-year contemporaries. Direct responses to selection and results from progeny-testing sires representative of the base population, YB, and YW were reported by MacNeil et al. (1998, 1999).

Data Analyses. Nonlinear regression was used to fit alternative growth functions (Brown et al., 1976) to the weight-age data from each female. Convergence of these models is known to be problematic for animals that are culled before attaining most of their mature size (Morrow et al., 1978). Hence, the data set was limited to those cows attaining a minimum of 1,640 d of age (n = 738). Alternative growth models were evaluated in preliminary analyses. Goodness of fit and convergence of the nonlinear model for the greatest number of animals led to the choice of the Brody growth model (Brody, 1945) for use in this research. Thus, the model $W_t = A(1 - b_0 e^{-kt})$ was fit to the ageweight profile for each cow. In this model, t = age in days, W_t = weight (kg) at age t, A = mature size parameter, b_0 = parameter relating weight at t = 0(i.e., at birth) to mature size, and k = maturing rate parameter. When convergence of the nonlinear model was obtained, the resulting parameter estimates were used as data in subsequent analyses.

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 as follows:

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

where y_1 represents the estimate for one of the Brody growth model parameters affected by the fixed effect

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of year of birth (β_1) , random direct additive genetic effects (\boldsymbol{u}_1) , and random residual effects (\boldsymbol{e}_1) ; \boldsymbol{y}_2 represents birth weights of both male and female Line 1 Hereford calves affected by fixed effects (β_2), random direct (\boldsymbol{u}_2) and maternal (\boldsymbol{m}_2) genetic effects, and random residual effects (e_2); and y_3 represents 365-d weights for Line 1 Hereford calves of both sexes affected by fixed effects (β_3), random direct (\boldsymbol{u}_3) and maternal (m₃) genetic effects, permanent environmental effects due to dams (d), and random residual effects (e_3). Fixed effects applicable to birth weight (β_2) were contemporary groups composed of year-sex-age-ofdam subclasses, linear and quadratic regressions on Julian date of birth, and linear regressions on inbreeding of calf and dam. Fixed effects applicable to 365-d weight (β_3) were contemporary groups composed of year-sex-age-of-dam subclasses and linear regressions on inbreeding of calf and dam. Expectations of y_i are $x_i\beta_i$ and the variance covariance structure of random effects was assumed to be as follows:

$$\operatorname{Var} \left(egin{array}{c} u_1 \\ u_2 \\ u_3 \\ m_2 \\ m_3 \\ d \\ e_1 \\ e_2 \\ e_3 \end{array} \right) =$$

$$\begin{bmatrix} \boldsymbol{A}\boldsymbol{\sigma}_{u1}^2 \\ \boldsymbol{A}\boldsymbol{\sigma}_{u1,u2} & \boldsymbol{A}\boldsymbol{\sigma}^2_{u2} \\ \boldsymbol{A}\boldsymbol{\sigma}_{u1,u3} & \boldsymbol{A}\boldsymbol{\sigma}_{u2,u3} & \boldsymbol{A}\boldsymbol{\sigma}^2_{u3} \\ 0 & \boldsymbol{A}\boldsymbol{\sigma}_{u2,m2} & \boldsymbol{A}\boldsymbol{\sigma}_{u3,m2} & \boldsymbol{A}\boldsymbol{\sigma}^2_{m2} \\ 0 & \boldsymbol{A}\boldsymbol{\sigma}_{u2,m3} & \boldsymbol{A}\boldsymbol{\sigma}_{u3,m3} & \boldsymbol{A}\boldsymbol{\sigma}_{m2,m3} & \boldsymbol{A}\boldsymbol{\sigma}^2_{m3} \\ 0 & 0 & 0 & 0 & \boldsymbol{I}_d\boldsymbol{\sigma}^2_d \\ 0 & 0 & 0 & 0 & 0 & \boldsymbol{I}_s\boldsymbol{\sigma}^2_{e1} \\ 0 & 0 & 0 & 0 & 0 & \boldsymbol{I}_s\boldsymbol{\sigma}_{e1,e2} & \boldsymbol{I}_s \boldsymbol{\sigma}^2_{e2} \\ 0 & 0 & 0 & 0 & 0 & \boldsymbol{I}_s\boldsymbol{\sigma}_{e1,e3} & \boldsymbol{I}_s\boldsymbol{\sigma}^2_{e3} \end{bmatrix}$$

The numerator relationship matrix among all animals is denoted by **A**. Pedigree data included animals predating initiation of the base population and this selection experiment (MacNeil et al., 1998). The identity matrices I_d and I_s correspond to Line 1 dams (n = 907) and Line 1 calves (n = 6,663), respectively. Components σ^2_{u1} and σ^2_{e1} are direct additive genetic and residual variances for the Brody growth curve model parameter estimate. The $\sigma_{u1,u2}$ and $\sigma_{u1,u3}$ are direct genetic covariance components for the growth curve parameter estimate being analyzed with birth weight and 365-d weight, respectively. Likewise, $\sigma_{e1.e2}$ and $\sigma_{e1,e3}$ are environmental covariance components for the growth curve parameter estimate being analyzed with birth weight and 365-d weight, respectively. That portion of the preceding model for birth weight and 365d weight is identical to that used in analyzing the primary selection experiment (MacNeil et al., 1998). Thus, the following variance and covariance components were set equal to the parameter estimates previously obtained:

$$\begin{bmatrix} \sigma^{2}_{u2} \\ \sigma_{u2,u3} & \sigma^{2}_{u3} \\ \sigma_{u2,m2} & \sigma_{u3,m2} & \sigma^{2}_{m2} \\ \sigma_{u2,m3} & \sigma_{u3,m3} & \sigma_{m2,m3} & \sigma^{2}_{m3} \end{bmatrix}$$

$$\begin{bmatrix} 6.00 \\ 29.03 & 418.65 \\ 0.07 & 13.15 & 3.30 \\ -4.90 & -0.33 & 10.37 & 79.36 \end{bmatrix}$$

 $\sigma^2_d = 124.71$, and

$$\begin{bmatrix} \sigma_{e2}^2 \\ \sigma_{e2,e3} & \sigma_{e3}^2 \end{bmatrix} = \begin{bmatrix} 11.72 \\ 18.08 & 717.83 \end{bmatrix}$$

These variances and covariances were held constant throughout the analyses reported here. The remaining variance and covariance components were estimated with derivative-free REML (Graser et al., 1987; Meyer, 1989) using multiple-trait derivative-free restricted maximum likelihood programs developed by Boldman et al. (1995). MacNeil et al. (1998) could not fit permanent environmental effects due to dams on birth weight and on yearling weight simultaneously. Hence, because birth weight and yearling weight have a partwhole relationship with each other and the model including permanent environmental effects due to dams on yearling weight was the better-fitting model, the assumption that the variance of permanent environmental effects due to dams on birth weight equaled zero was retained in this research.

Various starting values for σ^2_{u1} , σ^2_{e1} , $\sigma_{u1,u2}$, $\sigma_{u1,u3}$, $\sigma_{e1,e2}$, and $\sigma_{e1,e3}$ were used in the analysis of each trait. Convergence was determined by the variance of the simplex of parameter estimates being less than 10^{-9} . Global convergence was assumed when analyses with different starting values converged to similar parameter estimates and no further improvement in the log-likelihood resulted with several restarts of the analysis. The more complete five-trait model and the fitting of maternal effects on growth curve parameters were not attempted due to the small number of animals with growth curve parameter estimates and limitations in computing resources.

In order to compute breeding values for maternal genetic effects on gain from birth to weaning the two-trait model used in previous analysis of this selection experiment (MacNeil et al., 1998) was transformed into a three-trait model and the data were analyzed again. Birth weight remained in this new model with gain from birth to weaning and gain from weaning to yearling replacing yearling weight. Thus, the new model was as follows:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \\ \mathbf{y}_3 \end{bmatrix} = \begin{bmatrix} \mathbf{x}_1 \boldsymbol{\beta}_1 + \mathbf{z}_1 \mathbf{u}_1 + \mathbf{z}_1 \mathbf{m}_1 \\ \mathbf{x}_2 \boldsymbol{\beta}_2 + \mathbf{z}_2 \mathbf{u}_2 + \mathbf{z}_2 \mathbf{m}_2 + \mathbf{C} \mathbf{d} \\ \mathbf{x}_3 \boldsymbol{\beta}_3 + \mathbf{z}_3 \mathbf{u}_3 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \mathbf{e}_3 \end{bmatrix}$$

where y_1 represents the birth weight phenotype affected by fixed effects (β_1) of year-sex-age-of-dam contemporary groups, linear and quadratic regressions on Julian date of birth, and linear regressions on inbreeding of calf and dam, random direct (\mathbf{u}_1) and maternal (m_2) additive genetic effects, and random residual effects (e_1) ; y_2 represents the 180-d gain from birth to weaning affected by fixed effects (β_2) of year-sex-ageof-dam contemporary groups and linear regressions on inbreeding of calf and dam, random direct (u_2) and maternal (\mathbf{m}_2) additive genetic effects, permanent environmental effects due to dams (d), and random residual effects (e_2); and y_3 represents the 185-d gain from weaning to 365-d of age affected by fixed effects (β_3) of year, sex, and age-of-dam subclasses and the linear regression on inbreeding of calf, random direct additive genetic effects (u_3), and random residual effects (e_3) . Expectations of y_i are $x_i\beta_i$ and the variance covariance structure of random effects was assumed to be as follows:

$$\begin{array}{c}
u_1 \\
u_2 \\
u_3 \\
m_1 \\
m_2 \\
d \\
e_1 \\
e_2 \\
e_3
\end{array}$$

$$\begin{bmatrix} \boldsymbol{A}\boldsymbol{\sigma}_{u1}^2 & \boldsymbol{A}\boldsymbol{\sigma}_{u2}^2 & & & & \\ \boldsymbol{A}\boldsymbol{\sigma}_{u1,u2} & \boldsymbol{A}\boldsymbol{\sigma}_{u2}^2 & & & & \\ \boldsymbol{A}\boldsymbol{\sigma}_{u1,u3} & \boldsymbol{A}\boldsymbol{\sigma}_{u2,u3} & \boldsymbol{A}\boldsymbol{\sigma}_{u3}^2 & & & \\ \boldsymbol{A}\boldsymbol{\sigma}_{u1,m1} & \boldsymbol{A}\boldsymbol{\sigma}_{u2,m1} & 0 & \boldsymbol{A}\boldsymbol{\sigma}_{m1}^2 & & \\ \boldsymbol{0} & \boldsymbol{A}\boldsymbol{\sigma}_{u2,m2} & 0 & \boldsymbol{A}\boldsymbol{\sigma}_{m1,m2} & \boldsymbol{A}\boldsymbol{\sigma}_{m2}^2 & & \\ \boldsymbol{0} & 0 & 0 & 0 & 0 & \boldsymbol{I}_d\boldsymbol{\sigma}_d^2 & & \\ \boldsymbol{0} & 0 & 0 & 0 & 0 & \boldsymbol{I}_s\boldsymbol{\sigma}_{e1}^2 & & \\ \boldsymbol{0} & 0 & 0 & 0 & 0 & \boldsymbol{I}_s\boldsymbol{\sigma}_{e1,e2} & \boldsymbol{I}\boldsymbol{\sigma}_{e2}^2 & \\ \boldsymbol{0} & 0 & 0 & 0 & 0 & \boldsymbol{I}_{\sigma_{e1,e2}} & \boldsymbol{I}\boldsymbol{\sigma}_{e2}^2 & & \\ \boldsymbol{0} & 0 & 0 & 0 & 0 & \boldsymbol{I}_{\sigma_{e1,e3}} & \boldsymbol{I}\boldsymbol{\sigma}_{e2,e3} & \boldsymbol{I}\boldsymbol{\sigma}_{e3}^2 & & \\ \boldsymbol{0} & 0 & 0 & 0 & \boldsymbol{0} & \boldsymbol{I}\boldsymbol{\sigma}_{e1,e3} & \boldsymbol{I}\boldsymbol{\sigma}_{e2,e3} & \boldsymbol{I}\boldsymbol{\sigma}_{e3}^2 & & \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{I}\boldsymbol{\sigma}_{e1,e3} & \boldsymbol{I}\boldsymbol{\sigma}_{e2,e3} & \boldsymbol{I}\boldsymbol{\sigma}_{e3}^2 & & \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{I}\boldsymbol{\sigma}_{e1,e3} & \boldsymbol{I}\boldsymbol{\sigma}_{e2,e3} & \boldsymbol{I}\boldsymbol{\sigma}_{e3}^2 & & \\ \boldsymbol{0} & \boldsymbol{I}\boldsymbol{\sigma}_{e1,e3} & \boldsymbol{I}\boldsymbol{\sigma}_{e2,e3} & \boldsymbol{I}\boldsymbol{\sigma}_{e3}^2 & & \\ \boldsymbol{0} & \\ \boldsymbol{0} & \\ \boldsymbol{0} & \boldsymbol{0} &$$

MacNeil and Mott (2000) demonstrated the use of genetic evaluations for birth weight, mature weight, and maternal gain from birth to weaning in predicting genetic differences in energy required for maintenance, gestation, and lactation. These genetic evaluations, combined with estimated means for the base population and a lactation curve for the population, provide several of the inputs needed by the NRC (1996) model for energy requirements. For this study, rather than use NRC (1996) default values for milk composition, estimates of milk composition were obtained from analysis of milk samples obtained by oxytocin-stimulated hand-milking of 20 Line 1 Hereford cows 8 d postpartum. The average values for percentage fat,

Table 1. Estimates of phenotypic means (\overline{x}) , phenotypic variances (σ_p^2) , and heritability (h^2) for estimated parameters of the Brody (1945) growth model, and genetic (r_g) and phenotypic (r_p) correlations of the estimated parameters with birth weight (BWT) and yearling weight (YWT)

Statistic	Growth model parameter ^a		
	A	$\mathbf{b_0}$	k
\overline{x}	595.9	.934	1.72×10^{-3}
$\sigma_{\mathrm{p}}^2 \ \mathrm{h}^2$	71.9	$3.18 imes 10^{-2}$	$5.20 imes 10^{-4}$
$h^{\hat{2}}$.32	.27	.10
$r_{\rm g}-BWT$.34	11	.55
$r_p - BWT$.11	20	.11
$r_g - YWT$.65	17	.11
$r_p - YWT$.18	32	.29

 $^{a}Growth$ model: W_{t} = A(1 - $b_{0}exp(-kt)),$ where t = age in days and W_{t} = weight at age t.

protein, and solids-not-fat (4.4, 3.8, and 9.3%, respectively) were considered constant for all animals throughout lactation. These values are numerically greater than, but within one SD of, the respective constants assumed by NRC (1996) for all beef breeds. The NE $_{\rm m}$ required by a 60-mo-old cow calving annually was calculated for each animal based on its profile of breeding values without further adjustment for environmental stress or previous plane of nutrition.

Genetic trends were determined by regression of breeding values on birth year. These regressions were tested for homogeneity across sublines. Statements regarding the significance of genetic trends result from these analyses. Note that regression on birth year is similar to regression on generation number, because the progression of generations through time was similar in both sublines (MacNeil et al., 1998).

Results and Discussion

Average values for the growth curve parameter estimates, associated phenotypic SD, and heritability estimates are shown in Table 1. Heritability estimates for all three parameters from these data were lower than most other estimates in the literature (Brinks et al., 1964; Brown et al., 1972; Smith et al., 1976; Jenkins et al., 1991). However, these differences may result not only from differences among populations studied but also from differences in estimation procedures. As in this study, there is virtually universal agreement that the genetic correlation of mature weight with weights at younger ages is positive (Smith et al., 1976; Jenkins et al., 1991). Little information was found in the literature concerning the empirical genetic correlation of the parameter b₀ with weights at birth through 365-d of age. However, increasing birth weight, other things being equal, reduces b₀. Fitzhugh (1976) asserted that selection for increased size will increase the time taken to mature, implying negative genetic covariances of the

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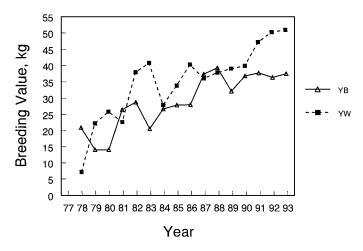


Figure 1. Breeding values for mature size of Line 1 Hereford females in sublines selected for either below-average birth weight and high yearling weight (YB) or for high yearling weight (YW) by year of birth.

maturing rate parameter (k) with both birth and yearling weight. Jenkins et al. (1991) observed interbreed genetic correlations supportive of the previous assertion but zero or positive genetic correlations within breeds, consistent with the present results.

Differences between the YB and YW lines were used as the primary basis of biological inference. In addition to arising from the imposed selection, genetic trends from unreplicated selection lines may result from random drift (Falconer, 1989). Proportions of male calves selected as sires were approximately 9% in YB and 8% in YW, and nearly every sire left at least one male offspring that was used for breeding in the subsequent generation (MacNeil et al., 1998). However, without replication of the selection lines the effect of random drift cannot be taken into account.

Shown in Figure 1 are changes in average breeding values for mature size of females in the YB and YW sublines each year over the course of this experiment. Mature cow size increased in both YB and YW sublines in response to selection applied. However, response in YB was approximately 80% of that observed in YW. This slower rate of increase in mature size of YB than of YW was anticipated from the selection applied and the genetic correlations of mature size with birth weight and yearling weight (Table 1).

The b_0 parameter decreased similarly over generations in both YB and YW sublines (Figure 2). The quantity $1-b_0$ approximates the ratio of birth weight to mature size. Thus, it seems birth weight increased similarly as a fraction of mature size in both sublines. It has been postulated that the ratio of birth weight of the calf to weight of the dam is related to the frequency of calving difficulty (Monteiro, 1969). This may help explain the lack of improvement in calving ability in response to selection for below-average birth weight and increased yearling weight that was observed by MacNeil et al. (1998). Given the observed changes in

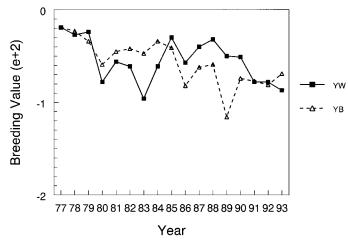


Figure 2. Breeding values for Brody growth curve initial size parameter of Line 1 Hereford females in sublines selected for either below-average birth weight and high yearling weight (YB) or for high yearling weight (YW) by year of birth.

mature size and b_0 , a genetic difference in birth weight between sublines of 1 kg was predicted to result from the 4.2 generations of selection applied. This predicted difference is approximately 42% of the difference in breeding values for birth weight observed by MacNeil et al. (1998). However, the Brody (1945) growth function is known to fit weight-age data recorded early in life less accurately than subsequent data (Brown et al., 1976).

An apparent founder effect caused the maturing rate parameter (k) to have diverged in the establishment of the YB and YW selection lines (Figure 3). However, some further divergence in maturing rate of the sublines is also apparent (P < 0.05). Throughout the course of this experiment breeding values for k in the YB subline were numerically less than corresponding breeding

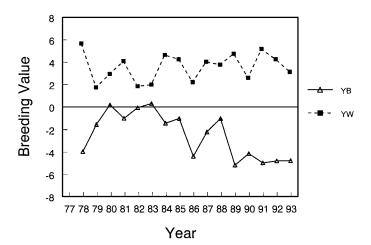


Figure 3. Breeding values (× 1,000) for maturing rate of Line 1 Hereford females in sublines selected for either below-average birth weight and high yearling weight (YB) or for high yearling weight (YW) by year of birth.

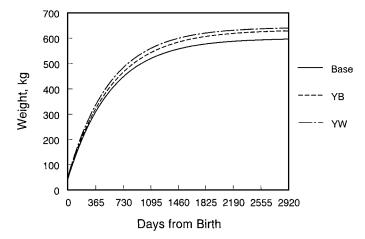


Figure 4. Growth curves of Line 1 Hereford females representative of the base population before selection was imposed and of sublines selected for either below-average birth weight and high yearling weight (YB) or for high yearling weight (YW) after approximately four generations of selection.

values in YW. Thus, the absolute value of k (which is negative) was larger in YB than in YW, and the YB subline is indicated as being earlier-maturing than the YW subline. The usual expectation is that greater values of k are associated with increased fatness at constant ages, and steer progeny of YB sires had greater genetic potential for fat deposition than contemporary YW-sired steers (MacNeil et al., 1999).

Using the average breeding values from females born in 1990 to 1993 for each of the growth curve parameters to adjust the respective mean values for females in the base population results in distinct growth curves for YB and YW (Figure 4). Granted, some differences in these growth curves may reflect the particular choice of the mathematical model used to describe growth in this research. Preliminary investigations with alternative mathematical models for describing growth resulted in the selection of the Brody growth function due to smaller average variance due to lack of fit for individual animals, especially at younger ages, and convergence of the nonlinear regression algorithm for a greater number of animals over the logistic, Gompertz, and Richards equations. These experiences in model selection are consistent with those of Brown et al. (1976). It seems both YB and YW have increased in genetic potential for mature size, the increase in YW being approximately 10 kg greater than in YB. The YB population of 1990 to 1993 reached two-thirds mature size approximately 29 d earlier than did the YW population, indicating their earlier maturity. The base population reached two-thirds mature size only 2 d earlier than YW. Thus, it seems that selection by independent culling levels for below-average birth weight and high vearling weight resulted in earlier maturation whereas selection for high yearling weight alone had little effect on maturing rate. These results are consistent with

the conclusions of Eisen (1976) summarizing selection experiments with mice and rats in that selection for body weight did little to alter the shape of the growth curve, but multiple-trait selection was effective in altering the maturation pattern. However, the results of the present experiment and the conclusion of Eisen (1976) seem at odds with the conclusion of Fitzhugh (1976), who suggested that selection for increased size increases time taken to mature.

Genetic trends in maternal effects on calf gain from birth to weaning are shown in Figure 5. A clear pattern of divergence between sublines emerged during later years of the experiment, with the maternal effect in YW being greater than in YB. However, the absolute difference between the YW and YB sublines was relatively small, corresponding to an approximately 3.5-kg difference in calf weight gain from birth through 180 d. MacNeil and Mott (2000) demonstrated the relationship between predicted breeding values for maternal genetic effect on weight gain of calf from birth to weaning and actual milk production as measured using weigh-suckle-weigh techniques. Based on these breeding values and the results of MacNeil and Mott (2000), it seems that the genetic potential for milk production of YW may have increased approximately 52% more rapidly than that of YB.

Because YW has greater breeding values for birth weight and mature size and greater genetic potential for milk production than YB, it was predicted that more energy would be required to support them (Figure 6). The average annual predicted NE $_{\rm m}$ required by YW cows born in 1990 to 1993 was 123 Mcal greater than that required by contemporary YB cows and was offset by a 5-kg greater total breeding value for gain from birth to weaning. In the commercial cow herd, natural selection for reproductive performance places a ceiling

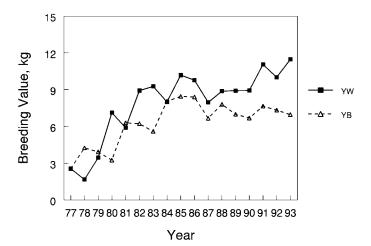


Figure 5. Breeding values for maternal genetic effects on calf weight gain from birth to weaning of Line 1 Hereford females in sublines selected for either below-average birth weight and high yearling weight (YB) or for high yearling weight (YW) by year of birth.

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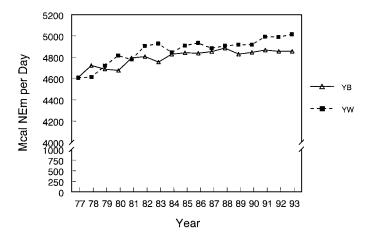


Figure 6. Genetic trends in predicted total energy requirements (sum of NE required for maintenance, growth, gestation, and lactation based on NRC, 1996) of Line 1 Hereford females in sublines selected for either below-average birth weight and high yearling weight (YB) or for high yearling weight (YW) by year of birth.

on milk production and growth (Willham, 1972). It follows that, with a fixed calving season in a limiting environment, excessive genetic potential for cow size or milk production can result in a reduced calf crop. Whether the small increase in energy required to support production of YW vs YB approaches this threshold is debatable. However, at some point genetic improvement strategies must consider not only production but also the costs of increasing production.

Implications

Selection for below-average birth weight and high yearling weight simultaneously is a selection strategy that has popular appeal. Although this strategy can result in improved postnatal performance relative to random selection, growth performance is compromised somewhat and the resulting cattle become earlier-maturing and smaller at all ages than under selection for high yearling weight alone. However, hastening maturation and reducing cow size and milk production may improve efficiency of beef production by reducing energy required by the cow herd in some production systems. The popular appeal of selecting for low birth weight and high yearling weight may stem from the perception that this strategy should change the relationship between cow size and calf birth weight while maintaining an increasing genetic trend in juvenile growth. Based on the relationship of birth weight to mature size found in this research, this perception may be flawed.

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