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Influence of Miles City Line 1 on the United States Hereford population[1,2,3]

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ABSTRACT: The goal of this research was to document the influence of Line 1 (L1) Hereford cattle, developed by the USDA at its research facility in Miles City, MT, on the U.S. Hereford population. The L1 Hereford population originated in 1934 and has been thereafter maintained as a closed herd at that location. Dissemination of germplasm began in 1948. Pedigree data for approximately 14 million cattle recorded by the American Hereford Association (AHA) were used. A preliminary experiment was conducted to establish sample size necessary to estimate the pedigree relationship between L1 and the recorded Hereford population. Five random samples of 100, 400, 500, and 3,000 calves were drawn from the sets of calves born in 1980, 1990, and 2000. Sampled calves were pseudo mated to L1 sires from the decades 1968 to 1978, 1978 to 1988, and 1988 to 1998, respectively. Inbreeding coefficients were calculated for the resulting "offspring" and the relationship of each sampled animal to L1 was taken to be twice the maximum inbreeding coefficient for the set of L1 sires used in the pseudo matings. Based on the results of this experiment, it was decided that a sample size of 400 animals per replicate was sufficient to estimate the relationship between L1 and the general Hereford population recorded by the AHA. In a second experiment, 5 sets of 400 animals were drawn from the AHA herdbook representing each year from 1980 to 2008 and pseudo mated to L1 sires and their relationship to L1 calculated as described above. Over the period, the number of animals recorded by the AHA that were related to L1 increased by $1.69 \pm 0.07\%$ per year. The L1 Hereford population was ancestral to 79% of Hereford cattle recorded in 2006 through 2008. The greatest concentration of animals related to L1 was in the Great Plains and eastern Corn Belt of the United States, but animals related to L1 were found in 48 states. In a third experiment, 240 L1 Hereford cattle and 311 sires representative of the Hereford breed in the United States were genotyped using the Illumina BovineSNP50 BeadChip. Resulting genotypes were used to assess the probability that the animals sampled from the U.S. population were members of L1. The average probability of membership in L1 was 0.20 and the regression of genomic probability of membership on pedigree relationship was 1.73 ± 0.11 ($r = 0.65$). These results document the far-reaching and profound impact of a long-term research program.

Key words: beef cattle, genomic, migration, pedigree, relationship

INTRODUCTION

Following on the agronomic success of hybrid corn (Sprague, 1962), the USDA began developing inbred lines of Hereford cattle with superior performance for economically important traits (Winters, 1931; Knapp et al., 1951). The first and several of these lines were developed at Fort Keogh, the USDA laboratory at Miles City, MT. The most important and productive of these lines was the Line 1 (**L1**) Hereford cattle (Knapp et al., 1951). Line 1 was founded with 2 purebred bulls, Advance Domino 20 (American Hereford Association [**AHA**] registration number 2035127) and Advance

Domino 54 (AHA registration number 2120894), purchased from Fred C. DeBerard of Kremmling, CO, in 1932 through 1933. These bulls were half-sibs sired by Advance Domino 13 (AHA registration number 1668403) and were unrelated to the 50 Hereford foundation cows purchased from George M. Miles and sons of Miles City, MT (Knapp et al., 1951). There has been no immigration from the industry into Miles City L1 since its founding.

Dissemination of L1 Hereford cattle from Fort Keogh began in 1948 with sales of bulls and females to local producers. Although initially not popular in the beef industry, the L1 breeding program produced a faster growing animal relative to contemporary cohorts. In time, buyers came from across the United States to purchase Miles City L1 Hereford cattle. To date, producers from 34 states have purchased L1 bulls and/or females. Several successful seedstock herds were founded with L1 germplasm. In 1983, Dickenson (1984) observed that 68% of all purebred Hereford sires advertised in the July 1983 issue of the breed magazine were related to L1. However, there has been no systematic study of the geographic distribution of genetic material from Miles City L1 or the degree to which that material is manifest in the U.S. Hereford population. Therefore, the goal of this project was to quantify the influence of Miles City L1 Hereford cattle on the general Hereford population of the United States.

MATERIALS AND METHODS

Institutional Animal Care and Use Committee approval was not obtained for this study because the pedigree data were accumulated by the AHA as part of their breed improvement program and genotypic data used herein was first reported elsewhere (Huang et al., 2012; Kuehn et al., 2011).

Determining Influence

The AHA Hereford herdbook contains approximately 14 million animals registered between 1960 and 2009 and more than 26 million animals in its entirety. However, the herdbook is not completely digitized to contemporaries of Advance Domino 13's parents. (S. Sanders, AHA, personal communication, 2008). The distribution of numbers of animals recorded by the AHA from 1980 to 2008 is shown in Fig. 1. Explicit calculation of relationship coefficients for all animals in the U.S. herdbook with more than 9,000 L1 Hereford cattle produced at Fort Keogh (i.e., a complete A matrix) was deemed infeasible. Therefore, a sampling strategy was developed to estimate the relationship coefficients to be used in documenting the influence of Miles City L1 on the recorded population. Records from 3 yr (1980, 1990, and 2000) were used in a preliminary experiment
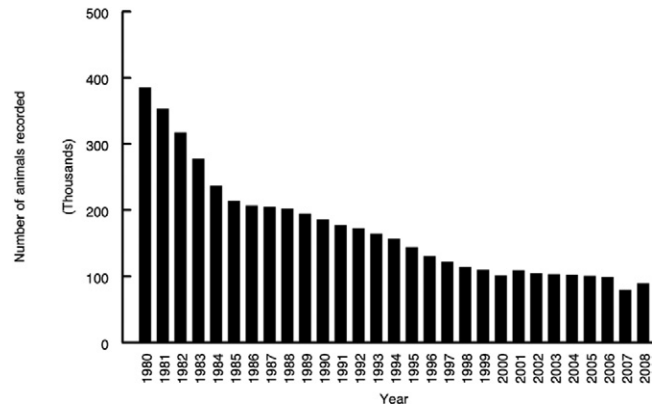

Figure 1. Number of animals recorded by the American Hereford Association in the years 1980 to 2008.

to determine the number of animals to sample from each year to calculate the CV across replicate samples ≤10%. Five independent random samples of 100, 400, 500, and 3,000 animals were drawn from the AHA herdbook for each of the 3 yr. The L1 sires born over the decade starting 2 yr previous to each birth year of interest were "pseudo mated" to the calves contained in each sample. Inbreeding coefficients were calculated for the resulting "progeny" using the algorithm developed by Henderson and Quaas (1976). Coefficients of relationship for each animal with the L1 sires were calculated as twice the inbreeding coefficients of their progeny. Finally, the influence of Miles City L1 on each sampled animal was taken to be the maximum relationship observed across the set of L1 sires. The mean and SD of the influence statistic across the 5 replicate samples were used to calculate the CV, which was used as a decision criterion.

Having established the appropriate sample size, 5 independent replicate sample sets of calves were randomly drawn from the population of calves recorded by the AHA as born in each year from 1980 to 2008, inclusively. The influence of Miles City L1 on each calf was calculated as described above. To provide context for the influence of Miles City L1 on the U.S. population as recorded by the AHA, industry sires born during the decade starting 2 yr before each birth year of interest (5 per birth year) were also sampled from the herdbook. Thus, for each annual cohort of recorded calves, their relationship to these 50 industry sires was calculated. The influence of these industry sires on the U.S. Hereford population was calculated as described above for the Miles City L1 sires.

Geographic Distribution of Hereford Cattle Related to Line 1

We were also interested in the geographic distribution of L1 germplasm across the United States. With 5 replicate random samples calves drawn from the AHA herdbook for each year there was a total of 2,000 animals

sampled each year from 1980 to 2008. The genetic influence of Miles City L1 on them was calculated as described above. The location of approximately 90% of these animals was identified by the postal zip code of their owner. A database of zip codes and their corresponding longitude and latitude was accessed at www.boutell.com/zipcodes/ (Boutell, 2008). The location (latitude and longitude) of each animal in the sample was mapped using ArcGIS software version 9.2 (ESRI, 2009).

Analysis of Genomic Data

Sires (n = 311) representative of the U.S. Hereford population (Thallman, 2009; Kuehn et al., 2011) and 240 L1 animals (Huang et al., 2012) were genotyped using the Illumina BovineSNP50 BeadChip (Matukumalli et al., 2009; Illumina inc., San Diego, CA). Here, the 311 sires are referred to as genotyped industry sires. The BeadChip includes a total of 52,156 SNP, of which 9,103 were from the genome sequence of L1 Dominette 01449 (AHA registration number 42190680). Ninety-six percent of the SNP had <0.1% missing genotypes and SNP that that had a call rate of <97% were not used. All animals had <0.5% missing genotypes. Single nucleotide polymorphisms that did not have chromosomal or position information in UMD3.1 map (Zimin et al., 2009) also were not used. Twenty-two percent of the SNP were monomorphic in these samples and were discarded. After editing, there were 33,154 polymorphic SNP loci that were used in subsequent analyses.

The program STRUCTURE (version 2.3.2; Pritchard et al., 2000) was used to analyze the genotypic data. STRUCTURE uses a Markov chain Monte Carlo sampling algorithm to investigate population structure and assign individuals to specific populations based on multilocus genotypic data. Here, we ran 110,000 iterations and discarded the first 10,000 as burn-in. Individual animals were identified a priori as being in 2 clusters (i.e., k = 2): L1 Hereford and the genotyped industry sires as representative of the United States Hereford population. The program predicts each animal's probability of membership in each cluster (Pritchard and Cox, 2002).

Pedigrees for the genotyped industry sires were also traced to the earliest entries in the AHA registry (American Hereford Cattle Breeders' Association, 1899) and an extended pedigree back to Cholestry 217, registration number 104 and born in 1841, for the sample of industry bulls was compiled. To compute the needed relationships, all possible matings between the L1 and genotyped industry sires were simulated and the maximum of the 240 coefficients of relationship for each industry bull was taken as a measure of that bull's relationship to L1. Correspondence between probability of membership in the L1 cluster and pedigree relationship was assessed by linear regression.

Table 1. Effect of sample size on variation in estimates of the average relationship between Line 1 and Hereford cattle recorded by the American Hereford Association

Year	Sample size	Statistic[1]			
		Frequency	Mean	SD	CV
1980	100	21.6	12.5	5.1	40.6
	400	23.0	11.5	0.4	3.6
	500	23.0	11.7	1.0	9.0
	3,000	22.0	12.2	0.7	5.7
1990	100	55.0	8.5	0.1	1.3
	400	50.0	9.1	0.2	2.5
	500	50.0	9.1	0.2	2.5
	3,000	51.0	8.8	0.3	3.6
2000	100	62.2	9.6	1.5	15.9
	400	65.0	8.6	0.2	2.8
	500	65.0	8.5	0.2	2.7
	3,000	65.6	8.8	0.2	2.8

[1]Frequency measures the average proportion of animals with nonzero relationship to Line 1 across 5 replicate samples. Mean measures the average relationship to Line 1 of the sampled animals with relationship to Line 1 > 0.0 and SD is the standard deviation of the means of 5 replicate samples of the designated size; CV = 100 × SD/mean.

RESULTS

Sample Size

Numbers of animals recorded by the AHA were 385,338, 186,255, and 101,450 in 1980, 1990, and 2000, respectively (Fig. 1). For 1980, samples of 100, 500, and 3,000 represent 0.025, 0.13, and 0.78% of the recorded calves, respectively, whereas for 2000, samples of 100, 500, and 3,000 represent 0.099, 0.49, and 2.96% of the recorded calves, respectively. Presented in Table 1 are summary statistics describing the variability among replicate samples of differing numbers of animals.

Based on the results presented in Table 1 and the a priori chosen threshold CV of 10%, samples of size n = 100 appear inadequate in 1980 and 2000. There were noteworthy differences among these samples with regard to number of animals that have L1 heritage and the degree of their relationship to L1. These discrepancies indicate inadequate sample size, because samples of the selected size were not large enough to reduce the variation among samples to an acceptable level (Lenth, 2001, 2007). Samples of sizes n = 500 and n = 3,000 were more consistent, and relative to the a priori chosen CV characterizing variability among replicate samples of 10%, they were acceptable for all 3 yr. Thus, for our purpose, there was little advantage of drawing samples of 3,000 animals from the AHA database relative to drawing samples of 500 animals. Lenth (2001) argues that it would be wise to use the smaller sample size, given the criterion for choice among samples of various sizes, so that additional time and resources are not wasted. Because samples of 500 animals appeared adequate and samples of

Table 2. Means and standard deviations of the mean of 5 replicate samples ($n = 400$) that characterize the relationship of animals recorded by the American Hereford Association to Line 1, summarized by year of birth

Year	Frequency, %	R_{rel}, %	R_{all}, %	Maximum R, %
		Statistic[1]		
1980	23.2 ± 2.8	10.4 ± 1.7	2.4 ± 0.6	64 ± 11
1981	30.6 ± 3.0	10.8 ± 1.4	3.2 ± 0.3	66 ± 13
1982	35.2 ± 3.0	9.6 ± 1.3	3.4 ± 0.7	62 ± 5
1983	37.8 ± 4.3	10.2 ± 1.6	3.8 ± 0.8	60 ± 3
1984	39.8 ± 2.5	10.8 ± 2.0	4.2 ± 1.1	50 ± 27
1985	42.6 ± 2.0	10.4 ± 1.1	4.4 ± 0.6	66 ± 7
1986	43.2 ± 1.7	9.6 ± 1.1	4.2 ± 0.5	52 ± 16
1987	46.2 ± 2.6	9.4 ± 1.2	4.2 ± 0.7	70 ± 9
1988	47.4 ± 3.0	10.8 ± 0.3	8.6 ± 0.9	60 ± 12
1989	50.4 ± 3.0	8.4 ± 1.2	4.2 ± 0.7	60 ± 16
1990	52.6 ± 2.8	8.2 ± 1.0	4.2 ± 0.7	64 ± 12
1991	50.2 ± 4.9	7.6 ± 1.6	4.0 ± 1.1	64 ± 24
1992	56.2 ± 4.1	7.8 ± 0.6	4.4 ± 0.4	74 ± 4
1993	57.2 ± 3.6	7.6 ± 0.6	4.4 ± 0.5	54 ± 16
1994	61.2 ± 4.3	8.4 ± 1.3	5.2 ± 0.4	64 ± 13
1995	61.8 ± 2.1	7.8 ± 0.7	4.8 ± 0.4	50 ± 27
1996	62.0 ± 2.4	8.4 ± 0.9	5.2 ± 0.5	66 ± 12
1997	63.4 ± 2.7	8.6 ± 1.0	5.4 ± 0.6	70 ± 19
1998	63.2 ± 3.7	8.2 ± 0.7	5.0 ± 0.6	64 ± 10
1999	62.2 ± 4.7	8.2 ± 0.9	5.0 ± 0.9	72 ± 17
2000	65.0 ± 2.9	8.4 ± 0.7	5.4 ± 0.3	56 ± 11
2001	62.2 ± 1.3	8.0 ± 1.1	5.0 ± 0.7	60 ± 18
2002	67.4 ± 1.5	7.4 ± 1.0	4.8 ± 0.7	60 ± 8
2003	68.8 ± 1.5	8.0 ± 1.0	5.4 ± 0.8	74 ± 16
2004	69.6 ± 1.8	7.8 ± 1.0	5.4 ± 0.8	76 ± 7
2005	72.0 ± 1.9	7.4 ± 1.1	5.2 ± 0.7	70 ± 17
2006	76.0 ± 1.2	7.2 ± 0.5	5.4 ± 0.4	76 ± 6
2007	80.0 ± 2.9	7.2 ± 0.8	5.6 ± 0.7	66 ± 15
2008	81.4 ± 1.9	6.6 ± 0.9	5.2 ± 0.6	76 ± 5

[1]Frequency = percentage of animals in sample having nonzero relationship to Line 1; R_{rel} and R_{all} = average coefficients of relationship for sampled animals that are related to Line 1 and for all animals in the sample, respectively. Maximum R = the coefficient of relationship for the animal contained in the sample that was most closely related to Line 1.

100 animals appeared insufficient, it was decided to investigate a slightly smaller sample size of $n = 400$. Results of the analysis of 5 replicate samples of $n = 400$ animals for each of the years 1980, 1990, and 2000 were found equally satisfactory as the samples of $n = 500$ animals from those years. Materially smaller sample sizes were not consistently satisfactory. Therefore, the results of the following analysis is based on 5 replicate samples of $n = 400$ animals for each year from 1980 to 2008.

Influence of Miles City Line 1 Hereford on the United States Population

Over time, the average proportion of animals influenced by the Miles City L1 population increased from an average of 23% in 1980 to 81% in 2008 (Table 2). The rate of increase in the proportion of animals recorded by the AHA that were related to Miles City L1 averaged 1.69 ± 0.07% per year. If this rate of increase were extrapolated into the future, every animal recorded by the AHA would contain genes originating from L1 by 2020. Considering only those calves in each annual sample from the AHA herdbook that were related to Miles City L1, the influence of L1 decreased by an average of 0.11 ± 0.01% per year over the period from 1980 to 2008. However, when the entire set of sampled calves was considered, it was found that the influence of Miles City L1 increased by an average of 0.06 ± 0.02% per year over the same time period. These findings result from the increasing proportion of cattle recorded by the AHA being related to Miles City L1 more than offsetting the trend to more distant relationship in the later years. The average coefficient of relationship being slightly greater than 5% in 2006 through 2008 can be characterized as the equivalent of each Hereford calf recorded by the AHA having a L1 Hereford from Fort Keogh as a great-great-grandparent.

The influence of the sampled industry sires was sporadic and without discernible trend in time. Across all years, 28.1 ± 6.1% of the 400 calves sampled annually were related to the 50 sampled industry sires born in the decade starting 2 yr before the birth of the calves. Overall, of the 155 industry sires sampled from the AHA herdbook only 28 of them were related to any of the sampled calves.

Geographic Distribution of Hereford Cattle in the United States and Their Relationship to Line 1

Our sampling found recorded Hereford cattle in every state except Alaska and Rhode Island. Most of the Hereford cattle were found in the Great Plains, eastern Corn Belt, and Pacific Northwest regions of the United States (Fig. 2). On a state by state basis, the greatest densities (n/km^2) of Hereford cattle are in northern Kansas, southern Oklahoma, and Texas. The presence of Hereford cattle, with a coefficient of relationship to L1 greater than 0.25, were distributed across the United States in a pattern that mimics the general distribution of Hereford cattle (Fig. 3). When the qualifying relationship (R) of animals to L1 was reduced (e.g., to the interval $0.125 < R \leq 0.25$), numbers of animals meeting the criterion increased and their geographic distribution became broader (Fig. 4). Geographic distributions specific to additional levels of relationship can be found in Leesburg (2011).

Genomic Relationship of the American Hereford Association Record Hereford Population to Line 1

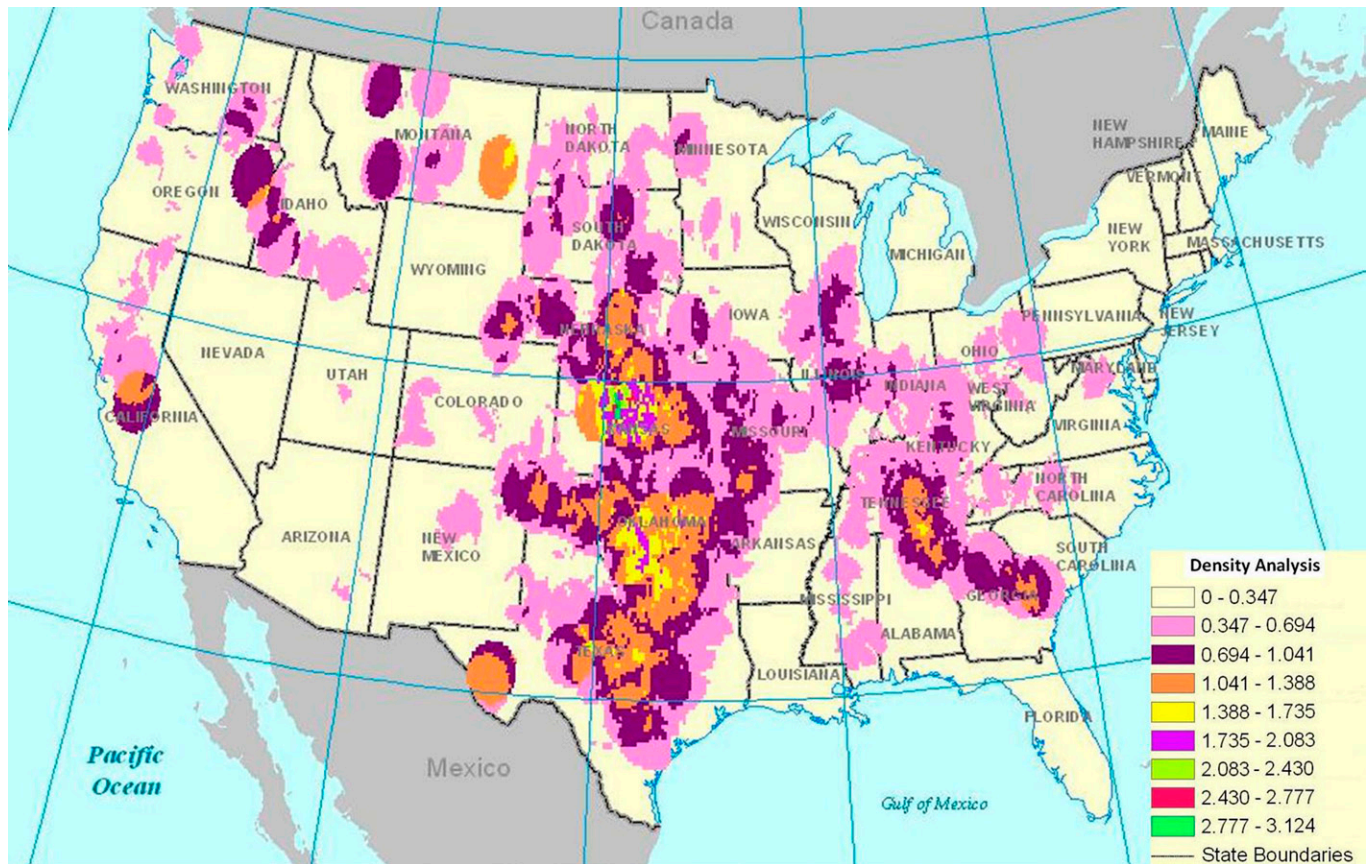Animals identified a priori as belonging to Miles City L1 were grouped in cluster 1 with an average probability of

Figure 2. Density of recorded Hereford cattle in the United States. The legend reflects numbers of animals per square kilometer.
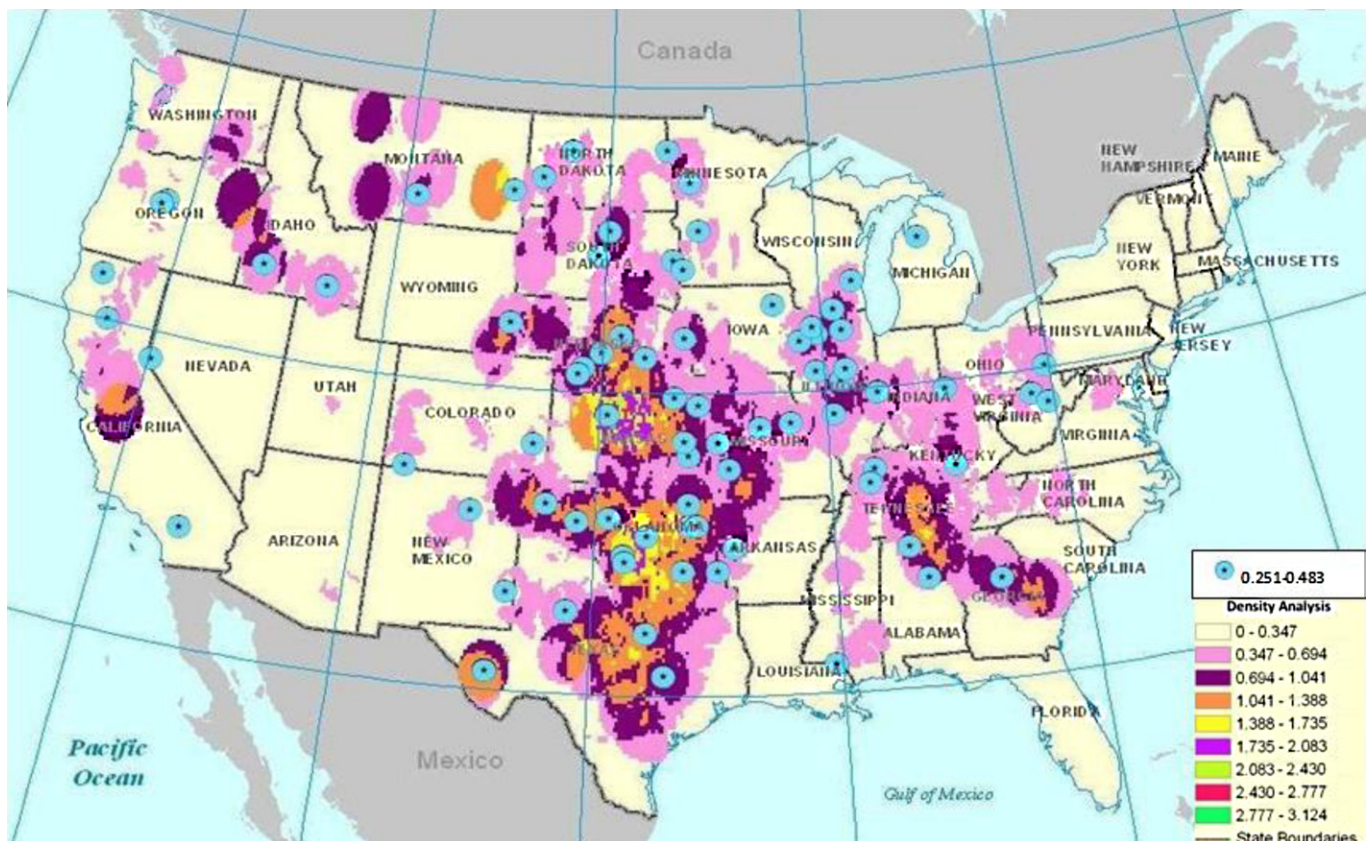

Figure 3. Density (number per square kilometer) of recorded Hereford cattle in the United States overlaid by symbols indicating the presence of animals with relationship to Line 1 Hereford cattle greater than 0.25.
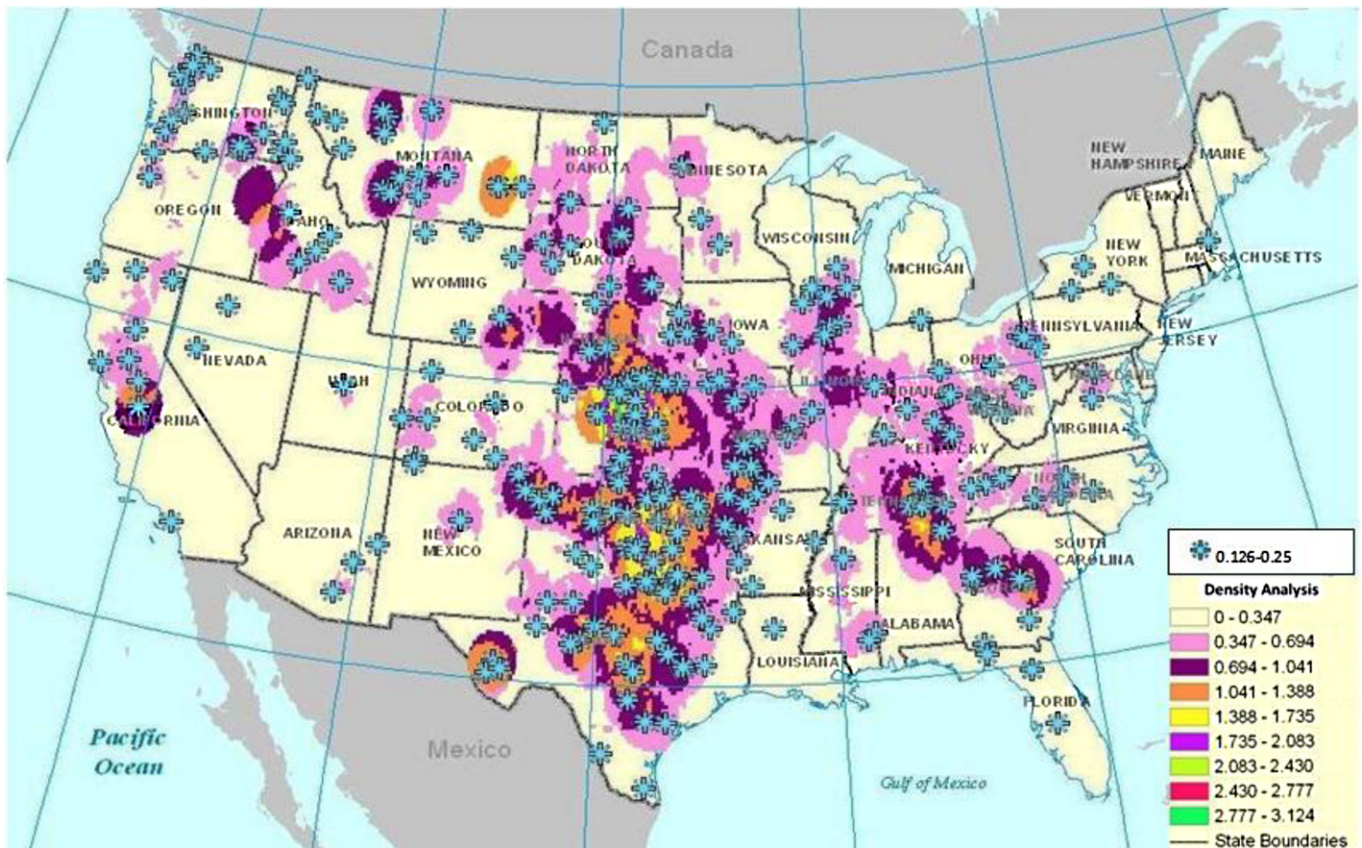
Figure 4. Density (number per square kilometer) of recorded Hereford cattle in the United States overlaid by symbols indicating the presence of animals with relationship (R) to Line 1 Hereford cattle in the interval $0.125 < R \le 0.25$.

membership >0.98 with SD = 0.05. The genotyped industry sires had varying probabilities of membership in the Miles City L1 cluster and the non-L1 cluster. The average probability of their membership in the L1 cluster was distributed on the interval from 0.00 to 1.00 with mean = 0.20, median = 0.14, and SD = 0.25. For the 5 bulls having greatest probability (>0.89) of membership in L1, 9 of their 10 collective parents were from the L1 Hereford herd at Fort Keogh and the 10th parent was linebred to members of Miles City L1.
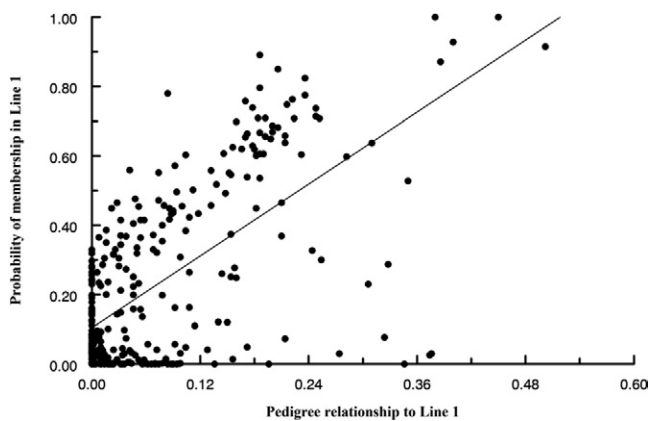

Figure 5. Correspondence between pedigree relationship with Miles City Line 1 Hereford cattle and genomic probability of membership in the Line 1 Hereford population for bulls sampled from the registry of the American Hereford Association.

Pedigree relationship of the 311 genotyped industry sires with L1 was distributed on the interval 0.00 to 0.50 with mean = 0.08, median = 0.04, and SD = 0.19. Shown in Fig. 5 is the relationship between probability of membership in the L1 cluster that was inferred using STRUCTURE and the pedigree relationships of the animals representative of the U.S. industry with L1 Hereford cattle. The scatter plot illustrates the joint distribution of individual animals from the industry Hereford sample. The regression of genomic probability of membership in Miles City L1 on pedigree relationship for the 311 genotyped industry sires from Thallman (2009) and Kuehn et al. (2011) was 1.73 ± 0.11.

DISCUSSION

Line 1 Hereford cattle have served as study material for numerous research projects from the mid 1930s to present day (MacNeil, 2009). Studying the use of L1 Hereford cattle provides insight into dissemination of one aspect of the research results to an industry where those results are applied. Here, we make a distinction between the influence of Miles City L1 on the U.S. Hereford population and the average relationship between these 2 groups. At least 2 factors complicate this analysis.

First, how is "influence" appropriately described? Bulls (and females) were sold from the Miles City L1 population, including bulls that sired progeny within the Miles City L1 population. These bulls were purchased by the "industry" and produced additional calves in the industry. It is contended that the correct metric to measure of the influence of L1 on those calves is their relationship to their sire as he is their connection to the Miles City L1 population. Obviously, their sire has maximum relationship between them of all of the L1 sires, and hence the maximum coefficient of relationship was used to quantify "influence." Alternative summary statistics (such as the mean) would include more convoluted relationships to additional Miles City L1 sires.

Second, how is the influence of Miles City L1 to be separated from ongoing external influence of common ancestry? Since it was founded in 1934 migration is entirely in 1 direction—from Miles City L1 to industry. Therefore, the common ancestor arguably best positioned to contribute to both industry and L1 as suggested above would be Advance Domino 13 (sire of both of the founding sires of L1; date of birth 1928). Here, the analysis began with industry calves born in 1980 and only included L1 sires from the previous 12 yr. Thus, the earliest L1 sires considered were born in 1968. Those sires are 8 or 9 generations removed from Advance Domino 13. All other L1 sires considered here are further removed from that point of common ancestry than are these sires. Thus, for the L1 sires we considered to have collateral relationship to the calves sampled from industry through common ancestry other than from Miles City L1 would require traversing a minimum of 9 or 10 generations with a maximum impact on the relationship coefficient of approximately 0.002. A further complication in making the relevant calculations arises because the entirety of the herdbook from the early 20th century has not been digitized (S. Sanders, AHA, personal communication, 2008). Here, this potential source of upward bias in the influence statistic has been ignored.

In the 1950s, dwarfism was recognized as a serious problem for Hereford breeders (McCann, 1974). The line-breeding and selection program that produced the L1 herd established it as being free of the recessive allele causing dwarfism and it became a resource breeders could use to purge dwarfism from their herds. At the end of the 1960s, in response to importation of Continental breeds from Europe, Hereford breeders again put greater emphasis on weight, maternal ability, and frame size. Years of L1 selection for performance again made Miles City L1 cattle popular and 68% of all purebred Hereford sires advertised in the July 1983 issue of the breed magazine were related to L1 (Dickenson, 1984). The obvious discrepancy between the 68% of advertised sires being related to L1 by pedigree and the present finding of $37.8 \pm 4.3\%$ may arise from the advertised sires being a highly selected sample of sires

then in use that was chosen at a time when the popularity of Miles City L1 cattle was high as indicated by record sale prices (result not shown). This popularity and research at Fort Keogh using the L1 cattle at a time when economics dictated that breeders needed to make better choices for their breeding programs created a stable demand for L1 genetics (Dickenson, 1984). It also coincided with the introduction of performance oriented breeding goals and the need for a different type of Hereford (Dickenson, 1984). Additionally, there are several reputation seedstock operations that use L1 germplasm and further disseminate it to the beef industry through their production sales as evidenced by sale reports in the popular press (e.g., Hereford America, 2013). The success of these private operations also affects the impact of the Miles City L1.

The results show L1 to be an important and widely distributed component of the U.S. Hereford breed. Regions with the greatest current-day densities of all Hereford cattle, and of L1 Hereford cattle as well, correspond to the historical record of areas where the Hereford breed gained strong footholds during the 1870s (Miller, 1902). Breeders with cattle having high relationships with L1 are typically identifiable as buyers at the Fort Keogh sales through which animals in excess to the research needs have been offered to the industry. Thus, wider dissemination of L1 germplasm appears to follow a tiered or pyramidal structure where a relatively small number of breeders purchase animals from the Miles City nucleus herd and multiply the germplasm for wider dissemination. Ultimately, cattle related to the L1 Hereford were located in every region and almost every state of the United States.

Here, both pedigree and genomic data were used to study the dissemination of L1 Hereford germplasm. The AHA continually prunes the digitized pedigree data set to contain only those animals that are influential in national cattle evaluation and ancestral animals that are of specific interest and demand to the general populace (S. Sanders, AHA, personal communication, 2008). Here, the digitized pedigree of the genotyped industry sires was augmented with pedigree information from the printed herdbooks beginning with volume 1 (American Hereford Cattle Breeders' Association, 1899). Pedigree data, as reported by breeders, may contain errors or be otherwise unavailable due to concerns over ownership of intellectual property (S. Sanders, AHA, personal communication, 2008). Use of genomic data may overcome these issues (Decker et al., 2012). In the present study and in the study of Angus cattle by Decker et al. (2012), there was general agreement between relationships indicated based on pedigree data and those inferred from genomic data. However, the scattering of points along the x axis of Fig. 5 indicating relatively high degrees of pedigree relationship without support from the genomic data and this is problematic (e.g., Purcell et al., 2007). These individuals may reflect

errors in pedigree recording, most likely in the set of industry sires. The positive *y*-intercept of the regression line shown in Fig. 5 was anticipated as it reflects background identity-by-descent and results from the assumption of no common ancestry for animals in the pedigree base population (Li et al., 2010; Decker et al., 2012).

In conclusion, since its inception in 1934, the scope and breadth of the genetic influence of Miles City L1 Hereford cattle is seen in the development of many fundamental evaluations still regarded as standards today. The L1 Hereford has contributed genetically to the U.S. beef industry through sales of animals that were surplus to the needs of the research program. The apparently successful use of L1 genetics in parts of the United States that are geographically distant from Montana provides an interesting counterpoint to the usual experience in exporting germplasm to regions where its adaptation is questionable. Given the multiplier effect derived from the use of L1 germplasm by other purebred breeders, it is apparent the L1 Hereford cattle from Miles City, MT, have a significant penetration into the U.S. Hereford population. Thus, L1 provides connectedness for current genetic evaluation systems that are used for the Hereford breed. In addition, germplasm from L1 aided the Hereford breed in the elimination of dwarfism and in responding to competition from breeds that have been imported from Europe. Thus, these results document the far-reaching and profound impact of a long-term research program.

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