Invited Review: Research contributions from seventy-five years of breeding Line 1 Hereford cattle at Miles City, Montana[1,2]

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ABSTRACT: For 75 yr, Line 1 Hereford cattle have been at the forefront of beef cattle breeding research. The goal of this review is to provide an overview of scientific contributions made using the Line 1 Hereford population. It was initially developed as contribution to a western regional program from which beef producers were envisioned to use heterosis by crossing selected inbred lines. Whereas this vision was never fulfilled, being largely supplanted by crossbreeding, Line 1 has had a profound influence on beef cattle breeding research and the Hereford breed. For more than 60 yr, Hereford breeders and commercial beef producers have purchased Line 1 Hereford germplasm for use in their herds. By example, Line 1 illustrates a successful line-breeding program through which a 39% additive relationship to the founding sire has been maintained over more than 18 generations. Procedures for performance testing beef cattle can be traced to original research with Line 1. Data from Line 1 contributed to the first estimates of heritability and genetic correlation for beef cattle. Work with Line 1 has also contributed greatly to the understanding of maternal genetic effects in beef cattle. Diallel crossing with other inbred lines provided early estimates of heterosis for beef cattle, complimented by the later observation that heterosis resulted in complete recovery of the accumulated negative effects of inbreeding. After exchanges of germplasm with the Northern Montana Agricultural Experiment Station at Havre and the Brooksville Beef Cattle Research Station in Florida, pioneering comprehensive evaluations of genotype × environment interaction were conducted. Breeding practices implemented by USDA Agricultural Research Service at Miles City make Line 1 the longest running selection experiment using beef cattle worldwide. This long-term database has provided an exceptional resource for prototype evaluations of procedures for national cattle evaluation, and the results make up an integral part of the foundation of modern-day genetic evaluation programs. Having used DNA from Line 1 in the development of a bacterial artificial chromosome library and the bovine genome sequence, Line 1 Hereford cattle are uniquely positioned for continued contributions in future research.

Key words: beef cattle, genetic evaluation, genetic resources, history, inbreeding, selection

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INTRODUCTION

Foundations for genetic improvement were laid by Robert Bakewell, in the latter half of the 18th century (Lush, 1945). He used inbreeding of highly selected animals to fix the desired type and then applied concepts of defined breeding goals, progeny testing, and assortative mating. Through work at the Carnegie Institution (Shull, 1908) and at the University of Connecticut (East, 1908), first commercialized by Henry Wallace in the mid-1920s, corn producers achieved great success with hybrid varieties (Jones, 1918). These scientific and practical foundations sparked development of inbred lines of livestock.

Until the early 1930s, there had been no systematic effort to develop, isolate, perpetuate, or catalog superior livestock germplasm (Anonymous, 1936). Thus, at the USDA Range Station in Miles City, in cooperation

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[2]This paper is dedicated to W. H. Black, B. Knapp Jr., R. T. Clark, R. R. Woodward, O. F. Pahnish, and J. J. Urick, innovators who made it possible, and to the cowboys who cared for the cattle and collected the data. The constructive comments of G. S. Lewis (USDA-ARS, Dubois, ID), K. A. Leymaster (USDA-ARS, Clay Center, NE), L. V. Cundiff (USDA-ARS, Clay Center, NE), J. O. Sanders (Texas A&M University, College Station), R. L. Willham (Iowa State University, Ames), and S. L. Rodriguez-Zas (University of Illinois, Urbana-Champaign) are greatly appreciated.

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with the Montana Agricultural Experiment Station, an attempt was made to develop true-breeding lines of Hereford cattle, especially adapted to western range areas, and possessing high fertility and superior quality (Black, 1936). According to Eller (2007), "Beef breeding at the USDA Range Station at Miles City, Montana beginning in 1924 was to change the direction of the beef industry… The early research work at Miles City led to developing a cattle production records program in Montana by 1936." Influenced by research done at Miles City, Montana cattlemen and the American Hereford Association were integral in forming the Beef Improvement Federation, which today is at the forefront of transforming performance concepts into industry action plans (R. L. Willham, Iowa State University, Ames, personal communication). Thus, Line 1 Hereford cattle have had enduring impacts on scientific advances in genetic improvement and the Hereford breed. This review examines the scientific and applied contributions of work with Line 1 Hereford cattle at this, the 75th anniversary of their founding.

MATERIALS AND METHODS

To fulfill the goal of developing true-breeding lines of Hereford cattle, 14 lines were established at Miles City between 1934 and 1955. Once established each line was closed and purposefully inbred as inbreeding was then the method of choice to produce true-breeding strains. Specifically, Line 1 was founded in 1934 from 2 sons of Advance Domino 13 (Advance Domino 20 and Advance Domino 54, Figure 1) purchased from Fred C. DeBerard of Kremmling, CO, and 50 cows purchased from George M. Miles of Miles City, MT. These were large-framed cattle with great potential for growth relative to many contemporary cattle of the day. Details of the breeding plan for Line 1 may very well have been based on studying the successful linebreeding program of C. G. Good (Pearson and Lush, 1933). Thus, daughters of Advance Domino 20 were bred to his paternal half-sib Advance Domino 54 and vice versa. Since the inception of Line 1, the line has been closed and the Line 1 Hereford cattle maintained by USDA at Miles City, MT, descend solely from foundation animals. The increase in inbreeding per generation has been reduced as Line 1 expanded in numbers and the mating of close relatives was avoided. The average genetic relationship of Line 1 Hereford calves born in 2008 with Advance Domino 13 remains just over 39%. Using 50 cows in the foundation of Line 1 was an unusually large commitment of resources compared with many other inbred lines being developed at the time. This commitment provided greater opportunity for selection to offset effects of inbreeding and likely contributed to the ultimate success of Line 1. Through the 75 yr since the inception of Line 1, several scientists have been responsible for breeding decisions and project management (Figure 2). Collaborations with numerous others have contributed greatly to the depth and breadth of accomplishments made using Line 1 Hereford cattle.

RESULTS AND DISCUSSION

In the 1930s, research with the Line 1 Hereford focused on methods of measuring performance of beef cattle. Progeny testing was a routine component of the breeding program (Figures 3 and 4). The implied breeding objective was economic return above feed costs, with return derived from carcasses of steers slaughtered at 408 kg of BW. It was established that BW gain per 45 kg of total digestible nutrients consumed had the greatest correlation with the economic breeding objective (Black and Knapp, 1936), and progeny groups of different sires varied significantly with respect to this objective and its indicator (Black and Knapp, 1938).

Motivated by contemporary popular practice, visual appraisal, numeric scoring, and linear measures were assessed as selection tools with the goal of simplifying evaluation of animals (Figure 5). These efforts proved unsatisfactory, and a need to develop methods of evaluation that are simple and practical was identified (Knapp et al., 1939). In some respects, these conflicting approaches for evaluating merit have not yet been reconciled.

Refinements of testing procedures became the focus of research in the 1940s. A feeding period of 168 d was found to be sufficient to measure efficiency of feed utilization, and 8 progeny per sire were deemed adequate to give a reasonably good test of additive genetic differences among bulls (Knapp et al., 1942). It was also found that ad libitum feeding, as opposed to limit feeding, was the best method by which differences in ability to grow may be determined (Knapp and Baker, 1943). In evaluating relationships between rate and efficiency of BW gain, it was concluded that "In time-constant feeding tests, selections should be made for rate of gain rather than observed gross efficiency" (Knapp and Baker, 1944). This result cemented the practice of basing future selection of Line 1 sires on growth to 1 yr of age.

Analysis of performance records required that correction factors be developed to account for differences in sex of calf, season of birth, and age of dam (Knapp et al., 1940; Koch and Clark, 1955a). Male calves were 2.5 kg heavier at birth and 11.9 kg heavier at weaning than female contemporaries. Calves from 3-, 4-, and 5-yr-old dams were 18.6, 8.2, and 2.7 kg lighter, respectively, than calves from mature (6-yr-old) cows. These correction factors remain remarkably similar to those recommended by the Beef Improvement Federation (2002).

The decade of the 1940s culminated with a series of papers in which the first estimates of heritability (Knapp and Nordskog, 1946a,b; Knapp and Clark, 1950) and genetic correlation (Knapp and Clark, 1947) for traits of beef cattle were published. The initial estimate of

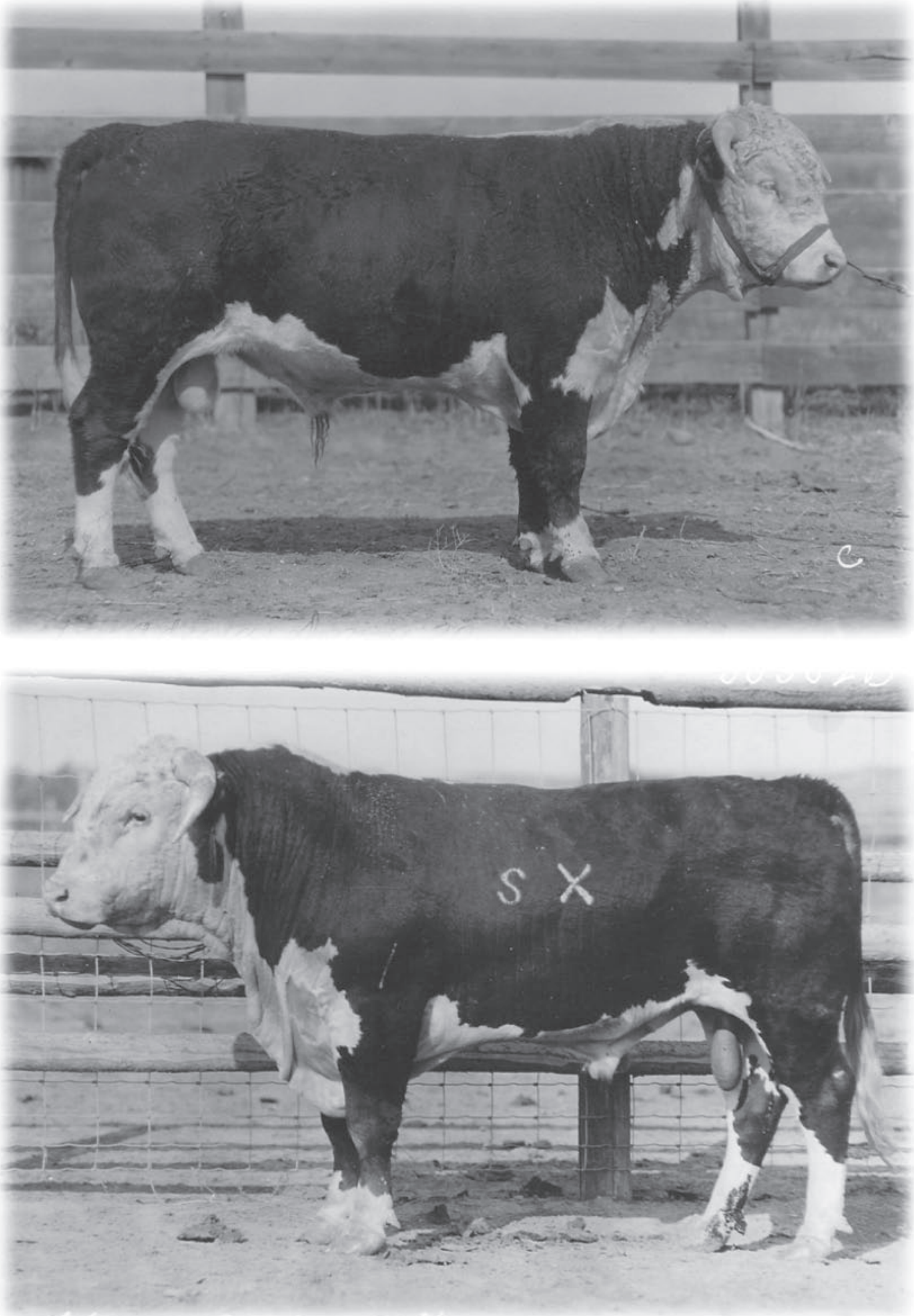


Figure 1. Foundation sires for Line 1, Advance Domino 20 (above) and Advance Domino 54 (below), in 1933 after their arrival at Miles City, MT.

heritability for daily BW gain on feed was almost 1.0, owing to then unrecognized confounding of sire progeny groups with pens to evaluate differences among sires in efficiency. Revised heritability estimates for BW at birth and weaning, BW gain in the feedlot, and area of the LM were 0.53, 0.28, 0.65, and 0.68, respectively (Knapp and Clark, 1950). It was concluded that heredity plays a most important part in determining the gains of calves in the feedlot. Progeny testing of bulls for gaining ability of calves was deemed unnecessary (Shelby et al., 1955). Thus, selection decisions could be made based on contemporary comparison of prospective herd sires, recognizing that evaluation of carcass traits still required slaughtering of progeny (Figure 6).

***W. H. Black** was a graduate of the State College of Agriculture at Ames, Iowa and leader of beef and dual purpose cattle investigations for USDA. Black was responsible for the initial research direction at Miles City. His collaboration with Prof. J. L. Lush had profound programmatic influence leading to the establishment of several inbred lines, their ultimate cross-line evaluation, and the research focus on methods of performance evaluation.*

***B. "Brad" Knapp Jr.** received a B.S. degree from Oklahoma A&M College and an M.S. degree from the State College of Agriculture at Ames, Iowa. Brad led the development of inbred lines at Miles City from 1943 until 1952. He traveled the U.S. speaking with ranchers and academics alike about the importance of record of performance programs. Brad was a recipient of the Beef Improvement Federation Pioneer Award in 1975.*

***R. T. "Scotty" Clark** emigrated to the U.S. from Scotland and was awarded a Ph.D. by the University of Minnesota. Scotty worked with Line 1 during its formative years (1938-1945) and was influential in the estimation of genetic parameters using data generated during that time. He was a builder of collaborations – and organized the cooperative regional beef cattle projects for USDA. As such, his impact on science and the beef industry was far-reaching. Scotty was a recipient of the Beef Improvement Federation Pioneer Award in 1980.*

***R. R. "Ray" Woodward** received his B.S. and M.S. degrees from Montana State College and was awarded a Ph.D. by the University of Minnesota. Ray was a beef cattle geneticist at Miles City from 1946 until 1960 and returned to Fort Keogh as Research Leader from 1976 to 1979. As a researcher, Ray was a developer and proponent of performance testing. He is a Fellow of the American Society of Animal Science, recipient of USDA Superior Service Award and Beef Improvement Federation Pioneer Award. In 1991, Ray's portrait was hung in the gallery of the Saddle and Sirloin Club Louisville, KY.*

***O. F. "Floyd" Pahnish** received a B.S. degree from Montana State College, a M.S. degree from University of Idaho, and was awarded a Ph.D. by the Oregon State University. Floyd was a beef cattle geneticist at the U.S. Range Livestock Experiment Station from 1964 until retiring in 1981. During much of this time, Floyd was also research leader. As a researcher, Floyd was noted for some of the earliest work on heterosis and genotype x environment interaction in beef cattle.*

***J. J. "Joe" Urick** received a B.S. degree from Montana State College and spent his career at the North Montana Agriculture Experiment Station (1948-1961) and U.S. Agricultural Experiment Station (1961-1989). Joe was a practical cattleman of tremendous insight. Many a Hereford producer sought his advice in the selection of Line 1 breeding stock offered to the industry. Integrally involved in the day-to-day implementation of research with Line 1, Joe insured data were always collected and accurate. Joe was a recipient of the Beef Improvement Federation Pioneer Award in 1979.*

***M. D. "Mike" MacNeil** received a B.S. from Cornell University, a M.S. degree from Montana State University and was awarded a Ph.D. by South Dakota State University. Mike started as leader of "the Line 1 project" at Fort Keogh, with the retirement of Joe Urick in 1989. He is recognized for work on various aspects of genetic improvement and biometry. Mike was inducted into the American Hereford Association Hall of Merit and is a recipient of the Beef Improvement Federation Continuing Service Award in 2005.*

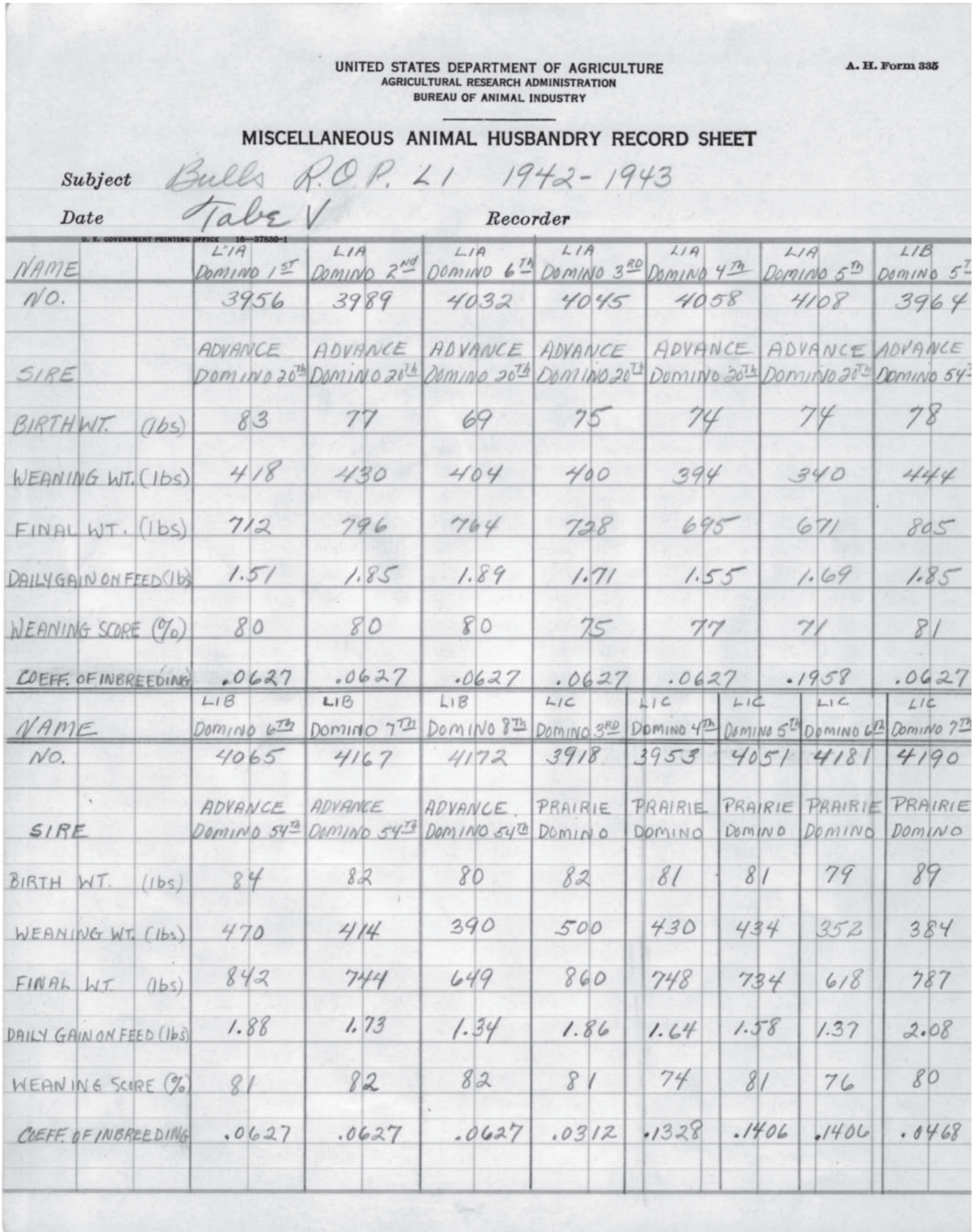
Figure 2. Scientists responsible for leading the Line 1 Hereford breeding program at Miles City, MT.

Figure 3. W. H. Black evaluating progeny of Advance Domino 20 at the St. Paul, MN, stockyards in 1938.

Body weight at 13 mo was deemed the most valuable criterion for selection (Shelby et al., 1960).

Dissemination of germplasm from Line 1 also began in the 1940s. Ray Woodward, then a USDA scientist, convinced his brothers-in-law (Jack Cooper and Les Holden) of the merits of linebreeding and selection based on performance. Record of performance concepts and Line 1 Hereford bulls were also accepted by commercial cattlemen in the region. At this time, the deleterious recessive gene causing dwarfism was a significant problem for the Hereford breed (McCann, 1974). Having established Line 1 Hereford cattle as being free of the gene for dwarfism through systematic mating of close relatives enhanced their acceptance. Owing to the historical selection of Line 1 for growth, industry interest in the cattle was renewed coincident with the importation of continental breeds from Europe. In 1980, the scientists that developed Line 1 were recognized with the USDA Superior Service Award for their impact on the beef industry. In 1984, 57% of the bulls listed in the American Hereford Association Sire evaluation were of predominantly Line 1 ancestry (Dickenson, 1984). Interest in Line 1 Hereford cattle from Miles City was renewed in the latter half of the first decade of the 21st century as the Hereford breed battled through another deleterious recessive condition, idiopathic epilepsy. Through 2008, 1,303 Line 1 bulls have been transferred from the research station at Miles City to registered Hereford breeders and commercial cattle producers. In addition to the many Hereford breeders using Line 1 germplasm (Figure 7), the cattle have contributed to research programs at USDA-ARS US Meat Animal Research Center, USDA-ARS Subtropical Agricultural Research Station, Northern Montana Agricultural Research Center, University of Arizona, University of Nevada—Reno, and University of Wisconsin.

Motivated in part by industry acceptance of Line 1 Hereford cattle, problems of cattle that manifest themselves as opportunity costs were studied in the 1950s. The incidence of bovine ocular squamous cell carcinoma (cancer eye) in Line 1 was found to be similar to its prevalence in other populations of Hereford (Woodward and Knapp, 1950). A genetic predisposition to cancer eye was also postulated based on differences between lines and the tendency of individual cows to produce an inordinate number of affected progeny. Prolapse of the vagina and uterus were a serious problem in many herds, particularly in the western range area and in Hereford cattle. In Line 1, the incidence of prolapse was found to be 1.7% annually and slightly greater than for other lines of Hereford cattle evaluated (Woodward and Quesenberry, 1956). These studies provided preliminary data for a subsequent more comprehensive investigation into factors affecting probability of cows being culled and expected herd life (Greer et al., 1980). The vast majority of culling decisions affecting cows through 10 yr of age were based on management rather than on physical impairment. Stillbirth of calves was found to be similar in Line 1 to other lines and to increase with the level of inbreeding (Woodward and Clark, 1959).



UNITED STATES DEPARTMENT OF AGRICULTURE
AGRICULTURAL RESEARCH ADMINISTRATION
BUREAU OF ANIMAL INDUSTRY

A. H. Form 335

MISCELLANEOUS ANIMAL HUSBANDRY RECORD SHEET

Subject Bulls R.O.P. L1 1942-1943

Date Table V *Recorder*

U. S. GOVERNMENT PRINTING OFFICE 16—37830-1

NAME	L1A DOMINO 1ST	L1A DOMINO 2ND	L1A DOMINO 6TH	L1A DOMINO 3RD	L1A DOMINO 4TH	L1A DOMINO 5TH	L1B DOMINO 5T
NO.	3956	3989	4032	4045	4058	4108	3964
SIRE	ADVANCE DOMINO 20TH	ADVANCE DOMINO 20TH	ADVANCE DOMINO 20TH	ADVANCE DOMINO 20TH	ADVANCE DOMINO 20TH	ADVANCE DOMINO 20TH	ADVANCE DOMINO 54
BIRTH WT. (lbs)	83	77	69	75	74	74	78
WEANING WT. (lbs)	418	430	404	400	394	340	444
FINAL WT. (lbs)	712	796	764	728	695	671	805
DAILY GAIN ON FEED (lbs)	1.51	1.85	1.89	1.71	1.55	1.69	1.85
WEANING SCORE (%)	80	80	80	75	77	71	81
COEFF. OF INBREEDING	.0627	.0627	.0627	.0627	.0627	.1958	.0627

NAME	L1B DOMINO 6TH	L1B DOMINO 7TH	L1B DOMINO 8TH	L1C DOMINO 3RD	L1C DOMINO 4TH	L1C DOMINO 5TH	L1C DOMINO 6TH	L1C DOMINO 7TH
NO.	4065	4167	4172	3918	3953	4051	4181	4190
SIRE	ADVANCE DOMINO 54TH	ADVANCE DOMINO 54TH	ADVANCE DOMINO 54TH	PRAIRIE DOMINO	PRAIRIE DOMINO	PRAIRIE DOMINO	PRAIRIE DOMINO	PRAIRIE DOMINO
BIRTH WT. (lbs)	84	82	80	82	81	81	79	89
WEANING WT. (lbs)	470	414	390	500	430	434	352	384
FINAL WT. (lbs)	842	744	649	860	748	734	618	787
DAILY GAIN ON FEED (lbs)	1.88	1.73	1.34	1.86	1.64	1.58	1.37	2.08
WEANING SCORE (%)	81	82	82	81	74	81	76	80
COEFF. OF INBREEDING	.0627	.0627	.0627	.0312	.1328	.1406	.1406	.0468

Figure 4. Record of performance data that resulted from progeny testing of Line 1 Hereford bulls; use of structured progeny testing in beef cattle breeding was pioneered by USDA researchers at Miles City, MT.

Figure 5. B. Knapp Jr. collecting linear measures to quantify body dimensions of cattle.

Even though dystocia was associated with greater birth weight and increased calf losses, stillbirth was more common for calves of below average birth weight.

Studies of heritability were augmented, in the early 1950s, by determining the extent to which weaning weights of Line 1 Hereford calves were permanent characteristics of their dams (Koch, 1951). Repeatability was found to be high enough to permit selection of cows on the basis of their first calf. Maternal environment was shown to have considerable effect on weaning score, but to be of negligible importance for BW gain from weaning to yearling and for yearling score (Koch and Clark, 1955b). With the advent of cryopreservation techniques in the early 1950s, semen was collected from three Line 1 bulls and frozen for use in future assessments of genetic trend. The original suggestion that negative correlations may exist between the genes directly affecting growth and genes affecting maternal environment was based on records from the lines of Hereford calves raised at the US Range Livestock Experiment Station, Miles City, MT, during the period 1926 to 1951 (Koch and Clark, 1955c). This finding has since been confirmed numerous times and manifests itself in contemporary national cattle evaluation as the negative covariance between direct and maternal effects on preweaning gain or weaning weight. The practical significance of these results is found in the recognition that "Selecting on the basis of gain from weaning to yearling age will increase the genic value for yearling gain but will cause a small loss in genic value for milking ability" (Koch and Clark, 1955d).

Later, Brinks et al. (1962, 1964) examined genetic and environmental factors affecting performance of performance-tested bulls and range-raised females and confirmed the absence of serious negative relationships that would hamper progress from selection for increased BW and BW gains. Brinks et al. (1962), through comparison with results from Koch and Clark (1955b), identified the potential for selection to bias within and between sire variance components. Effects of selection on genetic variability subsequently became topic of considerable interest owing to the landmark work of Bulmer (1971).

The vision of using highly selected inbred lines of beef cattle began to be evaluated at Miles City using Lines 1, 4, 6, 9, and 10 in a diallel crossing experiment

Figure 6. R. T. Clark recording carcass data from steers sired by Line 1 Hereford bulls.

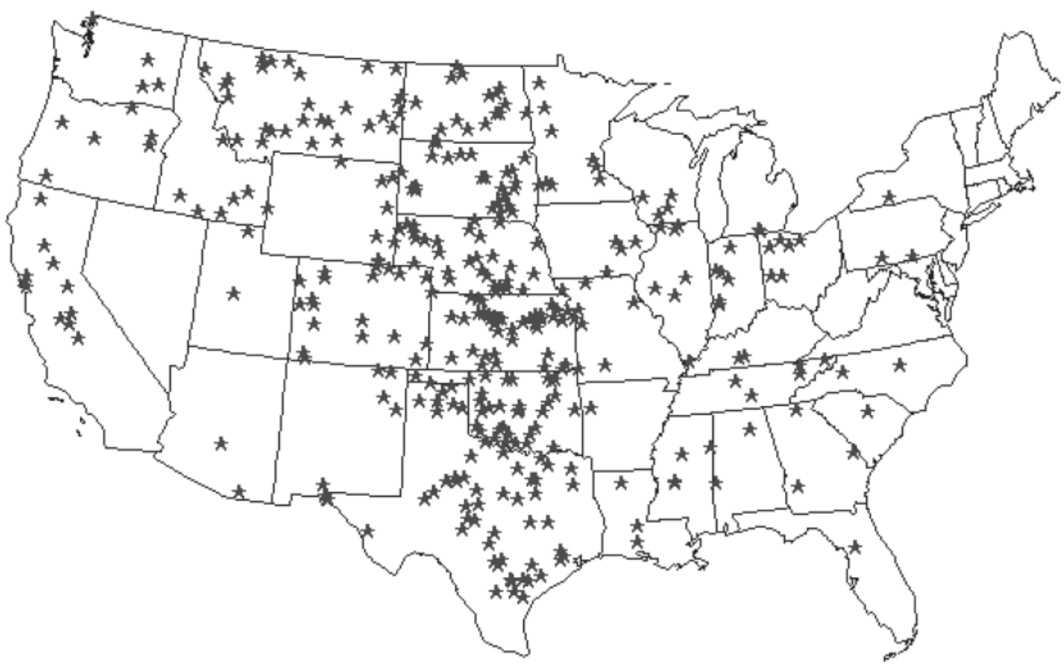


Figure 7. Locations of Hereford seedstock breeders using Line 1 Hereford germplasm in the 1990s.

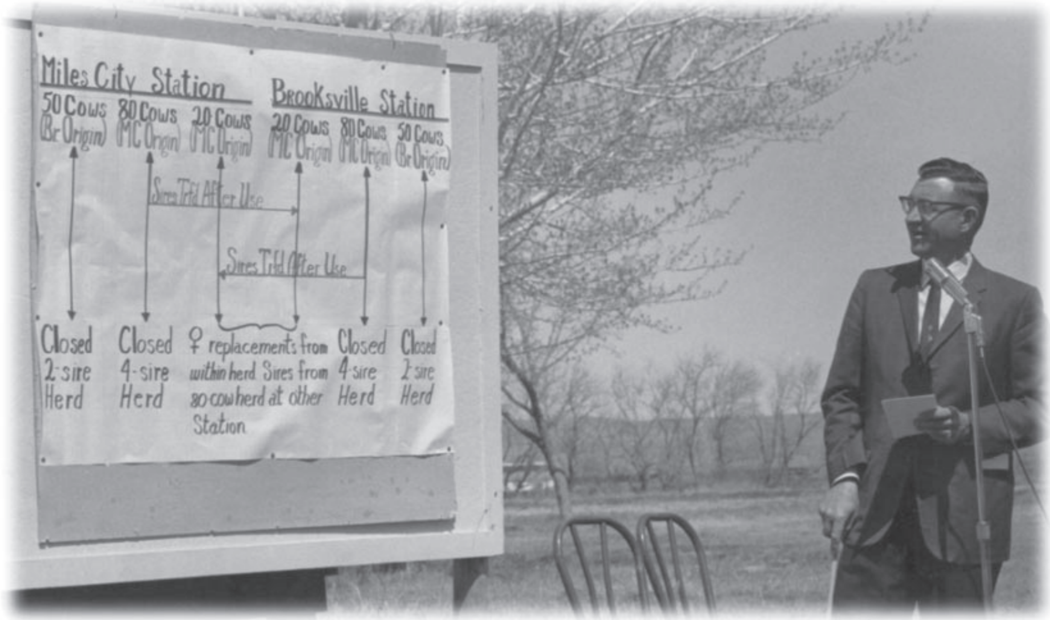


Figure 8. O. F. Pahnish presenting the design of the genotype × environment interaction study at a field day in Miles City, MT.

conducted in the 1960s. Initial observations included differences among parental lines in growth to weaning as influenced by direct and maternal effects, and significant direct heterosis (Brinks et al., 1967). Heterosis was greater for preweaning BW gain (8.1%) and weaning weight (7.2%) than for birth weight (3.4%) and weaning score (2.6%). Heterosis for yearling weight was similar to heterosis for weaning weight (Urick et al., 1968). From birth to yearling, heterosis for growth was consistently greater in heifers than in bulls. As a first test of the commercial applicability of topcrosses from selected inbred lines, the University of Arizona in cooperation with the San Carlos Apache Indian tribe pursued an evaluation of the most promising lines from Miles City (Ray et al., 1970). Profound among the results and supporting the negative covariance between direct and maternal effects was the observation that calves with the greatest weaning weight ordered by sire line weighed least when classified by dam line. Use of topcross dams resulted in a definite improvement in preweaning growth, although topcross sires offered no advantage. When subsequently estimated from inbred and cross-line females, maternal heterosis was found for preweaning gain (5.4%) and weaning weight (4.7%; Brinks et al., 1972). Revisiting these data some 30 yr later, heterosis was found to result in complete recovery of the accumulated negative effects of inbreeding (Pariacote et al., 1998).

In order for record of performance testing to be meaningful, progeny groups from different sires must have similar relative performance across herds and environments. An initial investigation in which Line 1 Hereford sires were used to produce calves at Miles City and the Montana Agricultural Experiment Station at Havre suggested the possibility of genotype × environment interaction affecting growth to 1 yr of age (Woodward and Clark, 1950). Had these results been subsequently verified, it would have been devastating to the seedstock industry because of the implied need to test seedstock in the environment of intended use.

Based on plausibility that genotypes might have differing value depending on the environment, comprehensive collaborative investigations were initiated between Fort Keogh and the Subtropical Research Station at Brooksville, FL (Figure 8). Line 1 Hereford cattle were transferred from Montana to Florida and Hereford cattle with approximately 10 yr of rigorous selection for ability to reproduce and grow in Florida were transferred to Montana (Butts et al., 1971). Initial evaluations suggested that the performance of Montana-originating cattle was superior in Montana and conversely Florida-originating cattle performed better in Florida (Figure 9). However, effects of genotype × environment interaction and physiological adaptation were confounded in the initial evaluations. Thus, in subsequent evaluation of potential genotype × environment interactions, all cows at both locations were descendants of sires born and selected in the respective environments (Koger et al., 1979). The high incidence of source by location interactions affecting reproduction (Koger et al., 1979), preweaning (Burns et al., 1979), and postweaning traits (Pahnish et al., 1983, 1985) suggested genotype × environment interactions may be of greater practical importance than was previously assumed.

Selection for growth and the importation of continental cattle led to a greater need to understand causes of calving difficulty. Upon identifying excessive birth weight as the primary factor contributing to calving difficulty (Bellows et al., 1971), a selection experiment was initiated to evaluate a strategy of using sires with below average birth weight and high yearling weight (MacNeil et al., 1998). This strategy resulted in less

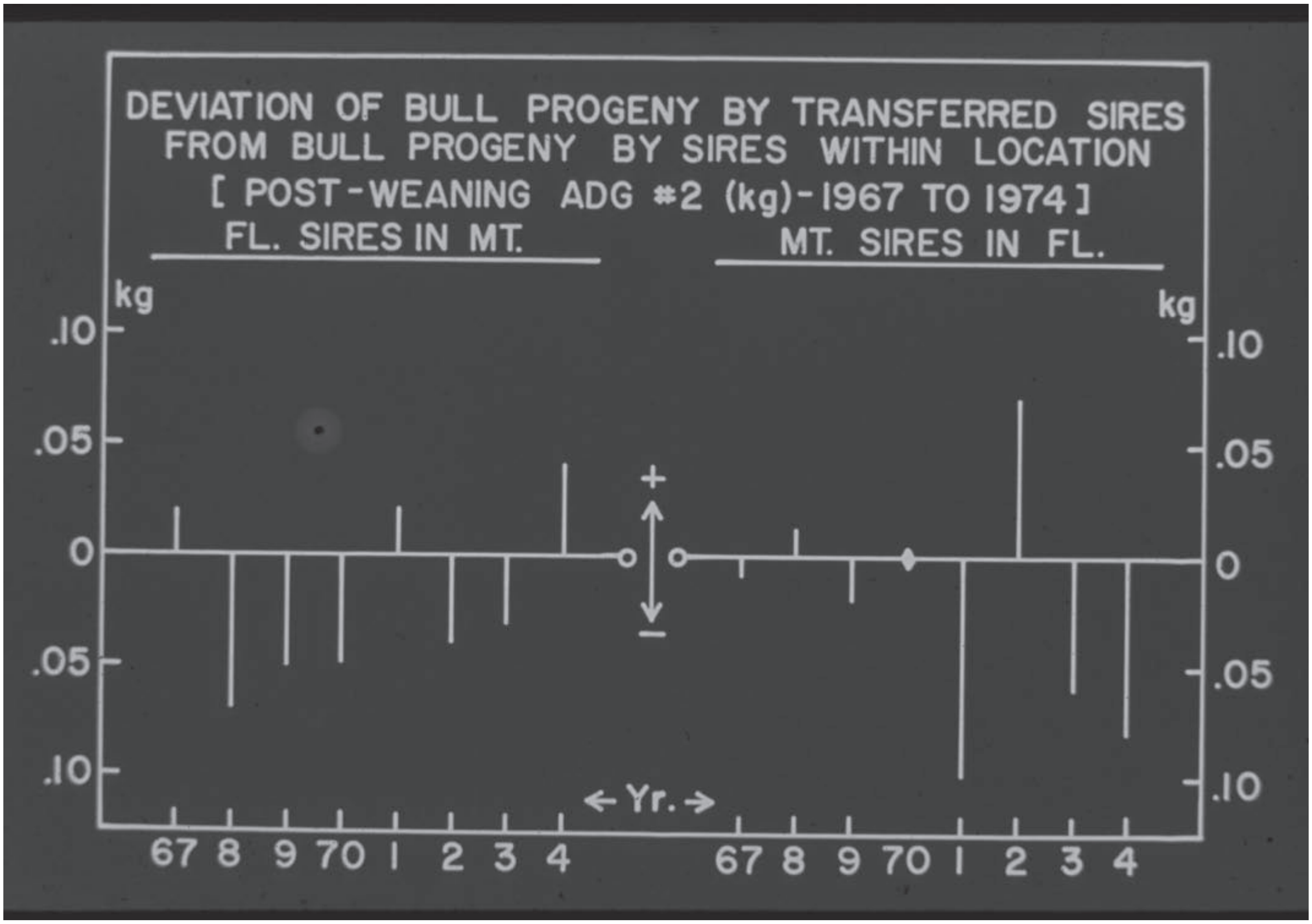


Figure 9. Original results supporting existence of genotype × environment interaction manifest as inferiority of progeny of transferred sires relative to progeny from sires at the same location. These results are from the collaboration between USDA locations at Miles City, MT, and Brooksville, FL.

frequent need for assistance at parturition of 2-yr-old heifers but failed to establish a favorable genetic trend in calving ability. Increased fatness of market progeny (MacNeil et al., 1999) and earlier maturity of replacement females (MacNeil et al., 2000) were noted as correlated responses to this selection strategy compared with selection for yearling weight alone.

A comprehensive review of effects of inbreeding in 48 lines of cattle found birth weight and growth to 1 yr of age to decrease with increased inbreeding of Line 1 (Brinks and Knapp, 1975). Pregnancy rate of Line 1 Hereford cows also decreased with increased inbreeding. Thus, effects of dominance potentially influenced performance traits of Line 1 Hereford cattle (Gengler et al., 1997). Statistical modeling of dominance effects requires a significant body of data, and simple methods were found to be elusive. However, no important differences in estimates of breeding value were found whether or not inbreeding effects were modeled as continuous effects (Ferreira et al., 1999).

The long-term database resulting from consistent performance recording of Line 1 Hereford cattle has been useful to explore enhancements to systems of national cattle evaluation. Data from Line 1 Hereford cattle raised in 4 diverse environments across Montana indicated potential for heterogeneity of genetic and environmental variance across herds and herd-specific inbreeding, sex, and age of dam effects (Snelling et al., 1996). The commonly used strategy of preadjusting growth from birth to weaning for effects of age of dam was also shown to bias estimates of breeding value for maternal preweaning BW gain and consequently maternal weaning weight (MacNeil and Snelling, 1996). Maternal genetic effects on preweaning BW gain were shown to be indicative of direct effects on milk production (MacNeil et al., 2006). Sire models, as first used in national cattle evaluation, were found to produce reduced estimates of heritability and less precise measures of breeding value than more computationally intense animal models (Ferreira et al., 1999). Thus, use of sire models could compromise genetic improvement relative to that obtainable using the animal model for genetic evaluation. Contemporary systems of national cattle evaluation almost exclusively use the animal model. In addition to alternative statistical models, this database has also been useful to explore alternative traits that might be included in systems of national cattle evaluation. Two such traits are maternal or daughter calving

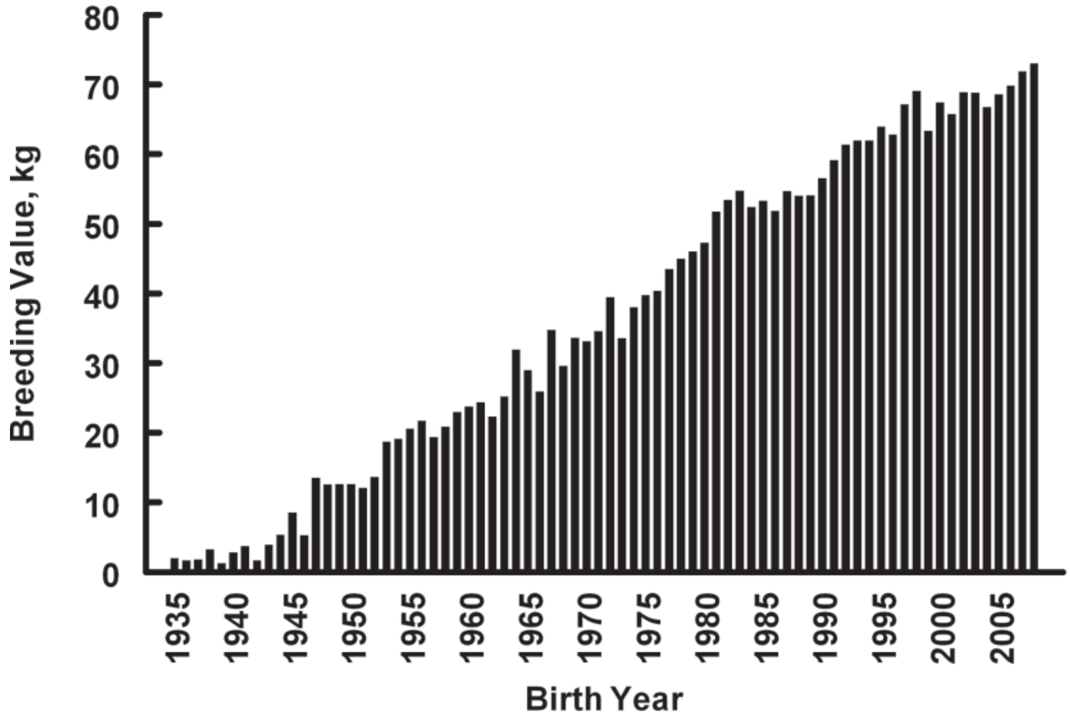


Figure 10. Genetic trend in 365-d weight from multiple trait animal model analyses. A sire summary is available (http://www.ars.usda.gov/Main/docs.htm?docid=3087).

date (MacNeil and Newman, 1994) and annual energy intake of cows (MacNeil and Mott, 2000). The latter is unique in that it is the only breeding value predicted entirely from indicator traits. The Red Angus Association of America reports a closely related breeding value for maintenance energy requirement to its member breeders (Evans et al., 2002).

Periodic assessments of genetic trends have shown selection for growth to 1 yr of age as efficacious throughout the 75 yr Line 1 has existed as a closed herd (Knapp et al., 1951; Brinks et al., 1965; MacNeil et al., 1992). Genetic potential for growth continues to increase at all ages less than 1 yr (Figure 10). A sire summary covering more than 18 generations is available (MacNeil, 2009). Even in populations with small effective size as a result from linebreeding and intense selection fostered with tools such as AI and embryo transfer, breeders should be encouraged that genetic improvement will continue.

Animal breeding research changed focus in the mid-1990s as laboratories were equipped to implement the PCR (Mullis et al., 1986) to amplify small fragments of DNA. Line 1 Hereford cattle were used in early studies of candidate genes affecting growth and milk production of beef cattle (Moody et al., 1996). Scaling up laboratory capability at Miles City made more intensive genomic investigations feasible, and genome-wide searches for QTL were initiated with crosses between Line 1 Hereford and a composite of Red Angus, Charolais, and Tarentaise (Grosz and MacNeil, 2001; MacNeil and Grosz, 2002). Some of the discovered QTL have since been incorporated into commercial tests for use by the beef industry. Broader application of Line 1 Hereford genetic material was realized by incorporation of DNA from a bull (L1 Domino 99375) into a bacterial artificial chromosome (BAC) library (http://bacpac.chori.org/bovine240.htm). This BAC library has subsequently been used nationally and internationally in discovery of causal mutations affecting economically important traits. Because increased homozygosity would allow easier matching of BAC end sequences and assembly of DNA sequencing reads, Line 1 was chosen to provide the basis for the bovine genome sequence. A tiling path that facilitates the sequencing was derived from the BAC library, and the sequence itself was based on DNA from L1 Dominette 01449 (Bovine Genome Sequence Consortium et al., 2009), a daughter of L1 Domino 99375. The genetic relationship of sire and daughter is approximately 93%.

Beyond reveling in the past accomplishments, looking back on the results of research conducted with Line 1 Hereford cattle clarifies potential future directions. Development of procedures for performance testing and the established importance of genotype-environment interaction affecting performance suggest working toward a system of national cattle evaluation with different genetic evaluations depending on the environment in which evaluated animals would be used. The bovine genome sequence and single nucleotide polymorphisms discovered in L1 Dominette 01449 together with the comprehensive phenotypic database from Line 1 open opportunities in developing a new generation of systems for national cattle evaluation that combine genomic and phenotypic information. Continued discovery of causal mutations affecting economically relevant traits and genetic markers that are closely linked to those mutations will help producers make more rational selection decisions and continue to keep beef affordable for American consumers. Gene expression studies conducted in diverse environments may elucidate the underlying basis for interactions between genotype and environment. Going beyond genetic evaluation, these same resources offer the opportunity to mechanistically understand the phenomena of inbreeding depression and heterosis. In application, beef producers could someday plan matings that would optimize the genotype of resulting progeny. The original vision that led to development of inbred lines might be revisited with the development of genomic lines characterized by optimal combining ability. Over all the years and into the future, Line 1 Hereford cattle have provided and will continue to provide an unrivaled vehicle for transferring scientific information to a much broader and in many cases more applied audience.

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