

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}

M. D. MacNeil^{*3}, J. J. Urick^{*}, and G. Decoudu[†]

^{*}Fort Keogh Livestock and Range Research Laboratory, USDA, ARS, Miles City, MT 59301 and

[†]Department of Mathematical Sciences, Montana State University, Bozeman 59717

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 three-parameter 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, b_0 , 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, b_0 , 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 ($\times 1,000$), -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

©2000 American Society of Animal Science. All rights reserved.

J. Anim. Sci. 2000. 78:2292–2298

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.,

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 straightforward assessment of impacts on energy requirements or production systems. Nonlinear growth functions provide a convenient approach to reducing a large number of weights measured over the lifetime of each animal to a few biologically interpretable parameter estimates (Brown et al., 1976).

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

¹This research was conducted under a cooperative agreement between USDA, ARS and the Montana Agric. Exp. Sta. USDA, ARS, Northern Plains Area, is an equal opportunity/affirmative action employer. All agency services are available without discrimination.

²Mention of a proprietary product does not constitute a guarantee or warranty of the product by USDA, Montana Agric. Exp. Sta., or the authors and does not imply its approval to the exclusion of other products that may also be suitable.

³Correspondence: Rt. 1, Box 2021 (phone: 406/232-8213; fax: 406/232-8209; E-mail: mike@larrrl.ars.usda.gov).

Received October 1, 1999.

Accepted April 12, 2000.

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, needle-and-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 below-average 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 $W_t = A(1 - b_0e^{-kt})$ was fit to the age-weight 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:

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \end{bmatrix} = \begin{bmatrix} x_1\beta_1 + z_1u_1 \\ x_2\beta_2 + z_2u_2 + z_2m_2 \\ x_3\beta_3 + z_3u_3 + z_3m_3 + Cd \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \end{bmatrix}$$

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

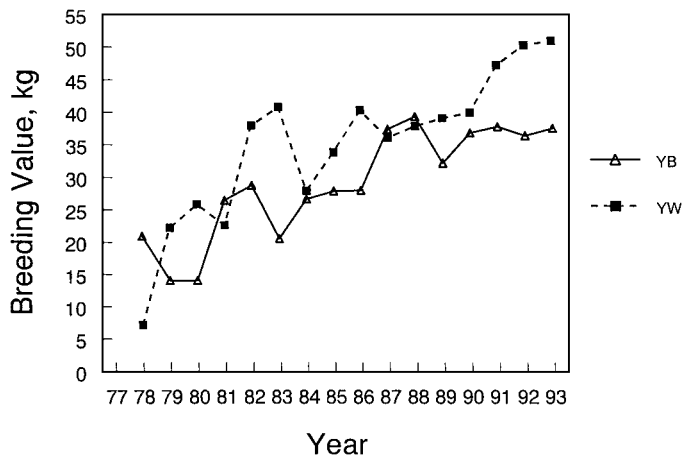


Figure 1. Breeding values for mature size of Line 1 Hereford females in sublines selected for either below-average birth weight and high yearling weight (YB) or for high yearling weight (YW) by year of birth.

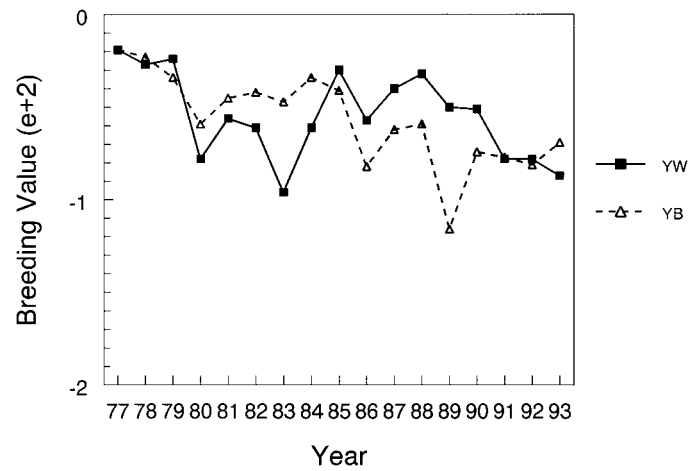


Figure 2. Breeding values for Brody growth curve initial size parameter of Line 1 Hereford females in sublines selected for either below-average birth weight and high yearling weight (YB) or for high yearling weight (YW) by year of birth.

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

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

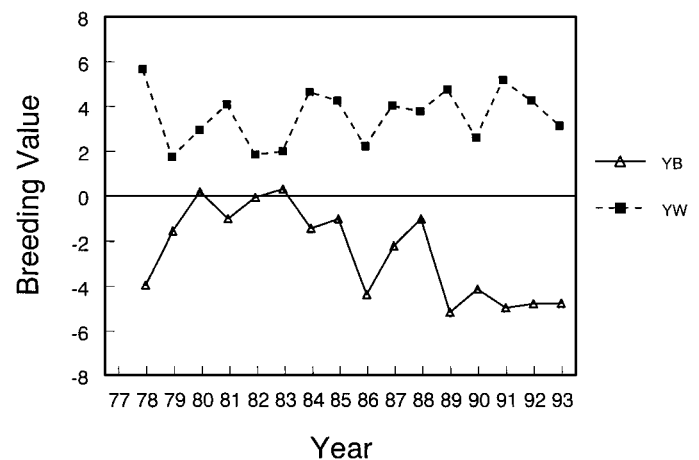


Figure 3. Breeding values ($\times 1,000$) for maturing rate of Line 1 Hereford females in sublines selected for either below-average birth weight and high yearling weight (YB) or for high yearling weight (YW) by year of birth.

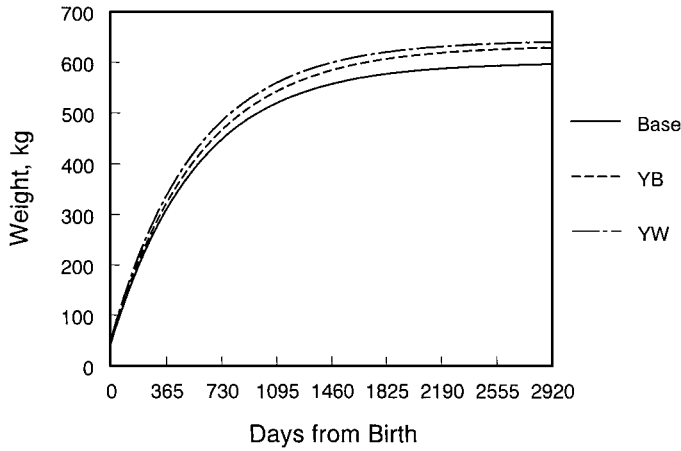


Figure 4. Growth curves of Line 1 Hereford females representative of the base population before selection was imposed and of sublines selected for either below-average birth weight and high yearling weight (YB) or for high yearling weight (YW) after approximately four generations of selection.

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 yearling 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_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

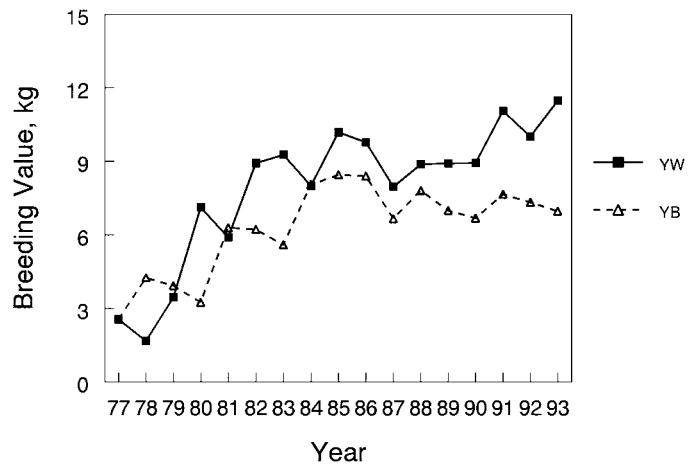


Figure 5. Breeding values for maternal genetic effects on calf weight gain from birth to weaning of Line 1 Hereford females in sublines selected for either below-average birth weight and high yearling weight (YB) or for high yearling weight (YW) by year of birth.

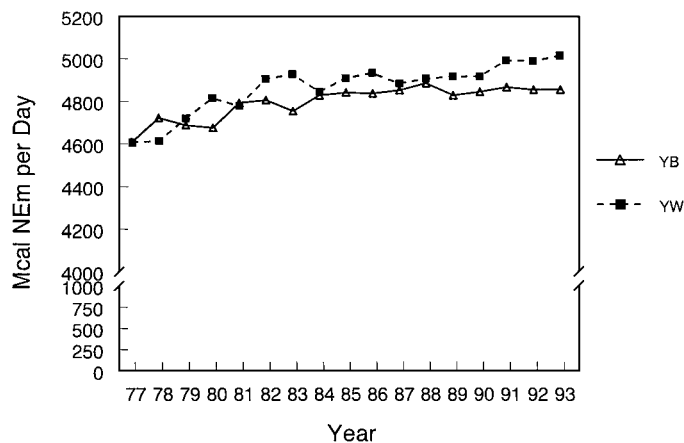


Figure 6. Genetic trends in predicted total energy requirements (sum of NE required for maintenance, growth, gestation, and lactation based on NRC, 1996) of Line 1 Hereford females in sublines selected for either below-average birth weight and high yearling weight (YB) or for high yearling weight (YW)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

Literature Cited

Boldman, K. G., L. A. Kriese, L. D. Van Vleck, C. P. Van Tassel, and S. D. Kachman. 1995. A manual for use of MTDFREML. A

set of programs to obtain estimates of variances and covariances (DRAFT). USDA, ARS, Washington, DC.

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 Publishing Corp., New York.

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.

Brown, J. E., H. A. Fitzhugh, and T. C. Cartwright. 1976. A comparison of nonlinear models for describing weight-age relationships in cattle. *J. Anim. Sci.* 42:810-818.

Cartwright, T. C. 1974. Net effects of genetic variability on beef production systems. *Genetics* 78:541-561.

Dickerson, G. E., N. Künzi, L. V. Cundiff, R. M. Koch, V. H. Arthaud, and K. E. Gregory. 1974. Selection criteria for efficient beef production. *J. Anim. Sci.* 39:659-673.

Eisen, E. J. 1976. Results of growth curve analysis in mice and rats. *J. Anim. Sci.* 42:1008-1023.

Falconer, D. S. 1989. *Introduction to Quantitative Genetics*, 3rd ed. Longman Scientific and Technical, Essex, U.K.

Fitzhugh, H. A., Jr. 1976. Analysis of growth curves and strategies for altering their shape. *J. Anim. Sci.* 42:1036-1051.

Graser, H.-U., S. P. Smith, and B. Tier. 1987. A derivative-free approach for estimating variance components in animal models by restricted maximum likelihood. *J. Anim. Sci.* 64:1362-1370.

Gregory, K. E. 1972. Beef cattle type for maximum efficiency: "Putting it all together." *J. Anim. Sci.* 34:881-884.

Heitschmidt, R. K., R. E. Short, and E. E. Grings. 1996. Ecosystems, sustainability, and animal agriculture. *J. Anim. Sci.* 74:1395-1405.

Jenkins, T. G., M. Kaps, L. V. Cundiff, and C. L. Ferrell. 1991. Evaluation of between- and within-breed variation in measures of weight-age relationships. *J. Anim. Sci.* 69:3118-3128.

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.

MacNeil, M. D., R. E. Short, and J. J. Urick. 1999. 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. *J. Anim. Sci.* 77:2345-2351.

MacNeil, M. D., J. J. Urick, S. Newman, and B. W. Knapp. 1992. Selection for postweaning growth in inbred Hereford cattle: The Fort Keogh, Montana Line 1 example. *J. Anim. Sci.* 70:723-733.

MacNeil, M. D., J. J. Urick, and W. M. Snelling. 1998. Comparison of selection by independent culling levels for below-average birth weight and high yearling weight with mass selection for high yearling weight in Line 1 Hereford cattle. *J. Anim. Sci.* 76:458-467.

Meyer, K. 1989. Restricted Maximum Likelihood to estimate variance components for animal models with several random effects, using a derivative-free algorithm. *Genet. Sel. Evol.* 21:317-340.

Monteiro, L. S. 1969. The relative size of calf and dam and the frequency of calving difficulties. *Anim. Prod.* 11:293-306.

Morrow, R. E., J. B. McLaren, and W. T. Butts. 1978. Effect of age on estimates of bovine growth-curve parameters. *J. Anim. Sci.* 47:352-357.

NRC. 1996. *Nutrient Requirements of Beef Cattle*, 7th ed. National Academy Press, Washington, DC.

Pollak, E. J., J. van der Werf, and R. L. Quaas. 1984. Selection bias and multiple trait evaluation. *J. Dairy Sci.* 67:1590-1595.

Smith, G. M., H. A. Fitzhugh, Jr., L. V. Cundiff, T. C. Cartwright, and K. E. Gregory. 1976. A genetic analysis of maturing patterns in straightbred and crossbred Hereford, Angus and Shorthorn cattle. *J. Anim. Sci.* 43:389-395.

Willham, R. L. 1972. Beef milk production for maximum efficiency. *J. Anim. Sci.* 34:864-869.