Genotype by environment interaction effects in genetic evaluation of preweaning gain for Line 1 Hereford cattle from Miles City, Montana[1]

M. D. MacNeil,*[2] F. F. Cardoso,† and E. Hay‡

*Delta G, Miles City, MT 59301 and Animal, Wildlife, and Grassland Sciences Department,
University of the Free State, P.O. Box 339, Bloemfontein 9300, South Africa; †Embrapa South Livestock,
Bagé, Brazil, and Animal Science Department, Federal University of Pelotas, 96010-900 Pelotas, Brazil; and
‡ USDA Agricultural Research Service, Fort Keogh Livestock and Range Research Laboratory, Miles City, MT 59301

ABSTRACT: It has long been recognized that genotype × environment interaction potentially influences genetic evaluation of beef cattle. However, this recognition has largely been ignored in systems for national cattle evaluation. The objective of this investigation was to determine if direct and maternal genetic effects on preweaning gain would be reranked depending on an environmental gradient as determined by year effects. Data used were from the 76-yr selection experiment with the Line 1 Hereford cattle raised at Miles City, MT. The data comprised recorded phenotypes from 7,566 animals and an additional 1,862 ancestral records included in the pedigree. The presence of genotype × environment interaction was examined using reaction norms wherein year effects on preweaning gain were hypothesized to linearly influence the EBV. Estimates of heritability for direct and maternal effects, given the average environment, were 10 ± 2 and $26 \pm 3\%$, respectively. In an environment that is characterized by the 5th (95th) percentile of the distribution of year effects, the corresponding estimates of heritability were 18 ± 3 ($22 \pm 3\%$) and $30 \pm 3\%$ ($30 \pm 3\%$), respectively. Rank correlations of direct and maternal EBV appropriate to the 5th and 95th percentiles of the year effects were 0.67 and 0.92, respectively. In the average environment, the genetic trends were 255 ± 1 g/yr for direct effects and 557 ± 3 g/yr for maternal effects. In the fifth percentile environment, the corresponding estimates of genetic trend were 271 ± 1 and 540 ± 3 g/yr, respectively, and in the 95th percentile environment, they were 236 ± 1 and 578 ± 3 g/yr, respectively. Linear genetic trends in environmental sensitivity were observed for both the direct ($-8.06 \times 10^{-4} \pm 0.49 \times 10^{-4}$) and maternal ($8.72 \times 10^{-4} \pm 0.43 \times 10^{-4}$) effects. Therefore, changing systems of national cattle evaluation to more fully account for potential genotype × environment interaction would improve the assessment of breeding stock, particularly for direct effects. Estimates of environmental sensitivity parameters could also facilitate identification of genetic limitations to production.

Key words: environmental sensitivity, genetic evaluation, preweaning growth, reaction norms

INTRODUCTION

Based on data from populations founded with germplasm from the Miles City, MT, Line 1 Hereford cattle, Burns et al. (1979) concluded that genotype × environment interaction deserves serious consideration in performance testing procedures, interregional exchange of seed stock, and sources of semen used for AI.

DeNise et al. (1988) observed fluctuating trends in estimated additive genetic variance of preweaning gain along an environmental gradient that was defined by 3 classes. Buchanan and Nielsen (1979) and Notter et al. (1992) also indicated that it might be necessary to account for sire × herd interaction effects on weaning weight in national cattle evaluations. However, they did not suggest that herd-specific breeding value prediction was necessary. Contrary to the aforementioned results, Tess et al. (1979) did not detect significant sire by geographical region effects on weaning weight among 3 disparate regions of the United States. Since the early investigations and with few exceptions (Corrêa et al., 2010; Cardoso and Tempelman, 2012; Ambrosini et al., 2016), strategies for national cattle evaluation have largely ignored effects of genotype × environment interaction (Huquet et al., 2012). However, individual producers could maximize genetic progress through the use of EBV that are more directly applicable to the environment in which they produce seed stock (Corrêa et al., 2010). Therefore, the objective of this work was to evaluate the sensitivity of genetic predictions for preweaning gain to the year effect that corresponded to the time of data collection.

MATERIALS AND METHODS

At the time of the inception of the Line 1 Hereford population, guidelines for the care and use of farm animals in research did not exist. The management of the cattle followed commonly accepted practices for commercial production. Since the publication of the first *Guide for the Care and Use of Agricultural Animals in Research and Teaching* (Federation of Animal Science Societies, 1988), the standards set forth therein and in subsequent editions were followed. Because this specific study makes use of this preexisting data, no specific review of it by the Institutional Animal Care and Use Committee of the USDA-ARS, Miles City, MT, was requested.

Data that were used in this research originated from a 76-yr selection experiment with the Line 1 Hereford cattle raised at Fort Keogh Livestock and Range Research Laboratory near Miles City, MT. Line 1 was founded using 2 half-sib bulls on 50 unrelated cows and has remained a closed population since its inception (MacNeil et al., 1992; MacNeil, 2009). The data comprised recorded phenotypes from 7,566 animals and an additional 1,862 ancestral records.

The topography varies from rolling hills to broken badlands with small, intersecting ephemeral streams flowing into the Tongue and Yellowstone Rivers in broad, nearly level valleys. The area is typical of the semiarid, mixed-grass prairie of the northern Great Plains. Indigenous vegetation on the 22,500-ha research station is a grama/needlegrass/wheatgrass (*Bouteloua/Stipa/Agropyron*) mix (Küchler, 1964). Elevation at Fort Keogh is approximately 720 m. Average annual temperature is 7.8°C, with daily extremes from −40 to 43°C. Average monthly temperatures are greatest during July and least during January. Average annual precipitation is 341 mm, with 75% occurring during the April through mid-August growing season.

Management of Line 1 remained relatively constant from 1935 to 2010. Cows grazed native range throughout the year. Each year they were moved to winter pasture on approximately January 1. Varying amounts of energy and protein supplement were fed, and hay was provided when excessive snow depth prevented normal winter grazing. Cows were placed in calving pastures in mid March. Calving heifers at 2 yr of age was initiated in 1977. Heifers have calved in lots of about 8 ha since that time. Since 1989, cows calved with the heifers and were given hay during the calving period. The 2,356 dams produced from 1 to 11 progeny each and had, on average, 3.2 calves. Cow–calf pairs were moved to native range spring pasture a few days after birth and from spring pastures to breeding pastures about June 1. A 45- to 60-d breeding season began about July 1 through 1945, about June 15 through 1992, and June 2 through the present. After the breeding season, cows and their calves were moved to rangeland summer pastures. Up to the late 1950s, cows and their calves were gathered on approximately September 1 of each year, and those male calves that were found lacking in structural soundness, breed character, or growth potential were castrated at that time. Subsequent to the late 1950s, all male calves were kept intact. Since the mid 1970s, calves have received preweaning vaccinations for stress-induced diseases at a late summer working. Calves were weaned during October at an average age of 180 d.

Following Cardoso and Tempelman (2012), a 2-step procedure was used to implement a genetic evaluation of preweaning gain that allowed for potential interaction between genotypes and continuous descriptors of environmental variation in the modeling of the data. In the first step, fixed year effects were estimated by REML as implemented by Boldman et al. (1995), fitting the model

$$y_{ijkl} = \mu + YR_i + SA_j + b_1 Fx_{ijkl} + b_2 Fd_{ijkl} + d_{ijkl} + m_{ijkl} + c_{ijk} + e_{ijkl,}$$

wherein y_{ijkl} is an observation of preweaning gain (kg) that had been linearly preadjusted to a constant age at weaning of 180 d for the *l*th calf out of the *k*th dam; μ is a constant applicable to all observations; YR_i is a fixed effect attributable to the *i*th year of birth in which the calf was produced; SA_j is a fixed effect attributable to the *j*th joint classification of sex of calf (bull or heifer) and age of dam (2, 3, 4, and 5+ yr); b_1 is the

fixed linear regression of y_{ijkl} on the inbreeding of the lth calf ($Fx_{ijkl} = 0$ to 0.47); b_2 is the fixed linear regression of y_{ijkl} on the inbreeding of the kth dam ($Fd_{ijkl} = 0$ to 0.45); d_{ijkl} is a random direct genetic effect of the lth calf; m_{ijkl} is a random maternal genetic effect of the lth calf; c_{ijk} is a random permanent environmental effect due to the kth dam; and e_{ijkl} is a random temporary environmental effect associated with each observation.

Then, in the second step, a random regression model was fit using the previously estimated year effects as covariate values (Calus et al., 2002; Kolmodin et al., 2002) to express the genetic value of each animal as a function of the environment in which it was produced (Falconer, 1990). Therefore, 2 additional terms were added to the model given above. These terms correspond to the random linear regressions of d_{ijkl} and m_{ijkl} on the previously estimated year effects. Under the reaction norm model, expectations and variances of the normal distributions specified in the first and second stage of the hierarchical model were

$$E\begin{bmatrix} y \\ yr \\ a \\ c \\ e \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix},$$

wherein X is a known design matrix relating the data y to the fixed effects β, and

$$\text{var}\begin{bmatrix} yr \\ a \\ c \\ e \end{bmatrix} = \begin{bmatrix} I\sigma_{rr}^2 & 0 & 0 & 0 \\ 0 & G & 0 & 0 \\ 0 & 0 & I\sigma_c^2 & 0 \\ 0 & 0 & 0 & I\sigma_e^2 \end{bmatrix},$$

wherein

$$G = \begin{bmatrix} A\sigma_1^2 & A\sigma_{1,2} & A\sigma_{1,3} & A\sigma_{1,4} \\ A\sigma_{2,1} & A\sigma_2^2 & A\sigma_{2,3} & A\sigma_{2,4} \\ A\sigma_{3,1} & A\sigma_{3,2} & A\sigma_3^2 & A\sigma_{3,4} \\ A\sigma_{4,1} & A\sigma_{4,2} & A\sigma_{4,3} & A\sigma_4^2 \end{bmatrix}$$

with the subscripts 1 through 4 designating the breeding values for the direct effects, linear reaction norm for direct effects, maternal effects, and linear reaction norm for maternal effects, respectively. Prior inverse χ^2 and Wishart distributions for variance components as well as all fully conditional posterior distributions used in the Markov chain Monte Carlo algorithms have been previously described (Cardoso and Tempelman, 2012). Intergen software (Cardoso, 2010) was used to carry out the computations. The analyses consisted of 110,000
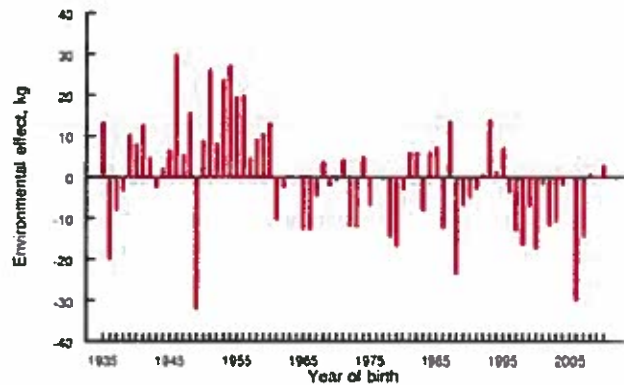

Figure 1. Environmental effects on gain from birth to weaning for Line 1 Hereford calves that were born between 1935 and 2011.

cycles, with the first 10,000 cycles discarded as burn-in, and using a thinning interval of 25 cycles. Global convergence was checked using the Geweke diagnostic. To summarize the genotype × environment interaction effects, EBV were calculated for each animal at the 5th, 50th, and 95th percentile of the environmental gradient. These EBV were used to estimate genetic trends and examine changes in the ranking of animals.

RESULTS AND DISCUSSION

Variability in weather across years and the dependence of the calves and their dams on naturally occurring vegetation for nutrients motivated our use of year effects as a measure of environmental variation. The year effects, centered on 0, had an approximately normal distribution over the range of −32.3 to 30.0 (Fig. 1). Including the reaction norms that linearly related direct and maternal additive effects to the environmental deviation for year effects reduced the variance of the year effects from 156.5 to 7.2. Therefore, it can be concluded that the linear effects of contemporary groups provide a quite useful basis to explain this known source of environmental variation.

Phenotypic expression of growth from birth to weaning was viewed as an integrative process combining direct and maternal genetic influences with those of the environment. Previous estimates of heritability for direct and maternal genetic effects on gain from birth to weaning in Line 1 were 13 to 16% and 20 to 25%, respectively (Tess and MacNeil, 1994; MacNeil and Mott, 2006). Here, the corresponding estimates of heritability, given the average environment, were 10 ± 2 and $26 \pm 3\%$, respectively. In an environment that is characterized by the 5th (95th) percentile of the distribution of year effects, the estimates of heritability for direct and maternal effects were 18 ± 3 ($22 \pm 3\%$) and $30 \pm 3\%$ ($30 \pm 3\%$), respectively. The rank correlation of direct EBV appropriate to the 5th and 95th percentiles of the

Table 1. Posterior mean (SD) estimates of variance components for direct, maternal, and reaction norm effects on gain from birth to weaning[1]

Effect	Direct	Reaction norm, direct	Maternal	Reaction norm, maternal
Direct	41.1935	0.0585	0.2124	0.2435
	(8.5610)	(0.2573)	(7.2145)	(0.2734)
Reaction norm, direct		0.1492	0.0922	−0.0359
		(0.0214)	(0.4487)	(0.0156)
Maternal			114.5070	−0.1092
			(14.4184)	(0.4081)
Reaction norm, maternal				0.1097
				(0.0179)

[1]Variance of permanent environmental effect due to dams = 70.4909 (9.0970) and variance of residual environmental effects = 207.0881 (6.7440).

year effects was 0.67. The corresponding rank correlation of maternal EBV was 0.92, respectively. Consistent with MacNeil and Mott (2006), the genetic correlation between direct and maternal effects that was estimated here was essentially nil (0.01 ± 0.11). Early estimates of this correlation were predominately negative (Baker 1980; Robinson, 1996). However, using simulation, Robinson (1996) and Lee and Pollak (1997) demonstrated the possibility for this negative correlation to result from an overlooked interaction between sire (additive genetic effect) and year. Permanent environmental effects due to dams accounted for $16 \pm 2\%$ of the phenotypic variance at the mean of the environmental gradient. Therefore, the estimated repeatability was 0.43 ± 0.02, which is not much different from estimates summarized by Bourdon (2000). The variance and covariance component values that were used in calculating these parameter estimates are shown in Table 1.

Approximately consistent genetic trends were observed for direct and maternal effects across the environmental gradient examined herein (Fig. 2 and 3, respectively). In the average environment, the trends were 255 ± 1 g/yr for direct effects and 557 ± 3 g/yr for maternal effects. In the fifth percentile environment, the corresponding estimates were 271 ± 1 and 540 ± 3 g/yr, respectively, whereas in the 95th percentile environment, the genetic trends for direct and maternal effects were 236 ± 1 and 578 ± 3 g/yr, respectively. One plausible explanation for the observed greater environmental effect across years on the EBV for direct effects than for maternal effects may be that the preweaning growth of an individual is expressed in a particular year and subject to one environment whereas the contribution of a dam is expressed across multiple years with the corresponding environmental effects being averaged. Irrespective of the environment, these estimates of genetic trends for preweaning gain are substantially greater than those observed by MacNeil et al. (1992) in an analysis of a substantial subset of the data that was analyzed here. At least
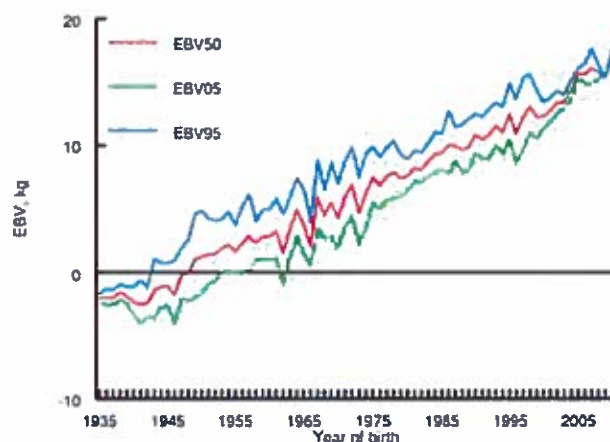
Figure 2. Genetic trends in direct additive effects on preweaning gain as related to the level of the environmental covariable year effect; EBV50 indicates the mean year effect, EBV05 indicates the fifth percentile year effect, and EBV95 indicates the 95th percentile year effect.

in part, this difference between studies may have resulted from the relatively strong direct-maternal correlation ($r_g = -0.40$) that was assumed in the earlier investigation.

At Fort Keogh, forage quality markedly changes across the preweaning period (Heitschmidt et al., 1993; Grings et al., 1995). On average, the growing season ended on August 13 (MacNeil and Vermeire, 2012), which is approximately 2 mo prior to weaning. Early in the preweaning period, when calves largely depend on milk from their dams for nutrition, forage quality is substantially greater than it is later when forages are senescing and decreasing in biological value and calves derive more of their diet from grazing. Senescence of rangeland forage would presumably be delayed in years characterized by longer, cooler growing seasons (Haferkamp et al., 2005; MacNeil and Vermeire, 2012). In such years, diet quality for the calves would be greater later in the preweaning period when forages contribute
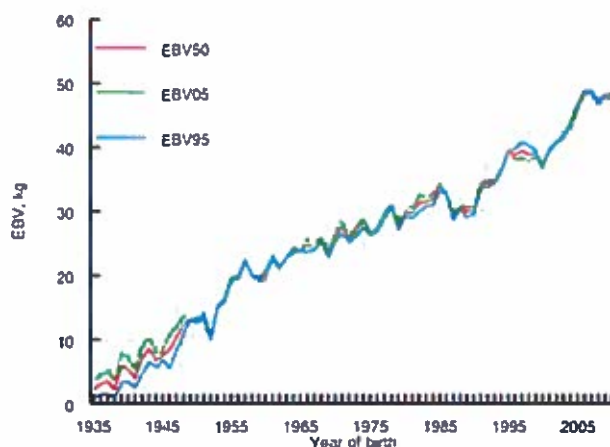
Figure 3. Genetic trends in maternal additive effects on preweaning gain as related to the level of the environmental covariable year effect; EBV50 indicates the mean year effect, EBV05 indicates the fifth percentile year effect, and EBV95 indicates the 95th percentile year effect.
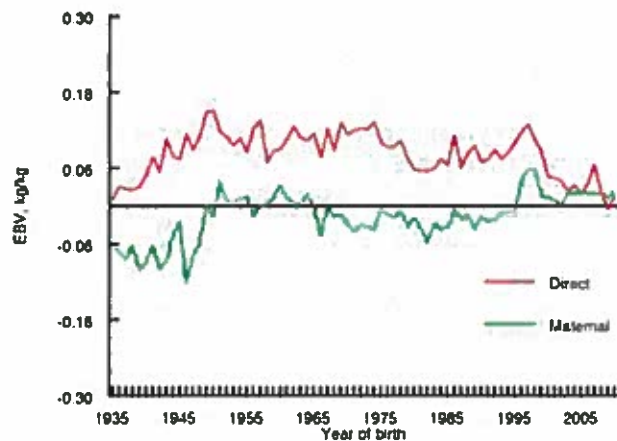
Figure 4. Genetic trends in environmental sensitivity of the direct and maternal EBV for preweaning gain.

more to their diet and, indeed, Line 1 Hereford calves grew more rapidly from birth to weaning than in warmer years. Small but significant linear trends over time in environmental sensitivity were observed for both the direct ($-8.06 \times 10^{-4} \pm 0.49 \times 10^{-4}$) and maternal ($8.72 \times 10^{-4} \pm 0.43 \times 10^{-4}$) effects (Fig. 4). In Line 1, selection has been continuously applied to increase growth to 1 yr of age (MacNeil et al., 1992). Both direct and maternal effects on preweaning gain contribute to the phenotype on which selection has been based. The contention that selection for greater performance in an unfavorable environment leads to reduced environmental sensitivity (Jinks and Connolly, 1973; Falconer, 1990), which would seem to suggest that the range environment at Fort Keogh and/or milk production by the Line 1 Hereford dams limits expression of genetic potential for growth. Likewise, the increasing maternal environmental sensitivity observed here could be interpreted to suggest that same environment was not limiting for milk production by Line 1 cows.

The present results provide additional motivation for examining the potential need for systems of national cattle evaluation to more fully account for potential genotype × environment interaction. Seed stock producers could use the average of environmental effects corresponding to their customer's individual operations to optimize genetic evaluation of candidates for selection given their circumstances. Estimates of environmental sensitivity parameters could also facilitate identification of genetic limitations to production.

LITERATURE CITED

Ambrosini, D. P., C. H. M. Malhado, R. Martins Filho, and P. L. S. Carneiro. 2016. Interação genótipo × ambiente via modelos de normas de reação para características de crescimento em bovinos Nelore. (In Portuguese.) Pesqui. Agropecu. Bras. 51:177–186. doi:10.1590/S0100-204X2016000200010

Baker, R. L. 1980. The role of maternal effects on the efficiency of selection in beef cattle – A review. Proc. N.Z. Soc. Anim. Prod. 40:285–303.

Boldman, K. G., L. A. Kriese, L. D. Van Vleck, C. P. Van Tassell, and S. D. Kachman. 1995. A manual for use of MTDFREML. A set of programs to obtain estimates of variance and covariances. USDA-ARS, Washington, DC.

Bourdon, R. M. 2000. Understanding animal breeding. 2nd ed. Prentice Hall, Upper Saddle River, NJ.

Buchanan, D. S., and M. K. Nielsen. 1979. Sire by environment interactions in beef cattle field data. J. Anim. Sci. 48:307–312. doi:10.2527/jas1979.482307x

Burns, W. C., M. Koger, W. T. Butts, O. F. Pahnish, and R. L. Blackwell. 1979. Genotype by environment interaction in Hereford cattle: II. Birth and weaning traits. J. Anim. Sci. 49:403–409.

Calus, M. P. L., A. F. Groen, and G. de Jong. 2002. Genotype × environment interaction for protein yield in Dutch dairy cattle as quantified by different models. J. Dairy Sci. 85:3115–3123. doi:10.3168/jds.S0022-0302(02)74399-3

Cardoso, F. F. 2010. Application of Bayesian inference in animal breeding using the Intergen program: Manual of version 1.2. Documentos, 112. Embrapa Pecuária Sul, Bagé, Brazil.

Cardoso, F. F., and R. J. Tempelman. 2012. Linear reaction norm models for genetic merit prediction of Angus cattle under genotype by environment interaction. J. Anim. Sci. 90:2130–2141. doi:10.2527/jas.2011-4333

Corrêa, M. B. B., N. J. L. Dionello, and F. F. Cardoso. 2010. Genetic evaluation of Devon cattle using a reaction norms model. Rev. Bras. Zootec. 39:128–133. doi:10.1590/S1516-35982010000100017

DeNise, S. K., M. Torabi, D. E. Ray, and R. Rice. 1988. Genetic parameter estimates for preweaning traits of beef cattle in a stressful environment. J. Anim. Sci. 66:1899–1906. doi:10.2527/jas1988.6681899x

Falconer, D. S. 1990. Selection in different environments: Effects on environmental sensitivity (reaction norm) and on mean performance. Genet. Res. 56:57–70. doi:10.1017/S0016672300028883

Federation of Animal Science Societies. 1988. Guide for the care and use of agricultural animals in research and teaching. Federation of Animal Science Societies, Champaign, IL.

Grings, E. E., D. C. Adams, and R. E. Short. 1995. Diet quality of suckling calves and mature steers on Northern Great Plains rangelands. J. Range Manage. 48:438–441. doi:10.2307/4002248

Haferkamp, M. R., M. D. MacNeil, and E. E. Grings. 2005. Predicting nitrogen content in the northern mixed-grass prairie. Rangeland Ecol. Manage. 58:155–160. doi:10.2111/04-01.1

Heitschmidt, R. K., J. D. Volesky, M. R. Haferkamp, and P. O. Currie. 1993. Steer performance on native and modified Northern Great Plains rangeland. J. Range Manage. 46:529–533. doi:10.2307/4002866

Huquet, B., H. Leclerc, and V. Ducrocq. 2012. Modelling and estimation of genotype by environment interactions for production traits in French dairy cattle. Genet. Sel. Evol. 44:35. doi:10.1186/1297-9686-44-35

Jinks, J. L., and V. Connolly. 1973. Selection for specific and general response to environmental differences. Heredity 30:33–40. doi:10.1038/hdy.1973.4

Kolmodin, R., E. Strandberg, P. Madsen, J. Jensen, and H. Jorjani. 2002. Genotype by environment interaction in Nordic dairy cattle studied using reaction norms. Acta Agric. Scand., Sect. A 52:11–24.

Küchler, A. 1964. Potential natural vegetation of the coterminous United States. Special Publ. 36. American Geographic Society, New York, NY.

Lee, C., and E. J. Pollak. 1997. Relationship between sire × year interactions and direct-maternal genetic correlation for weaning weight of Simmental cattle. J. Anim. Sci. 75:68–75. doi:10.2527/1997.75168x

MacNeil, M. D. 2009. Invited review: Research contributions from seventy-five years of breeding Line 1 Hereford cattle at Miles City, Montana. J. Anim. Sci. 87:2489–2501. doi:10.2527/jas.2009-1909

MacNeil, M. D., and T. B. Mott. 2006. Genetic analysis of gain from birth to weaning, milk production, and udder conformation in Line 1 Hereford cattle. J. Anim. Sci. 84:1639–1645. doi:10.2527/jas.2005-697

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. doi:10.2527/1992.703723x

MacNeil, M. D., and L. T. Vermeire. 2012. Effect of weather patterns on preweaning growth of beef calves in the Northern Great Plains. Agric. Sci. 3:929–935.

Notter, D. R., B. Tier, and K. Meyer. 1992. Sire × herd interactions for weaning weight in beef cattle. J. Anim. Sci. 70:2359–2365. doi:10.2527/1992.7082359x

Robinson, D. L. 1996. Models which might explain negative correlations between direct and maternal genetic effects. Livest. Prod. Sci. 45:111–122. doi:10.1016/0301-6226(96)00002-4

Tess, M. W., D. D. Kress, P. J. Burfening, and R. L. Friedrich. 1979. Sire by environment interactions in Simmental-sired calves. J. Anim. Sci. 49:964–971. doi:10.2527/jas1979.494964x

Tess, M. W., and M. D. MacNeil. 1994. Evaluation of cytoplasmic genetic effects in Miles City Line 1 Hereford cattle. J. Anim. Sci. 72:851–856.