THE INFLUENCE OF LINE 1 HEREFORDS ON THE GLOBAL HEREFORD POPULATION

by

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Thesis submitted to the Faculty of Natural and Agricultural Sciences, Department of
Animal, Wildlife and Grassland Sciences,
University of the Free State

In accordance with the requirements for the degree

PHILOSOPHIAE DOCTOR

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Bloemfontein

April, 2012

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PREFACE

I would like to express my sincere appreciation and gratitude to some outstanding people and institutions that have helped me on this crazy ride.

To:

Dr. Michael D. MacNeil: for his continuous encouragement, leadership and support; thank you for sharing your knowledge with me.

Prof. Frikke W.C. Neser: for taking a chance on me and supporting this project across an ocean. Your understanding and encouragement are greatly, greatly appreciated.

Dr. Este van Marle-Koster: for accumulating samples used to obtain DNA from Hereford cattle in South Africa.

The American Hereford Association and the Canadian Hereford Association: for providing such valuable data for this project and your continued support and interest. Namely: Stacy Sanders and Jack Ward, American Hereford Association and Ross MacDonald and Karin Schmid, Canadian Hereford Association.

Agricultural Research Council in Irene: namely Olivia Mapholi Tshipuliso, Norman Maiwashe, Ephraim Matjuda, and Helena Theron. Everything you have done on behalf of this project, coordinating data, supplies, semen and all the little things were invaluable to the result. You are dear friends and I hope to see you all again soon!

To my parents: thanks for raising all of us on a farm and giving us tremendous appreciation for hard work, sweat, blood and manure. Agriculture helps makes the world go ‘round, thanks for giving us some dirt and cows to play with!

My most wonderful husband: who was my champion from day zero; I couldn’t have done this without his love, support, and encouragement. There aren’t great enough words to describe how much you have done and supported me through all this - I am most truly blessed!

To my babies: I live for the hours I get to see you and watch you grow. You make me happy every second, and I only want more. You’re too little to understand this, but your constant hugs and kisses whenever I got home no matter how late made me want to work harder and harder for you.

And finally – Thank you to the University of the Free State, for accepting this thesis and allowing me to finish this idea I have had for many years!

ABSTRACT

The goal of this research was to document the influence of Line 1 Hereford cattle, developed by the United States Department of Agriculture at its research facility in Miles City, Montana, on Hereford populations in the United States, South Africa, Canada, Australia, Great Britain, and Uruguay. Line 1 Hereford cattle were line-bred at the USDA-Agricultural Research Service station of Fort Keogh in Miles City, Montana since 1934. The dissemination of germplasm from Fort Keogh began with the earliest recorded sales in 1948. Analytical approaches made use of both recorded pedigree and genomic markers. Pedigree records numbering nearly 14 million from the American Hereford Association, and 3 million from the Canadian Hereford Association were randomly sampled five times for each year from 1980-2008. Sampled animals were pseudo-mated to Line 1 sires, inbreeding coefficients of the resulting progeny were calculated and relationships of the sampled individuals to Line 1 were estimated as twice the maximum inbreeding coefficient. The Line 1 Hereford population was found to be ancestral to 82% of the current population of purebred Hereford cattle in the United States. The number of Hereford cattle in the Unites States that were related to Line 1 has increased by more than 2% per year. The greatest concentrations of Line 1 genetics were found in the central and Midwestern regions of the country, but Line 1 genetics were found in 48 of the 50 states. Proportion of Hereford cattle registered in Canada that were related to Line 1 increased from 26% to 68% between 1980 and 2007. Animals recorded in the Canadian Herdbook that had ancestors in the American Herdbook were found in 8 of the 9 provinces and of these, animals related to Line 1 Hereford were found in 6 provinces. Two hundred forty animals sampled from the Line 1 herd at Fort Keogh and 311 sires representative of the Hereford breed in the U.S. were genotyped for 50K SNP. Resulting genotypes were used to assess the probability that the animals sampled from the U.S. population were members of Line 1 Hereford. The average probability of membership was 0.20 and the regression of pedigree relationship on genomic probability of membership was 1.73 ± 0.11 ($r = 0.65$). A similar analysis of the relationship between Line 1 and a sample of the South African Hereford ($n = 36$) population was conducted using 34 microsatellite loci. It was found that the probability that South African Hereford cattle were descendants of the Line 1 Hereford population was 0.38 ± 0.08. Pedigree relationship of Hereford cattle registered in South Africa with Line 1 was 24%. Obtaining complete herdbooks from other countries proved infeasible. Therefore, pedigrees of highly used sires were used as inferred from the accuracy of their genetic evaluation for direct effects on weaning weight from Hereford populations in the United Kingdom, Australia, and Uruguay with that of Line 1 Hereford. Those estimated relationships were 0.22, 0.30, and 0.23, respectively. The apparent presence the Line 1 Hereford cattle maintain in Hereford cattle around the world is highly important. The observed relationship of Line 1 Hereford with other Hereford populations is indicative of the far-reaching and profound impact of a long-term research program.

CHAPTER 1

INTRODUCTION

Inbreeding and hybridization programs were started in the early 1920’s following upon the experiments of G. H. Shull and others (Sprague, 1962). These experiments provided the basis for the development of hybrid corn. Demonstration plantings and field observations proved the value of hybrids. The U.S. livestock industry was not to be left behind and in 1931, the U.S. Department of Agriculture (USDA), Bureau of Animal Industry, initiated projects on development of inbred lines of cattle that were superior in rate of gain, weight for day of age, carcass characteristics, and fertility (Winters, 1931; Knapp *et al.*, 1951). Fort Keogh, the USDA range livestock experiment station, played a large part in this project by developing the first and several of these inbred lines of cattle. The most important and productive of these inbred lines being Line 1 Hereford cattle (Knapp *et al.*, 1951).

To clarify, a breed is defined as a group of domesticated animals or plants with a homogeneous appearance, behavior, or other characteristics that distinguish it from other animals or plants of the same species; most often arrived at via selective breeding. Alternatively, an inbred line is the reproduction from the mating of two genetically related parents which results in increased homozygosity.

Although initially not popular among the beef industry, the Line 1 breeding program produced a faster growing animal relative to contemporary cohorts. In the 1950’s, dwarfism was recognized as a serious problem for Hereford breeders (McCann, 1974). The linebreeding and selection program that produced the Line 1 herd rendered it 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 1960's, in response to importation of continental breeds from Europe, Hereford breeders again put greater emphasis on weight and frame size and this also increased the popularity of Line 1 Hereford cattle.

Dissemination of Line 1 Hereford germplasm began in 1948 with sales of bulls and females that were excess to research needs to local cattle producers. In time, buyers came from across the U.S. to purchase Line 1 Hereford cattle from Fort Keogh. Additionally, several successful seedstock herds were founded using Line 1 germplasm. In 1983, it was noted that 68% of all purebred Hereford sires advertised in the July issue of the breed magazine were related to Line 1 (Dickenson, 1984). However, to date there has been no systematic study of the geographic distribution of genetic material from Line 1 or the degree to which that material is manifested in the world's Hereford population.

1.1 OBJECTIVES

The overall goal of this project was to quantify the influence of the Line 1 Hereford cattle, a product of research conducted by the United States Department of Agriculture, Agricultural Research Service and predecessor agencies, on certain major Hereford populations worldwide.

Specific objectives were to:

1. determine the requisite sample size to estimate the average relationship of Line 1 Hereford cattle at Fort Keogh Livestock and

Range Research Laboratory with animals in a pedigree recorded breed association database;

2. estimate relationship of Line 1 Hereford cattle at Fort Keogh Livestock and Range Research Laboratory with animals recorded by the American Hereford Association using pedigree and genomic information;
3. estimate relationship of Line 1 Hereford cattle at Fort Keogh Livestock and Range Research Laboratory with animals recorded in the South African Hereford Herdbook using pedigree and genomic information;
4. estimate relationship of Line 1 Hereford cattle at Fort Keogh Livestock and Range Research Laboratory with animals recorded by the Canadian Hereford Association using pedigree data; and
5. estimate the relationship between influential sires whose progeny have been recorded in the herd books of Australia, the United Kingdom and Uruguay with the Line 1 Hereford cattle at Fort Keogh Livestock and Range Research Laboratory.

1.2 HISTORY OF CATTLE

The ancestor of all existing domesticated cattle is universally accepted as being the now extinct aurochs, *Bos primigenius* (Zeuner, 1963; Grigson, 1978, 1980; Epstein and Mason, 1984; Payne, 1991). It’s thought that the aurochs had evolved in Asia from an ancestor known as *Bos acutifrons* (Pilgrim, 1947). The aurochs migrated across Asia, into Europe and North Africa and their remains have been found in far reaching geographical regions. It is thought that the migration of the aurochs led to the creation of several distinct subspecies across these areas (MacHugh, 1996).

Descending from aurochs cattle, the two major domesticated cattle species, *Bos taurus* and *Bos indicus,* are morphologically and physiologically different. The *Bos taurus* cattle are usually found in temperate climate zones with higher levels of rainfall and denser vegetation. While *Bos indicus* cattle are typically found in hot arid or semi-arid regions of the world like Africa and Asia. MacHugh (1996) offers a very detailed analysis of the paths of evolution these two species may have taken through history to arrive at the species and breeds of cattle we know today. Whatever the early origins of domesticated cattle, it's clear that many varieties existed on several levels even at the earliest stages before breeds were clearly defined or recognized as such.

Events surrounding cattle domestication have been studied by historians and archeologists alike. A widely accepted view for the foundation of the modern European cattle is that they have ancestors who were introduced by early farmers who migrated from India and the near East into Italy during a Neolithic changeover where a farming or agrarian society was cultivated away from the hunter-gatherer lifestyle (Cavalli-Sforza *et al.*, 1994, Beja-Pereira *et al.*, 2003). Aurochs cattle still existed at this time, but as the human population continued to expand in Europe their numbers declined rapidly and they survived mainly in remote isolated areas. They all eventually became extinct with the last auroch supposedly dying in a Polish game reserve in 1627 (Epstein and Mason, 1984).

How much genetic material was exchanged to aid in the development of the European cattle breeds between the native aurochs and the newly arrived domesticated cattle of new farmers is unknown (MacHugh, 1996). However, studies conducted by Medjugorac *et al.* (1994) utilizing classical polymorphisms, such as blood group systems and allozymes from 14 European cattle breeds suggest that some genetic exchange did take place. Medjugorac *et al.* (1994) shows the migratory model of expansion of the early European farmers is demonstrable in current present day studies of human population which can also be used to explain the distribution of genetic variation seen in today's existing cattle breeds. A pattern of gradual phenotypic and genetic differences was observed going from the southeast to northwest of Europe. Along with the genetic variation observed between the breeds studied suggested gene flow from the indigenous aurochs into the newly introduced herds did in fact happen, with the result being the modern day breeds now present in Europe.

Hanotte *et al*. (2002) determined the initial expansion of the African *Bos taurus* was likely from a singular region of origin. The route to the southern part of the continent was by an easterly route. Alternatively, the introduction of *Bos indicus* genetics found entry through Cape Horn and the east coast of Africa as well as two modes of introgression (Hanotte *et al*., 2002).

Ultimately, what has been determined thus far is that the development of modern day cattle populations were influenced by evolutionary pressures from the beginning of pastoralism and into the early 19th century when the modern concept of specific cattle breeds was initiated (Medjugorac *et al.*, 1994; and MacHugh, 1996). However, in the past 160+ years the situation is dramatically different with the introduction and extensive use of scientific breeding practices and reproductive technology.

1.3 ANIMAL AGRICULTURE

People have tended livestock and domesticated animals have provided food, transport, shelter and power for thousands of years (Zeuner, 1963). Selected plants and animals form the foundation of agriculture (Childe, 1957). In the last 200 years the focus has been on deliberately selecting animals to better serve the needs of the human population and breeding them accordingly (BOA, 1993; Zeuner, 1963). There has been a definite shift in the genetic makeup of domesticated animal populations. For example, cattle have been selected and bred specifically for either milk or meat production; sheep for either wool or meat production (Willham, 1982), and even chickens for either eggs or meat (Chambers *et al.*, 1981; Crawford, 1990). Diversity in genetics within these agricultural species is highly important as the ever expanding human population places increased demands on natural resources and strives to improve their living conditions (Cunningham, 1992).

The parallel migration of the human population and their domesticated animals led to the introduction of these species to regions where they would not likely have colonized without human assistance otherwise (Mason, 1984). Once a species was introduced the selective adaptation process began that acclimatized the species to the new environment, additionally it increased the genetic distance of the emigrating population away from its parent population (Su *et al.*, 2003). Over time the effects of isolation and selection resulted in populations that became genetically distinct from others maintained in alternative environments (Mason, 1984, Su *et al.*, 2003). The geographical center of the initial domestication of domestic species can be identified and the distribution of the various breeding populations about those centers adapted to different environments can be traced (Mason, 1984).

Livestock production has been greatly enhanced through new technologies and developments that altered their physiology and environment (Blackburn, 1993; Toro and Caballero, 2005). Cattle producers in Europe and North America have long been exposed to and used the practices of genetic selection and assortative mating. However, in several other regions of the world use of scientific methods and technologies is still in the formative stages. This could give breeds in Europe and North America a unique genetic history and diversity.

Most of the observed variation in livestock is genetic due to the differences in genes carried by various individuals (Frankham *et al.*, 2002). This variation can be quantified at several levels; among species, among major types within a species, among breeds within a major type, between breeders' lines within a breed, and among individuals (BOA, 1993). For example, differences in sheep species, hair sheep and wool sheep are types, Dorset and Merino are breeds, commercial stocks or strains of Merino are breeder's lines, and between individuals in the Merino breed can all be traced back to the variation at the level of the gene (FAO, 1986). Genetic diversity explains the expression of the degree of this variation.

In animal agriculture, genetic variation has been manipulated by controlling reproduction through selection and crossbreeding and these tools have been the foundation for improving livestock populations (Miller, 1969). Response of populations to the selection goals of breeders manifest through artificial selection and changes in their environment ultimately depends upon the reservoir of genetic variation (Gibson and Wilton, 1998).

Genetic selection has yielded amazing results. In the last century alone, milk production per dairy cow has increased rapidly while the number of cows has declined to less than one-half the peak number in the 1940's. Peak milk yield has increased more than three-fold from 37 kg/d in the 1960's to 116 kg/d in the 1990's (Hansen, 2000).

However, human needs and preferences encouraged even more varied populations over the years. Wool sheep were developed, as were dairy cattle and goats, while chickens and ducks were developed that had increased egg-laying capabilities. All these are examples of domestic populations bred to meet specific needs (Zeuner, 1963; Willham, 1982). Combining these needs with preferences for color patterns and morphological types brings about much differentiation among livestock populations (Sharp, 1987).

The origination of cattle breeds as a concept rather than local types is said thought to have originated with Robert Blakewell of the 18th century (Porter, 1992). Intensive culling and inbreeding were pervasive in an effort to realize specific breeding goals, thereby aiding the shift from draught animals to beef producing or milk producing animals. This influence lends to breeds that are very distinct from one another with regard to phenotype, the result of a history of rigorous breeding programs. Among the British Isles, there are approximately 30 distinct cattle breeds, there are those selected for dairy production, beef production, and those selected primarily for breed phenotype, with regard to coat color or pattern (Weiner *et al*., 2004).

The formation of breed societies in regions colonized by western Europeans solidified the subdivision of domestic species in response to human preferences in the 1800s (Wezyk, 1990). Breed individuality rested on the idea that consistency of type was an important component in livestock production and could only be achieved by the controlled mating among animals of known parentage (Wezyk, 1990). Initial entry into breed society records was restricted animals based on color and morphological type and if continuous membership was desired then ancestry needed to be documented. The best example of breed isolation is seen in the tremendous genetic diversity of horses and dogs. The idea of breed isolation also brought a rich array of livestock into Western Europe (Wezyk, 1990).

However, restricting the number of parents and application of artificial selection has resulted in a decline in the genetic diversity of some livestock and plant species (OTA, 1987). There has been an increased reliance on specific breeds of livestock for commercial and seedstock production at the expense of other recognized breeds and types (OTA, 1985). The reduced genetic diversity may limit options in the future for improving livestock populations or modifying them to meet as yet unforeseeable needs and demands (OTA, 1985).

Breed designation is generally considered a western European and North American notion, but it can and is applied to basically any livestock population that is reasonably identifiable (BOA, 1993). However, in much of the developing world breed designations can’t be used accurately, because breed identity is not maintained, nor is the choice of mates actually controlled (Wezyk, 1990). In these countries, distinct, identifiable populations are typically the result of geographic isolation and/or phenotypic selection. Yet, even in developed countries breed identity does not carry with it clear distinction of genetic exclusivity that is generally assumed (BOA, 1993). Breeds have been combined with other breeds to obtain rearrangements of the gene pool. Specific genes are not lost by this process; rather they are transferred to the new population (Wezyk, 1990).

1.4 GENETIC DIVERSITY STUDIES

The advancement of technology has aided in the widespread dissemination of animal germplasm the past 100 years, with likely affects calculable on genetic diversity of cattle populations. Research is available on genetic relationships and genetic variation within dairy cattle breeds (Cunningham and O’Byrne, 1977, Swalve and Van Vleck, 1986, and Jansen *et al.*, 1987), with few of these same or similar analyses conducted for beef cattle. Cleveland *et al.* (2005) researched genetic diversity in the U.S. Hereford population, establishing a level and rate of inbreeding and effective population size. Subsequent reasons for changes and levels of inbreeding coefficients were identified as well as strategies to maintain a specific level of genetic diversity. Mburu and Hanotte (2005) studied the large variation in genetic diversity among African cattle; estimating diversity was highest for *Bos taurus* cattle in north Africa and lowest in the western part of the continent. Furthermore, analysis of genetic structure supported isolation by distance in all but the South African region where there was extensive gene flow between populations.

A comprehensive pedigree analysis of a large portion of the Hereford pedigree by Cleveland *et al*. (2005) showed inbreeding of modern Hereford cattle was 9.8% with approximately 95% of individuals being inbred. Burrow (1993) analyzed the genetic diversity of Hereford subpopulations; identifiable fractions or subdivisions of the aforementioned Hereford population. Popular lines of Hereford cattle were sampled by Willham (1937) with a calculated mean inbreeding coefficient of 8.1%. Stonaker (1951) and Russell *et al.* (1984) each reported inbreeding on closed herds circa 1947 and 1984 respectively at 30.7% and 37%. Blott *et al.* (1998) reported on Hereford cattle from the United Kingdom and Canada, subsamples of the breed produced significant genetic differences between the two countries. A significant portion of domestic genetics in British Hereford cattle has been supplanted by contemporary germplasm from Canada. Canadian Hereford cattle were found to be more homozygous than Hereford cattle in other countries (Blott *et al.*, 1998).

Performance in beef cattle is reduced as documented by inbreeding studies conducted by Flower *et al.* (1963), Brinks *et al.* (1965), and Krehbiel *et al.* (1969). Typically growth rates and fitness levels are reduced in inbred cattle populations. MacNeil *et al.* (1989) studied the effects of inbreeding and heterosis as it was manifested in crossline matings on maternal characteristics. Their findings compared linecross, topcross and inbred lines. Methods used in these studies are similar to those developed for this project’s analysis of Line 1 cattle and their potential influence on Hereford herds around the globe.

Bennewitz *et al*. (2006) suggested extinction of farm animal breeds threatens genetic diversity of livestock species. The Foreign Agriculture Organization (2000) classifies a third of the recorded livestock breeds as high risk to extinction; with the loss of over 1000 breeds in the last 100 years. It is widely accepted that there is a distinct need to conserve genetic diversity of threatened populations so long as there is adequate time to establish a conservation plan and if the breed or population is a priority. A plentiful resource of genetic diversity within a livestock species is the requirement of coping with presumed future changes in livestock breeding and farming programs (Bennewitz *et al*., 2006).

Research by Taberlet *et al*. (2008) indicated many breeds of domesticated livestock suffer from inbreeding, with an effective population size below 50. Economic pressure is placed on farmers to develop industrial breeds, which leads to abandonment of traditional breeds which ultimately led to extinction in some cases as a result. These studies indicate genetic resources of cattle, sheep and goats are highly endangered, particularly in developed countries (Taberlet *et al*., 2008). These results can be directly compared to lines, families, or populations within breeds as well; a loss of genetic diversity leads to a loss of useful genetic resources as well.

The level of dynamics among Hereford cattle on a national and global scale make for an ideal study on genetic diversity, within and among segregated, isolated or inbred populations.

CHAPTER 2

HEREFORD HISTORY AROUND THE GLOBE

2.1 THE HEREFORD CONTRIBUTION

The true origin of the Hereford breed is lost to history, but as the name Hereford suggests these cattle are agreed to have evolved from the indigenous Red cattle which roamed the Welsh Border Counties and Western edges of England (Hereford Cattle Society, 1996). The origins of this breed in the county of Herefordshire have been mentioned in written documents as early as 1600. Willham (1937) reported the breed may have come from stock that originated in Holland.

Hereford cattle were believed to originally have been developed as draught oxen, bred to subsist on poor grazing while maintaining the ability to withstand hard work. Initially, pedigree information was not highly regarded. In the early part of the 19th century, Hereford cattle were considered your basic farmers cow, nothing fancy and not worthy of notice from fancy breeders or the aristocracy (Dixon, 1868). Formal selection and improvement practices began in the early 18th century when Benjamin Tomkins started a herd with a Hereford bull named Silver. Historical records identify the bull, Silver, as red with a white face and with a bit of white on its back (Hereford Herd Book Society, 1995).

International trade in the later part of the 19th century changed minds considerably with the ‘Yankee Boom” which called for legions of cattle to be exported to the United

States. Enthusiasm for pedigree information and entry in the herd book only gained more interest when breeding stocks were sold internationally. Formal association and record keeping allowed farmers access to the profitable exportation trade (Prentice, 1942).

In the late 19th century, when there was great need to increase and improve meat supplies, Hereford bulls were used extensively (Grundy, 2002). By the mid 1860's, Hereford cattle were imported into the United States from Great Britain and herds were mainly established in the Northern Great Plains. Conditions were right for breed expansion due to a strong demand for regular beef supplies from the growing industrial population (Grundy, 2002).

T.L. Miller is credited as having great influence on establishment of Hereford cattle in the U.S. In 1872, he founded a herd with purchases of Hereford cattle from Ohio and Ontario, Canada. Eight years later he traveled to England to purchase animals from primary Hereford breeders (Miller, 1902). He recognized the need and desire for this breed in their ability to improve the cattle of the Plains.

The Hereford breed enjoyed great success on the Great Plains of the U.S. It was early maturing, an excellent and economical converter of grass into quality beef and was long lived. Early demand from cattle producers on the ranges of the Great Plains was for a bull that had at least some Hereford breeding and buyers travelled great distances for bulls that were at least part Hereford (Sanders, 1914). Even a bull that was 25% Hereford was viewed as being able to impart considerable improvement to the range cattle. American breeders formed a breed society in 1881 and published their first herd book soon after (Sanders, 1914). Entry into the herd book met with restrictions in 1883, such that only calves that were the product of animals that were a part of Volumes 1 or 2, or one of the 13 volumes of the English herd book were allowed (Sanders, 1914). There was great monetary value in well-authenticated lineages.

Anecdotal evidence gives a few ideas for the demand and size of the trade as well as the scarcity of Hereford bulls in the early years of importation. Between 1882 and 1890, cattlemen placed over 10,000 Hereford bulls on the ranges of the Texas panhandle (Grundy, 2002). The demand for purebred and or close to purebred cattle was so high that nearly all males were kept for breeding, so much so that there were shortages of steers for livestock shows and general slaughter. Before 1880, only about 200 animals had been imported to the United States. However, importation increased to between 3900 and 6000 bulls from 1880-1884 (Grundy, 2002). The distribution of Hereford cattle at the time is represented in Table 2.1 (Sanders, 1914). Hereford cattle foraged well in tough environments from wintering in the foothills of the Rocky Mountains to thriving in desert and arid places like New Mexico, Texas and Arizona. Their reputation of docility and being easy calving garnered them further attention among ranchers and stockmen. Hereford-cross steers, virtually unknown only 5 years earlier were garnering top prices in 1883. The breed seemingly invaded the Great Plains after 1886 with reports of widespread Hereford breeding programs in Texas, New Mexico, and Arizona. By 1910, Longhorn cattle were rarely seen in stockyards (Walton, 1986). A mere decade later still the beef industry in the United States appeared to have been revolutionized. The once accepted four to five year old, 2000 pound oxen was effectively trumped by a fifteen to eighteen month high quality steer (Wallace and Watson, 1923).

Table 2.1 Distribution of U.S. Hereford Cattle, late nineteenth century to 1920

	Eastern States %	States W of Mississippi River	Total
Cattle Imported 1848-86	57.3	42.7	3703
Registered cattle alive 1914a	19.3	79.1	118,130
Registered cattle 1920	6.7	84.3	369,111

a – based on an estimated 120,000 registered cattle living in 1914: the table excludes states with fewer than 250 head.

Sources: 1848-86 and 1914; Sanders (1914) estimates no more than 200 prior to 1880; 1920: data give the location of 91% of the total 405,482 registered Hereford cattle as of January 1, 1920 (United States Department of Agriculture, 1922). (Adapted from Grundy, 2002)

In the earliest days of the 20th century of all the Hereford cattle exported from Great Britain nearly 51% went to North America, with 40% going to South America, while animals were also exported to Australia and South Africa (Hereford Cattle Society, 1996). Three decades into the twentieth century saw more than 62% of Hereford cattle exported from Great Britain to South America, with less than 1% coming to North America. However, during the early 20th century, the number of recorded Hereford cattle also underestimated the breed's influence on commercial ranches, as nearly all recorded data at the time was for purebred animals. The United States census of pedigree cattle in 1920 reported only 3% of cattle registered were purebred, while hundreds of thousands of high grade Hereford crosses were not accounted for (Walton, 1986).

In more recent times, Hereford cattle have been in demand as breeding animals because of their good temperament, and their adaptability and efficiency across a wide range of environments. Porter (1992) identified the Hereford as the most numerous and widely distributed beef breed in the world, while also contributing to the genetic make-up of at least two dozen other cattle breeds worldwide. Many countries had developed their own Hereford herd books, with more than 30 million cattle registered worldwide (Hereford Cattle Society, 1996).

Frederick William Stone was an Englishman from Warwickshire who introduced the Hereford breed into Canada. Stone arrived in Canada in 1831, settled onto 200 acres south of the modern city of Guelph. After initially importing Shorthorns into Canada after a visit to the English Royal Show, Stone was impressed with the quality of the Hereford cattle. Hereford cattle were purchased at Lord Bateman's sale and brought to Canada in 1860 (Canadian Hereford Association, 2010).

Hereford's have been credited with having played a major role in the development of the beef industry in South Africa. The first two Hereford bulls were imported into South Africa in 1890, followed by additional imports between 1894 and 1899. No females were imported with these, only bulls as they were used to progress the national herd.

A bull named Southern Cross was imported in 1901 by George Moorcroft; the first Hereford cows are thought to have been imported at this same time. Later bulls and cows were imported by James Gray, Abe Bailey, and G.J. Young. These men are commonly referred to as the fathers' of the Hereford breed in South Africa (South African Hereford Cattle Breeders' Society, 2010). In 1903, 27 cows and 4 bulls were imported by the Transvaal Government. This event fostered considerable interest in the Hereford breed within the country and further improved the South African national cattle herd. Pedigreed herds were maintained on government farms and were regularly infused with new genetics year after year from the best herds in England (South African Hereford Cattle Breeders' Society, 2010). The breed was credited with great prepotency, or the ability of one parent to transmit more characteristics to its offspring than the other parent, possibly due to long pedigreed breeding lines (Bruni, 1895).

Cattle first came to Australia on the First Fleet in 1788. These cattle were of Zebu origin and did not fare well initially, and were actually lost for several years only to be found later among a small but growing herd of descendants (Primary Industries, 2010). The first Hereford cattle exported to Australia occurred in 1825. Four bulls were boarded on a ship and traveled for 6 months to Tasmania, three of the bulls names have survived history; Billy, Beauty and Matchless. They were taken to a farm in Cressy, when that farm sold the cattle were sold to John Taylor whose descendants still breed Hereford cattle in Tasmania. A cow named Novelty Winton, in the modern Australian Hereford Society database can be traced back to Matchless (Henson, 2005).

In South America, the Hereford breed had become famous for its grazing properties and for its ability to improve native cattle (MacDonald and Sinclair, 1909). The first importations of Hereford cattle took place around 1858. Importations of Hereford cattle into Uruguay were plentiful, with the country being dubbed the "best customer" (MacDonald and Sinclair, 1909). When importation of Hereford cattle ebbed in the United States, countries in South America increased their demand. In 1907 the imports into Uruguay were at their highest and were expected to continue to increase due to the fact that the Hereford breed adapted well to the country and climate (MacDonald and Sinclair, 1909). Stockmen of Uruguay recognized the Hereford breeding graded up their herds quickly and efficiently.

2.2 HISTORY AND SIGNIFICANCE OF LINE 1 HEREFORD CATTLE

Many state and federal inbreeding and hybridization programs were started in the early 1920's in the USA. In general, these programs were motivated by the thought that basic genetic theory was an inadequate guide and new procedures were required (Sprague, 1962). Hundreds of inbred lines were developed and later evaluated in thousands of crosses (Sprague, 1962). G.H. Shull, a geneticist had started experiments in 1906 on inheritance in corn and other experimental stations soon followed suit. From these experiments came important observations of reduced vigor due to inbreeding and restoration of vigor upon crossing (Sprague, 1962). These experiments also provided the basis for development of hybrid corn. The general opinion was that hybrid corn was not feasible because of the reduced vigor of the inbred parents (Sprague, 1962). Further, when the initial hybrids became commercially available, many producers were reluctant to adopt them. However, demonstration plantings and field observations were implemented to prove the value of hybrids. By 1935 the demand for hybrid seed exceeded production in the Corn Belt and from that point on the hybrid seed industry developed rapidly (Sprague, 1962). Livestock producers were soon to follow lines of similar research and development.

Inbred lines of cattle had been developed by breeders since the beginning of historical records of beef cattle, but with the development of inbred lines where selection was based on gains, weight per day of age, carcass characteristics, and several other factors related to economics was and still is unique in the history of beef cattle breeding (Knapp *et al.*, 1951). In 1924, a herd of Hereford cattle was purchased from George

Miles and Sons in Miles City, MT. This herd was the foundation for the longest running beef cattle experiment in the world.

In 1931, the Bureau of Animal Industry, a part of the United States Department of Agriculture (USDA) initiated projects involving development of inbred lines of cattle that were superior in rate of gain, weight for day of age, carcass characteristics, and high fertility (Winters, 1931; Knapp *et al.*, 1951). These characteristics were deemed most important to commercial breeders and feeders of the day. Fort Keogh, the USDA range livestock experimental station, played a large part in this project developing the first and several of these inbred lines of cattle. The most important and productive of these inbred lines was the Line 1 (Knapp *et al.*, 1951). The breeding program started with the purchase of 2 purebred Hereford bulls, Advance Domino 20 (Figure 2.1) and Advance Domino 54 (Figure 2.2) from Fred C. DeBerard of Kremmling, Colorado. These bulls became foundation sires for the Line 1 Hereford breeding program (Knapp *et al.*, 1951). They were half-sibs out of Advance Domino 13 and were unrelated to the Hereford cattle to which they were initially bred at Fort Keogh, 50 cows purchased from George M. Miles and sons (Knapp *et al.*, 1951). Advance Domino 20 and 54 were used in breeding herds through 1941. Several years after the initial phase reciprocal crosses were made between the progeny of both sires producing progeny that were between 1 and 28.7% inbred, they averaged 7.9% inbred. Subsequent generations were produced from selected progeny that were *inter se* mated with the rate of inbreeding being controlled through avoidance of mating of close relatives.

Figure 2.1 Advance Domino 20

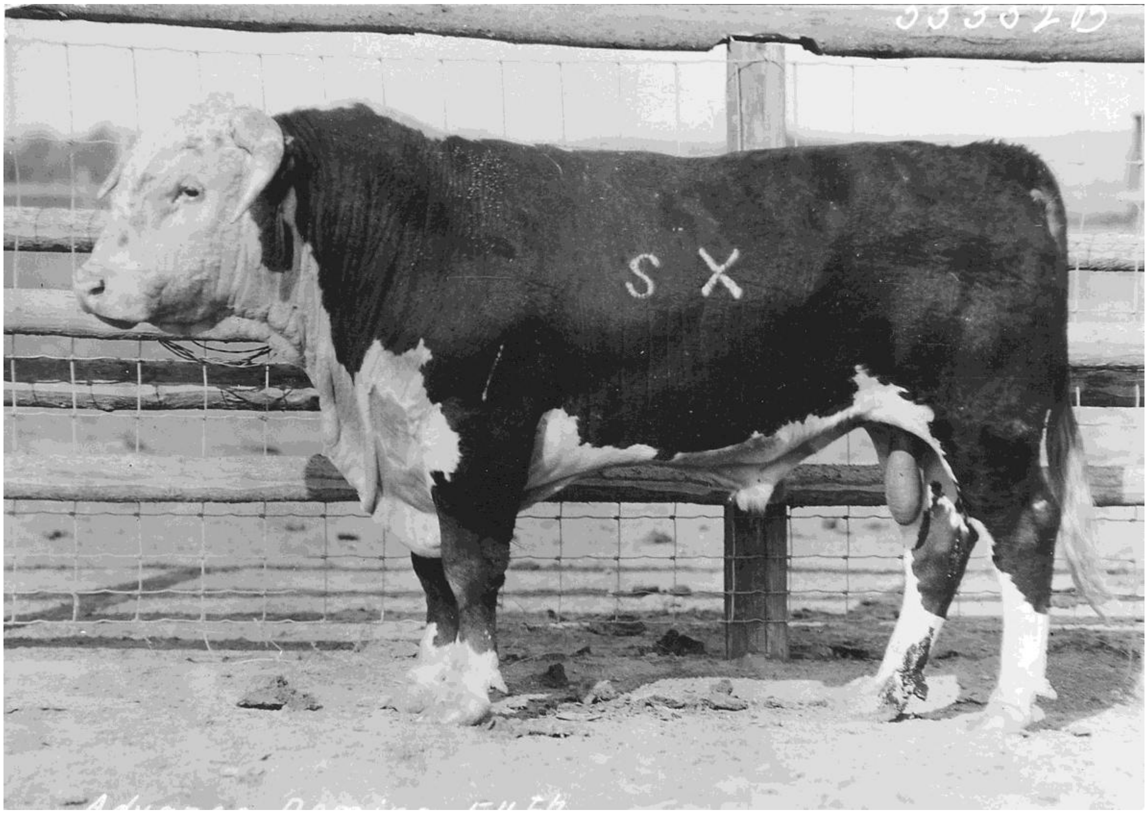

Figure 2.2 Advance Domino 54

Specific genetic evaluation methods were developed at Fort Keogh beginning in 1935. All beef performance testing programs in the USA and around the world were built on this groundwork. Including, the first heritability estimates for performance traits in beef cattle (Knapp and Nordskog, 1946), and separation of the impact of heredity and environment on ultimate performance (Knapp and Nordskog, 1946; Woodward, 1984).

Fourteen inbred lines were ultimately developed at Fort Keogh; eleven of those lines were established by purchasing related heifers and bulls from individual herds. All lines were maintained as closed herds with no outside genetic introductions or contributions. In 1962, six of those herds were culled due to poor performance or other problems (Brinks and Knapp, 1975; Woodward, 1984). Also at this time line crosses were made among five of the lines. This was done to measure the heterosis that is expressed when the inbred lines were crossed (Chambers and Whatley, 1951; Brinks *et al.*, 1972; Kress *et al.*, 1979; Fogarty *et al.*, 1984; Anderson *et al.*, 1986; MacNeil *et al.*, 1989; Pariacote *et al.*, 1998). Of all the inbred lines developed, only Line 1 remains today.

Popular lines of cattle typically come and go in a space of about 10 years and any influence they have on their breed is short lived. Such is the case of several well known family lines that are part of Hereford history, such as Prospector, Don, Brae Arden, Monarch, and Tarrington. Yet, Line 1 cattle made an impact on the Hereford breed because of years of selection for performance (Dickenson, 1984). This and the fact that Line 1 came about at a time when economics dictated that breeders needed to make better choices for their breeding programs created a stable demand for Line 1 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).

Although initially not popular with Hereford breeders, Line 1 was a faster growing animal than contemporary Hereford cattle. Before the 1940’s, dwarfism was not recognized as a problem among Hereford breeders. However, in 10 years time it had become a serious issue (McCann, 1974). The mature weight of a dwarf Hereford was around 600 lbs, while normal cattle reached about 1,800 lbs (McCann, 1974). Some well known, very popular, and much used herd sires carried the causative recessive allele (McCann, 1974), but Line 1 cattle did not. Thus, Line 1 became a resource that breeders could use to purge dwarfism from their herds.

Performance recording schemes developed by researchers from Fort Keogh so long ago have had tremendous influence on genetic improvement of all livestock species. Refined recording and testing techniques now used in modern-day genetic improvement programs were pioneered with the development of the inbred lines of cattle at Fort Keogh.

The importance of Line 1 Hereford cattle to beef cattle genetics research is also reflected by the selection of a Line 1 bull for construction of a bacterial artificial chromosome library (Liu *et al.*, 2009; Bovine HapMap Consortium, 2009, Bovine Genome Sequencing and Analysis Consortium *et al.*, 2009; MacNeil, 2009) and his daughter, L1 Dominette 01449 (Figure 2.3), for the sequencing of the beef cattle genome (Liu *et al.*, 2009; Bovine HapMap Consortium, 2009, Bovine Genome Sequencing and Analysis Consortium, 2009; MacNeil, 2009). This selection was based, at least in part, on the greater homozygosity of Line 1 relative to non-inbred cattle.

Figure 2.3 Line 1 Dominette 01449

Since the earliest recorded sale of cattle from Fort Keogh it should be noted that purchases of Line 1 cattle over the years have been to producers in 34 states in the United States and 5 Canadian provinces; namely Alberta, Manitoba, Nova Scotia, Ontario and Saskatchewan (Figure 2.4). Furthermore, in 1983, it was noted that 68% of all purebred sires advertised in the July (herd sire) issue of the American Hereford Association breed magazine were related, to some degree, to Line 1 (Dickenson, 1984).

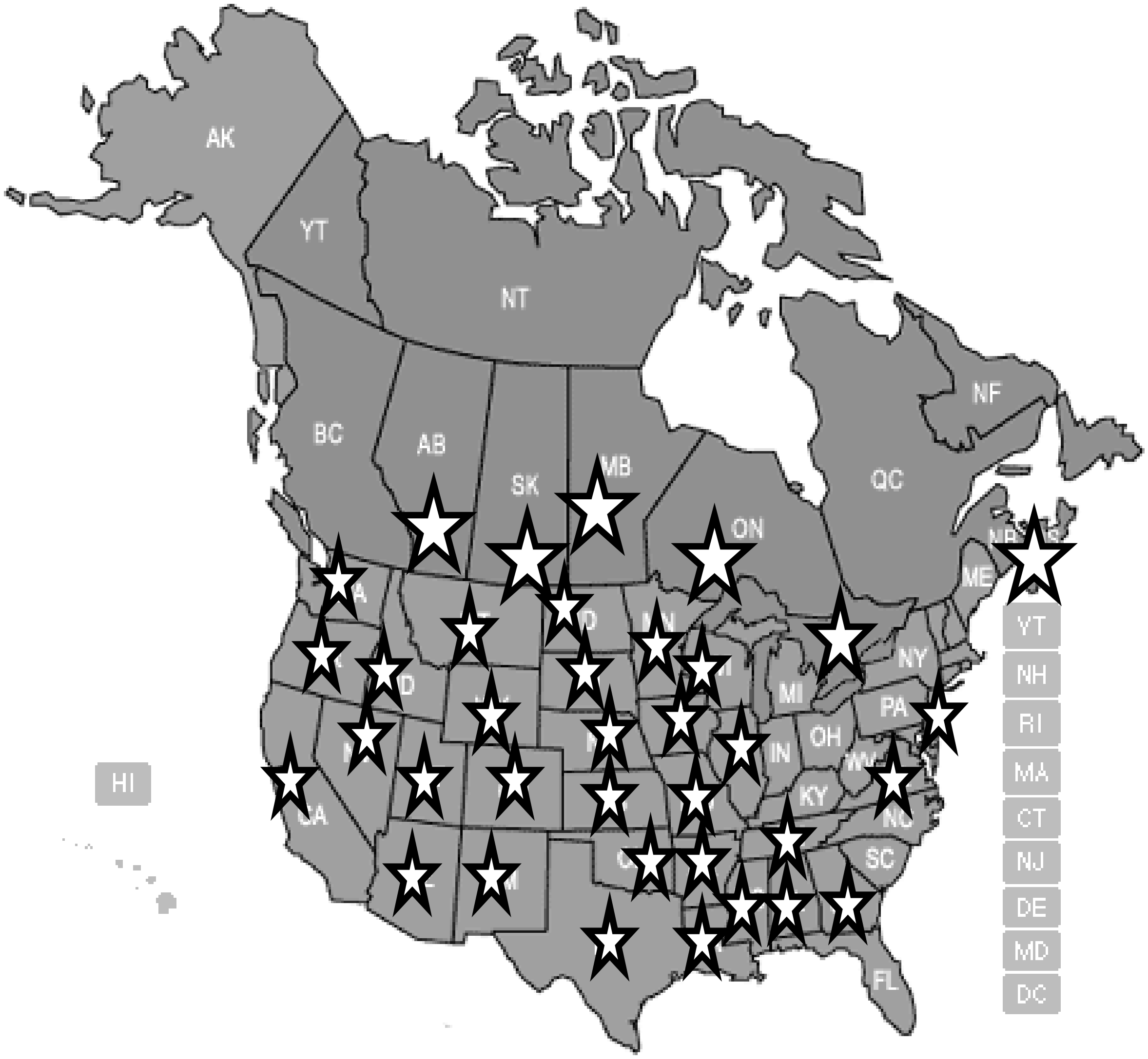

Figure 2.4 Line 1 Hereford distributions through annual production sale, 1947-present

The U.S. Department of Labor Bureau of Labor and Statistics maintains the consumer price index (CPI) which allows calculations to be made to measure the average price of consumer goods and services purchased from one period of time to the next (USDL, 2010). The percent change in CPI is a measure estimating inflation. The CPI was used to adjust for the effect of inflation on the real value of money. An index maintained online by the Federal Reserve Bank of Minneapolis (2010) beginning in the year 1800 to the present also has a formula for calculating the change in the value of money. By using this formula, it was determined that sales of Line 1 bulls and heifers since 1955 have generated the equivalent of $12,670,253.76, in 2010 dollars. The single largest sale occurred in 1979 with receipts being greater than $1.2 million. Additionally, the highest price ever received for a Line 1 bull was in 1980 with the purchase of Line 1 Domino 77618 for $160,000; equivalent to more than $425,000, in 2010 dollars. It was not uncommon for sales of top performing bulls in the 1970's to sell for upwards of $5,000, equivalent to more than $20,000 in 2010 dollars. Still other bulls of special interest, with regard for particular sires and dams in their pedigree, garnered anywhere from $10,000 to $40,000 for their purchase. Top females sold for anywhere from $1,000 to over $5,000 during this era. In 2010, those prices are the equivalent of approximately $4,000 to over $22,000. Historical records kept from each sale are a testament to Fort Keogh's work in the field of genetics and to the longevity and continuing influence and importance of the Line 1 Hereford breeding project.

2.3 HEREFORD CATTLE AROUND THE WORLD

The Hereford breed has been credited with building the cattle industry in Canada (Canadian Hereford Association, 2010). In 1860, Frederick William Stone, a Warwickshire Englishman, arranged to purchase eight Hereford heifers and a young Hereford bull, Lord Bateman; in England. His intention was to show these cattle at a provincial exhibition in Ontario to attract some attention to the breed. An editorial in an agriculture publication noted these Hereford cattle from Lord Bateman stood "unequalled in purity, size, and symmetry in England" and Stone was congratulated for his purchase of these animals (Canadian Hereford Association, 2010). The Canadian Hereford Association was formed in 1890 with its primary objective being maintaining purity of the Hereford breed. In 2011, they estimated there were 120,000 purebred Hereford females in production in Canada, with upwards of 350,000 straight-bred commercial Hereford females as well. They also estimate well over 30% of the beef cattle population in Canada has Hereford influence (Canadian Hereford Association, 2010).

The first Hereford bulls were imported into South Africa in 1890. Since that time, a substantial number of Hereford cattle have been imported into South Africa with the goal of improving the national herd (South African Hereford Cattle Breeders' Society, 2010). Furthermore, Hereford semen and embryos are frequently exported from the United States to South Africa (Coe, personal communication). Hereford cattle adapted well to conditions in southern Africa were often compared to the native cattle and touted as healthy, hardy, and prolific (South African Hereford Cattle Breeders' Society, 2010). Dr. Jan Bonsma, considered the father of the Bonsmara breed, once wrote that "the Hereford is the best grazing animal of the British Beef Breeds; it has a wonderful temperament and utilizes sour pasture well" (South African Hereford Cattle Breeders' Society, 2010). In 2007, the South African Hereford Breeders Society marked its 90th anniversary.

In the United Kingdom (UK), the Hereford is one of the oldest native beef breeds. They originated in the Herefordshire County in the mid 1700's. They have since spread to most parts of the UK and then the rest of the world. Under the patronage of Queen

Victoria the Hereford Cattle Society was founded in 1878. The Hereford Herd book opened in 1846 and has been closed since 1886 to any animal whose sire or dam had not been previously recorded. This has kept the purity of the breed intact for over 120 years (Hereford Cattle Society, 2011). Over the centuries the breed has progressed through various proposals put into service by its Society (Hereford Cattle Society, 2011).

The first Hereford cattle imported to Australia occurred in 1825 with the inauguration of the Australian Hereford Herd Book Society occuring in 1890 (Hereford Herd Book Society, 1995). Hereford cattle in Uruguay are considered the choice of the country where over 65% of the national herd is Hereford.

The Hereford Breeders Association of Uruguay was formed in 1946. Currently there are now over 500 breeders working with the association to continue to move the breed forward into the future (Sociedad Criadores de Hereford del Uruguay, 2011).

There are many more countries with Hereford associations and societies, but with datasubsets for major Hereford populations from these countries any significance to the Line 1 Hereford contribution should be attainable and definable.

2.4 SUMMARY

Essentially gene flow or genetic migration is the transfer of alleles of genes or genetic material from one population to another. Su *et al.* (2003) found in a study of plant populations around the Great Wall of China versus mountain paths in the similar region that individuals from the same subpopulation tended to cluster together, while individuals from two subpopulations derivative of one population along a path were mixed. Su *et al.* (2003) found the total genetic variation of a population was distributed among individuals within their subpopulations. The subpopulations of all species were significantly genetically differentiated in the control and test populations. However, the degree of genetic differentiation between the subpopulations along the Great Wall test sites was significantly higher.

In this same way the oceans can act as a barrier to the flow of genetics from one population to another in different countries. Considering the history of the Hereford breed and its movement across the world in the early 20th century, importation of live animals was challenging yet still accomplished and helped to establish base populations of these breeds in several countries. Live animals were brought into these countries for several decades and then importation from England basically stopped or slowed significantly. Geographic isolation is expected to have significant effects on the genetic structure of populations (Smith, 1999). Yet, these cattle were shuffled around their respective countries, as well as out of them and used in numerous breeding programs and their own genetic bases developed. In the latter part of the 20th century when semen and embryo collection were a more convenient means to importing fresh genetics and aiding in gene flow the transfer and trade of genetics resumed once again (BOA, 1993).

Logistics and the many rules and regulations with regard to importing semen and embryos still act as a barrier to the transfer of genetics around the globe. However, when particular bulls or cows gain much favor their genetics are bound to cross these boundaries and in this way the influence of the Line 1 Hereford cattle was influential in the Australian Hereford cattle in the early 1980's (Neilson, personal communication). Producers (Cooper Hereford and Holden Hereford) with a long history of purchasing and purveying Line 1 genetics were the supply of Line 1 genetics to Australia at this time, via semen and embryos.

Throughout the long 77 year history of the Line 1 Hereford, the scope and breadth of their genetic influence is seen in the development of many fundamental evaluations still regarded as standards today. As well as aiding in the elimination of dwarfism from the breed. The Line 1 Hereford has contributed genetically through distribution of its genetics through production sales; rarely would this type of influence from one herd be seen throughout the world. Barriers to gene flow are often physical and considered a hindrance, however with technology and easier transportation between and across countries moving influential and desirable genetics is far more effective in the increasingly modern age and Line 1 genetics are particularly able to perform in this environment and benefit Hereford herds around the world.

CHAPTER 3

SAMPLE SIZE NEEDED TO DETERMINE COEFICIENT OF RELATIONSHIP BETWEEN LINE 1 HEREFORD AND THE U.S. HEREFORD POPULATION

3.1 INTRODUCTION

Research studies need to be carefully planned. Good planning is influenced by several factors. The problem should be defined carefully and prepared, including asking questions about the purpose of the study, the population size, the risk of getting a bad sample and an allowable sampling error (Israel, 1992). Experimental units should be randomly selected from the population to which inference is to be made (Lenth, 2001).

Sample size should be adequate and relative to the particular goals. However, sample size is also important for economic reasons. A study that is "big enough" generates enough data that an effect of sufficient magnitude to be important has a high probability of being statistically significant. An oversized study will declare "statistically significant" an effect that is too small to be important, and consume too many resources. An undersized study can be a waste of resources in that the probability of detecting an important effect is low.

Criteria to be specified are: the probability level at which effects are declared significantly different, the probability with which important effects are to be detected, and the magnitude of the effect to be declared different. Finally the degree of variability for the characteristics of interest must be known. Taken together, these factors can be used to determine the required sample size (Miaoulis and Michener, 1976). While formulas for calculation of required sample size for comparison of groups are well recognized, similar formulas to determine sample size necessary to determine the coefficient of relationship are unknown.

Fort Keogh Livestock and Range Research Laboratory had marketed bulls and females that were excess to research needs since 1947. Culturally speaking, the Line 1 Hereford serves as a visual document of Fort Keogh’s research history and impact.

The U.S. Hereford herdbook contains approximately 14 million animals registered between 1960 and 2009 and over 26 million animals in the entire herdbook so far (Sanders, personal communication). Explicit calculation of relationship coefficients for all animals in the U.S. herdbook with the Line 1 Hereford sires used at Fort Keogh was seen as being computationally unfeasible. Thus, an experiment was designed to examine the precision with which the mean of the maximum relationship coefficient between a Line 1 sire and randomly selected animals in the U.S. Hereford herdbook, was estimated as a function of the sample size.

3.2 MATERIALS AND METHODS

Fourteen million records were obtained from the American Hereford Association covering the period from 1960-2009. The distribution of those records across years is shown in Table 3.1. Records from three years (1980, 1990, and 2000) were used in this experiment. Samples of 100 calves, 500 calves, and 3000 calves were to be extracted from the herdbook 5 times for each of the three selected years. Thus, there were 15 independent samples for each year. Sampled calves from 1980, 1990, and 2000 were pseudo-mated to Line 1 sires from the decades 1968 to 1978, 1978 to 1988, and 1988 to 1998, respectively. Inbreeding coefficients were then calculated for the "offspring" resulting from these "matings" using the algorithm developed by Henderson and Quaas (1976). The relationship of each "calf" to Line 1 was taken to be twice the maximum inbreeding coefficient for the set of Line 1 sires used in the pseudo-matings.

For the purpose of characterizing the distribution of relationship between Line 1 and the Hereford population as recorded by the American Hereford Association, the distribution of maximum inbreeding coefficient of a "progeny" resulting from the pseudo-mating of sampled animals to Line 1 sires, for the subset of sampled animals that were related to Line 1, was deemed appropriate. Sample size was deemed adequate when the coefficient of variation for the replicate samples drawn from this distribution was less than 10%.

Table 3.1 Number of Hereford calves registered in USA by year

Year	**N recorded**
1980	385338
1981	353080
1982	317569
1983	277689
1984	236705
1985	213689
1986	206686
1987	204856
1988	202183
1989	194884
1990	186255
1991	177484
1992	173119
1993	165094
1994	156930
1995	144406
1996	130689
1997	122120
1998	114306
1999	110263
2000	101450
2001	109457
2002	104964
2003	103522
2004	102730
2005	100917
2006	99066
2007	80036
2008	89751

3.3 RESULTS AND DISCUSSION RANDOM SAMPLING SIZE

The numbers of calves registered with the American Hereford Association for the three years used in this initial analysis phase are 385,338, 186,255, and 101,450 for 1980, 1990 and 2000, respectively (Table 1). Thus, the number of calves registered in 1990 and 2000 compared to those registered in 1980 decreased by 52% and 74%, respectively. Across years the sample sizes evaluated are increasing proportions of the annually recorded Hereford cattle. For 1980, samples of 100, 500, and 3000 represent 0.025%, 0.13%, and 0.78% of the recorded calves, respectively. Whereas for 2000, samples of 100, 500, and 3000 represent 0.099%, 0.49%, and 2.96% or recorded calves, respectively. Presented in Tables 3.2 (1980), 3.3 (1990), and 3.4 (2000) are results from this analyses.

Analysis of the five 100 animal samples in 1980 of the distribution of maximum inbreeding coefficient of a “progeny” resulting from the pseudo-mating of sampled animals to Line 1 sires, for the subset of sampled animals that were related to Line 1 returned a CV of 41.2% which greatly exceeded the specified 10% limit. The standard deviation of the variation among replicates related to with Line 1 pedigree relationship is notable relative to the mean of the replicates. Thus, there were noteworthy differences between replicates of 100 with regard to number of animals sampled that have Line 1 heritage and the degree of their relationship to Line 1. These discrepancies indicate inadequate sample size, because the sample of the selected size were not a large enough population to “even out” inconsistencies among them (Lenth, 2001, 2007).

The samples of 500 pseudo-progeny were more consistent. The CV of the inbreeding coefficient of the pseudo-progeny with relationship to Line 1 produced by

Line 1 sires and those animals sampled was 9%, less than the 10% a priori threshold. The standard deviation of the proportion of animals that were related to Line 1 was smaller (P= 0.01) than when sample size was 100. Thus, the number of animals in each sample with relationship to Line 1 was more consistent. The maximum inbreeding coefficient of a “progeny” resulting from the pseudo-mating of sampled animals to Line 1 sires, for the subset of sampled animals that were related to Line 1 was also less than (P < 0.01) in the previous set of samples indicating significantly less variation in average relationship to Line 1. Relative to a sample size of 100, the samples of 500 animals drawn from the American Hereford Association database captured a greater overall range in relationship to Line 1.

In assessing the relationship of the general Hereford population to Line 1, means and standard deviations of both frequency of related animals and the degree of relationship were similar when based on sample sizes of 500 and 3000. Thus, there was little, if any, advantage of drawing samples of 3000 animals from the American Hereford Association database relative to drawing samples of 500 animals. It would be wise to use the smaller sample size, and possibly characterize sample sizes between 100 and 500 so that additional time and resources are not wasted in use of excessively large samples (Lenth, 2001).

Table 3.2 Effect of sample size on estimated relationship of Hereford cattle born in 1980 and recorded in the herdbook of the American Hereford Association to Line 1.

Samples of 100 calves born in 1980							
Sample	**Freq**	**Fx_r**	**R_r, %**	**Fx_a**	**R_a, %**	**Min**	**Max**
A	14	0.069	14	0.009	2	0.0059	0.31
B	20	0.102	20	0.019	4	0.0056	0.28
C	26	0.035	7	0.009	2	0.0059	0.19
D	27	0.060	12	0.016	3	0.0059	0.27
E	21	0.046	9	0.010	2	0.0059	0.11
Mean	**21.6**	**0.062**	**13**	**0.130**	**2.6**	**0.0058**	**0.25**
SD	**5.2**	**0.026**	**5**	**0.005**	**0.9**	**0.0001**	**0.08**
Samples of 500 calves born in 1980							
Sample	**Freq**	**Fx_r**	**R_r, %**	**Fx_a**	**R_a, %**	**Min**	**Max**
A	25	0.052	10	0.013	3	0.0015	0.26
B	22	0.054	11	0.012	2	0.0007	0.37
C	22	0.065	13	0.014	3	0.0015	0.32
D	23	0.059	12	0.014	3	0.0011	0.30
E	24	0.055	11	0.013	3	0.0007	0.29
Mean	**23**	**0.057**	**11**	**0.013**	**2.8**	**0.0011**	**0.31**
SD	**1.3**	**0.005**	**1.1**	**0.001**	**0.4**	**0.0004**	**0.04**
Samples of 3000 calves born in 1980							
Sample	**Freq**	**Fx_r**	**R_r, %**	**Fx_a**	**R_a, %**	**Min**	**Max**
A	21	0.058	12	0.012	2	0.0007	0.30
B	22	0.055	11	0.012	2	0.0015	0.34
C	22	0.056	13	0.012	2	0.0011	0.36
D	23	0.061	12	0.014	3	0.0005	0.38
E	23	0.063	13	0.015	3	0.0011	0.36
Mean	**22**	**0.059**	**12**	**0.013**	**2.4**	**0.0010**	**0.35**
SD	**1.2**	**0.005**	**0.8**	**0.001**	**0.5**	**0.0004**	**0.03**

Sample = Designates replicate of the experiment; Freq = Frequency of animals in sample having non-zero relationship to Line 1; Fx_r = Mean of maximum inbreeding coefficient of a “progeny” resulting from the pseudo-mating of sampled animal to Line 1 sires, for the subset of sampled animals that were related to Line 1; $R_r = (2*Fx_r)*100$, i.e. the percentage relationship between Line 1 and those sampled animals that were related to Line 1.; Fx_a = Mean of maximum inbreeding coefficient of a “progeny” resulting from the pseudo-mating of all sampled animal to Line 1 sires; R_a = the percentage relationship between Line 1 and all sampled animals; Min and Max = minimum and maximum of distribution of Fx_r, respectively.

Analysis of the five 100 animal samples in 1990 of the distribution of maximum inbreeding coefficient of a “progeny” resulting from the pseudo-mating of sampled animals to Line 1 sires, for the subset of sampled animals that were related to Line 1 returned a CV of

4.5% which was well within the specified 10% limit (Table 3.3). The standard deviation for the proportion of animals related to Line 1 pedigree relationship is also relatively small in comparison to the mean of the replicates. Thus, for 1990 drawing a sample of 100 animals appeared sufficient to characterize the relationship of Line 1 to the general Hereford population as recorded by the American Hereford Association.

For a sample size of 500, the inter-replicate standard deviation of relationship to Line 1 for those animals that were related to Line 1 was 2.74 and the associated CV was 1%, again substantially less than the a priori selected threshold of 10%. This indicated relatively little variation among the replicates, which was consistent with the standard deviation of the inbreeding coefficients returned at 0.0011, and their range being 0.044 to 0.04 resulting in an estimated average relationship of 9%.

Samples of 3000 drawn from 1990 were consistent with the samples of 500, for almost all measures. The most notable difference was in the range in maximum high inbreeding coefficients. In the samples of 500, the maximum inbreeding coefficients ranged from 0.23 to 0.38, while in samples of 3000 the range was from 0.40 to 0.43. For all sample sizes, these results show less variation among all sample sizes than corresponding samples from 1980, and indicate that, in this instance, a sample size of 100 would be sufficient.

While the overall average relationships remained consistent among the 500 and 3000 sample sizes the much larger maximum inbreeding coefficients may simply result from the larger sample size. The same observation would hold true when an increased proportion of a population was sampled. The number of animals registered in 1980 was 385,338, whereas the number of animals registered in 1990 was 187,255, which is a 51%

reduction in animals available for selection. As the population pool gets smaller the chances of selecting more consistent, representative sample subsets increases and smaller samples sizes could be appropriate.

Table 3.3 Effect of sample size on estimated relationship of Hereford cattle born in 1990 and recorded in the herdbook of the American Hereford Association to Line 1.

Samples of 100 calves born in 1990							
Sample	**Freq**	**Fx_r**	**R_r, %**	**Fx_a**	**R_a, %**	**Min**	**Max**
A	49	0.042	8	0.02	4	0.0017	0.21
B	53	0.043	9	0.023	5	0.0022	0.13
C	61	0.042	8	0.026	5	0.0016	0.19
D	54	0.043	9	0.023	5	0.0015	0.17
E	57	0.042	8	0.024	5	0.0022	0.16
Mean	**55**	**0.0424**	**8**	**0.023**	**5**	**0.002**	**0.21**
SD	**4.5**	**0.0005**	**1**	**0.002**	**0.4**	**0.0003**	**0.03**
Samples of 500 calves born in 1990							
Sample	**Freq**	**Fx_r**	**R_r, %**	**Fx_a**	**R_a, %**	**Min**	**Max**
A	53	0.044	9	0.024	5	0.0005	0.23
B	49	0.046	9	0.023	5	0.0005	0.39
C	52	0.045	9	0.023	5	0.0005	0.27
D	46	0.045	9	0.021	4	0.0005	0.33
E	50	0.047	9	0.023	5	0.0003	0.38
Mean	**50**	**0.0454**	**9**	**0.023**	**5**	**0.0005**	**0.32**
SD	**2.74**	**0.0011**	**0**	**0.001**	**0.4**	**0.0001**	**0.07**
Samples of 3000 calves born in 1990							
Sample	**Freq**	**Fx_r**	**R_r, %**	**Fx_a**	**R_a, %**	**Min**	**Max**
A	51	0.045	9	0.023	5	0.0003	0.40
B	51	0.042	8	0.021	4	0.0003	0.43
C	51	0.046	9	0.023	5	0.0005	0.42
D	50	0.044	9	0.022	4	0.0003	0.43
E	52	0.043	9	0.023	5	0.0005	0.42
Mean	**51**	**0.044**	**9**	**0.022**	**5**	**0.0004**	**0.42**
SD	**0.71**	**0.0016**	**0.4**	**0.001**	**0.5**	**0.0001**	**0.01**

Sample = Designates replicate of the experiment; Freq = Frequency of animals in sample having non-zero relationship to Line 1; Fx_r = Mean of maximum inbreeding coefficient of a “progeny” resulting from the pseudo-mating of sampled animals to Line 1 sires, for the subset of sampled animals that were related to Line 1; $R_r = (2*Fx_r)*100$, i.e. the percentage relationship between Line 1 and those sampled animals that were related to Line 1.; Fx_a = Mean of maximum inbreeding coefficient of a “progeny” resulting from the pseudo-mating of all sampled animal to Line 1 sires; R_a = the percentage relationship between Line 1 and all sampled animals; Min and Max = minimum and maximum of distribution of Fx_r, respectively.

For the samples from 2000, the average proportion of animals with Line 1 heritage was 62.2%, 65%, and 65.5%, with associated standard deviations among replicates of 3.8, 1.4, and 0.54 for 100, 500, and 3000 samples, respectively (Table 3.4). The corresponding inter-replicate standard deviations of the inbreeding coefficients were 0.0077, 0.0011, and 0.0001. For those animals that were related to Line 1, relationship was 10%, 8%, and 9% for samples sizes of 100, 500, and 3000, respectively. Thus, the average relationships for all chosen animals were 6%, 5%, and 6% for the samples of 100, 500, and 3000 animals. Again the range in maximum inbreeding coefficients increased with sample size, from 0.38, to 0.41, and 0.43. However, variation among the separate samples sizes remained more variable in the smaller samples ranging from 0.12 to 0.38. Samples of 500 still showed considerable variation ranging from 0.25 to 0.41. Finally, samples of 3000 animals were more consistent with a range from 0.41 to 0.43. In summary, the pre-established threshold for the coefficient of variation among replicates of estimated relationship to Line 1 was breached by the samples of 100 at 16%. However, samples of 500 and 3000 returned CV of 2.6% and 2.7%, respectively.

Table 3.4 Effect of sample size on estimated relationship of Hereford cattle born in 2000 and recorded in the herdbook of the American Hereford Association to Line 1.

Samples of 100 calves born in 2000							
Sample	**Freq**	**Fx_r**	**R_r, %**	**Fx_a**	**R_a, %**	**Min**	**Max**
A	60	0.046	9	0.028	6	0.0001	0.21
B	63	0.049	10	0.031	6	0.0001	0.30
C	62	0.061	12	0.039	8	0.0006	0.38
D	58	0.042	8	0.025	5	0.0001	0.12
E	68	0.043	9	0.029	6	0.0001	0.30
Mean	**62.2**	**0.048**	**10**	**0.030**	**6**	**0.0002**	**0.26**
SD	**3.8**	**0.0077**	**1.5**	**0.005**	**1.1**	**0.0002**	**0.10**
Samples of 500 calves born in 2000							
Sample	**Freq**	**Fx_r**	**R_r, %**	**Fx_a**	**R_a, %**	**Min**	**Max**
A	63	0.043	9	0.027	5	0.0001	0.25
B	66	0.044	9	0.029	6	0.0001	0.38
C	64	0.041	8	0.023	5	0.0001	0.35
D	66	0.043	9	0.028	6	0.0001	0.49
E	66	0.042	8	0.028	6	0.0001	0.41
Mean	**65.0**	**0.042**	**8**	**0.027**	**5**	**0.0001**	**0.36**
SD	**1.4**	**0.0011**	**0.5**	**0.002**	**0.5**	**0.0000**	**0.09**
Samples of 3000 calves born in 2000							
Sample	**Freq**	**Fx_r**	**R_r, %**	**Fx_a**	**R_a, %**	**Min**	**Max**
A	66	0.045	9	0.030	6	0.0001	0.42
B	65	0.045	9	0.029	6	0.0001	0.41
C	66	0.044	9	0.029	6	0.0001	0.43
D	66	0.044	9	0.029	6	0.0001	0.42
E	65	0.042	8	0.027	5	0.0001	0.40
Mean	**65.6**	**0.0444**	**9**	**0.0288**	**6**	**0.0001**	**0.42**
SD	**0.54**	**0.0001**	**0.4**	**0.001**	**0.4**	**0.0000**	**0.01**

Sample = Designates replicate of the experiment; Freq = Frequency of animals in sample having non-zero relationship to Line 1; Fx_r = Mean of maximum inbreeding coefficient of a "progeny" resulting from the pseudo-mating of sampled animals to Line 1 sires, for the subset of sampled animals that were related to Line 1; $R_r = (2*Fx_r)*100$, i.e. the percentage relationship between Line 1 and those sampled animals that were related to Line 1.; Fx_a = Mean of maximum inbreeding coefficient of a "progeny" resulting from the pseudo-mating of all sampled animals to Line 1 sires; R_a = the percentage relationship between Line 1 and all sampled animals; Min and Max = minimum and maximum of distribution of Fx_r, respectively.

Sample sizes of 500 and 3000 consistently provided estimates of relationship of Hereford cattle recorded by the American Hereford Association to Line 1 that were within acceptable limits of variability. Further, for animals sampled from 1990, a sample size of 100 animals was also satisfactory. Thus, it was decided to investigate a slightly smaller sample size of 400. Results of the analysis of five replicates of a sample size of 400 for each 1980, 1990, and 2000 were found equally satisfactory as the samples of 500 animals from those years (Table 3.5). Consequently, because these smaller samples represented a more efficient use of resources, it was decided to use samples of 400 in future analyses of the American Hereford Association database. These analyses are included at Table 3.5. The samples of 400 identify great similarities and frequency of selected animals with relationship to Line 1, along with inbreeding coefficient of these selected samples, the relationship of parental units, as well as the minimums and maximums for relationship coefficients. Finally, the standard deviations for these measures fall within their counterparts for samples of 500 and 3000. Clearly these results indicate samples of 400 to be adequate and justifiable representation of the populations of interest.

Table 3.5 Effect of sample size (400) on estimated relationship of Hereford cattle born in 1980, 1990, and 2000 and recorded in the herdbook of the American Hereford Association to Line 1.

Samples of 400 calves born in 1980							
Sample	**Freq**	**Fx_r**	**R_r, %**	**Fx_a**	**R_a, %**	**Min**	**Max**
A	22	0.055	12	0.013	3	0.0015	0.38
B	23	0.059	12	0.013	3	0.0011	0.37
C	24	0.056	11	0.012	2	0.0007	0.31
D	22	0.060	12	0.014	3	0.0005	0.29
E	25	0.057	12	0.014	3	0.0015	0.32
Mean	**23**	**0.057**	**12**	**0.013**	**3**	**0.0011**	**0.33**
SD	**1.3**	**0.0021**	**0.4**	**0.001**	**0.4**	**0.0005**	**0.04**
Samples of 400 calves born in 1990							
Sample	**Freq**	**Fx_r**	**R_r, %**	**Fx_a**	**R_a, %**	**Min**	**Max**
A	50	0.045	9	0.023	5	0.0005	0.34
B	49	0.046	9	0.024	5	0.0005	0.36
C	52	0.045	9	0.021	4	0.0003	0.29
D	51	0.044	9	0.023	5	0.0005	0.37
E	50	0.047	9	0.024	5	0.0005	0.29
Mean	**50**	**0.0454**	**9**	**0.023**	**5**	**0.0005**	**0.33**
SD	**0.14**	**0.0011**	**0.0**	**0.001**	**0.4**	**0.0001**	**0.04**
Samples of 400 calves born in 2000							
Sample	**Freq**	**Fx_r**	**R_r, %**	**Fx_a**	**R_a, %**	**Min**	**Max**
A	66	0.044	9	0.029	6	0.0001	0.38
B	64	0.041	8	0.030	6	0.0001	0.35
C	66	0.044	9	0.027	5	0.0001	0.30
D	63	0.043	9	0.028	6	0.0001	0.32
E	66	0.043	9	0.028	6	0.0001	0.34
Mean	**65**	**0.042**	**9**	**0.028**	**6**	**0.0001**	**0.34**
SD	**1.4**	**0.0012**	**0.4**	**0.001**	**0.4**	**0.0000**	**0.03**

Sample = Designates replicate of the experiment; Freq = Frequency of animals in sample having non-zero relationship to Line 1; Fx_r = Mean of maximum inbreeding coefficient of a “progeny” resulting from the pseudo-mating of sampled animals to Line 1 sires, for the subset of sampled animals that were related to Line 1; $R_r = (2*Fx_r)*100$, i.e. the percentage relationship between Line 1 and those sampled animals that were related to Line 1.; Fx_a = Mean of maximum inbreeding coefficient of a “progeny” resulting from the pseudo-mating of all sampled animals to Line 1 sires; R_a = the percentage relationship between Line 1 and all sampled animals; Min and Max = minimum and maximum of distribution of Fx_r, respectively.

CHAPTER 4

INFLUENCE OF LINE 1 HEREFORD CATTLE ON HEREFORD CATTLE IN THE UNITED STATES

4.1 INTRODUCTION

By the mid 1860’s Hereford cattle were imported into the United States from Great Britain and herds were mainly established in the Northern Great Plains. Conditions were right to start exploitation of the breed due to strong demand from the growing industrial population that wanted regular beef supplies (Grundy, 2002). Many State and Federal inbreeding and hybridization programs were started in the early 1920’s. In 1931, the United States Department of Agriculture’s Bureau of Animal Industry initiated development of inbred lines of cattle that were superior in rate of gain, weight for day of age, carcass characteristics, and high fertility (Winters, 1931; Knapp *et al.*, 1951). The most important and productive of these inbred lines was Line 1, produced at the Fort Keogh research station in Miles City, Montana (Knapp *et al.*, 1951).

Dissemination of Line 1 Hereford bulls and females that were excess to research needs began in 1947, with sales primarily to breeders in the United States. In 1984, Dickenson noted that 68% of all purebred Hereford sires advertised in the July issue of the breed magazine published by the American Hereford Association were related to Line 1. Heitschmidt (2005) edited a review of agricultural research for a meeting before congress and viewed the development of Line 1 Hereford cattle as one of the greatest genetic accomplishments of the past century and suggested that the present-day herd was the oldest and purest line of Hereford cattle in the entire world. The 75th anniversary of the founding of the Line 1 population was celebrated in 2009.

What is the continuing impact of Line 1 on purebred Hereford cattle in the United States? Simply querying “L1 Domino” against the registration name field in the American Hereford Association website returned the earliest recorded reference to L1 Dominette and L1 Domino occurring around 1949, when the use of the name L1 Domino and L1 Dominette became the standard for the calves reared at Fort Keogh Livestock and Range Research Laboratory. The objective of this study was to quantify numbers of animals recorded in the American Hereford registry that are descendants of Line 1 and the degree to which they are related to Line 1 Hereford cattle from Fort Keogh. A second objective was to examine the geographic distribution of Line 1 germplasm across the United States.

4.2 MATERIALS AND METHODS

Fourteen million pedigree records were obtained from the American Hereford Association covering the period from 1960-2009. These records included all sires used in propagation of Line 1 at Fort Keogh. The intent was to estimate the relationship of Line 1 Hereford cattle among cattle recorded in the American Hereford database. Please refer to Table 3.1,which itemized the number of calves recorded by the American Hereford Association from 1980 to 2008.

4.2.1 Relationship to Line 1

Five random samples of 400 calves were to be extracted from each the Hereford's herdbook for each year from 1980 to 2008. Thus, 2000 calves were sampled each year. Sampled calves for each of the years were pseudo-mated to Line 1 sires from the decade beginning 12 years prior to the year sampled. Inbreeding coefficients were calculated for the "offspring" resulting from these "matings" using the algorithm developed by Henderson and Quaas (1976). The relationship of Line 1 to each calf sampled from the herdbook was taken to be twice the maximum inbreeding coefficient for the set of Line 1 sires used in the pseudo-matings. Hereafter, this measurement is identified as the relationship of the animal to the Line 1 Hereford population.

4.2.2 Geographic distribution of Hereford cattle related to Line 1

A sample of 400 calves per year was drawn from the American Hereford Association database. The location of approximately 90% of these animals was identified by the postal zip code of their owner (N = 10,700). The location (latitude and longitude) of each of the chosen calves was mapped using ArcGIS[1] software (ESRI, 2009). A list of all zip codes and longitudinal and latitudinal data was compiled relating to the entire United States accessed from http://www.boutell.com/zipcodes/ (Boutell, 2008).

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[1] ArcGis, ESRI Headquarters, Redlands, California

4.3 RESULTS AND DISCUSSION

4.3.1 Relationship of U.S. Hereford population to Line 1

Over time, the average proportion of animals related to the Line 1 population increased from an average of 23% in 1980 to 81% in 2008 (Table 4.2). The rate of increase in proportion related to Line 1 was 2.07% per year (Figure 4.2). If that rate of increase were to continue into the future every registered Hereford in the United States could contain genes originating from Line 1 by 2024. However, the average relationship of just those animals related to Line 1 decreased from 10% in 1980 to 7% in 2008. Yet the average relationship of all recorded Hereford calves to Line 1 increased from 2% in 1980 to 5% in 2008. This 5% relationship can be characterized as the equivalent of each Hereford calf recorded by the American Hereford Association having a Line 1 Hereford from Fort Keogh as a great-great grandparent.

Table 4.2 Relationship of Hereford calves recorded by the American Hereford Association to Line 1, by birth year of recorded calves. Summarized are 5 replicates of 400 samples randomly drawn from each year.

Sample	Sample Size	Freq	Fx_r	R_r, %	Fx_a	R_a, %	Min	Max	SD
1980	92	23%	0.052	10%	0.012	2%	0.00154	0.32	2.83
1981	122	30%	0.054	11%	0.016	3%	0.00174	0.33	3.00
1982	139	35%	0.048	10%	0.017	3%	0.00188	0.31	3.04
1983	151	38%	0.051	10%	0.019	4%	0.00128	0.30	4.27
1984	158	39%	0.054	11%	0.021	4%	0.00166	0.25	2.45
1985	170	42%	0.052	10%	0.022	4%	0.00096	0.33	2.00
1986	173	43%	0.048	10%	0.021	4%	0.00082	0.26	1.66
1987	184	46%	0.047	9%	0.021	4%	0.00136	0.35	2.60
1988	190	48%	0.043	9%	0.054	11%	0.00056	0.30	2.96
1989	202	51%	0.042	8%	0.021	4%	0.00048	0.30	3.04
1990	211	53%	0.041	8%	0.021	4%	0.00062	0.32	2.78
1991	200	50%	0.038	8%	0.020	4%	0.00068	0.32	4.92
1992	224	56%	0.039	8%	0.022	4%	0.0002	0.37	4.09
1993	228	57%	0.038	8%	0.022	4%	0.00024	0.27	3.57
1994	245	61%	0.042	8%	0.026	5%	0.0001	0.32	3.94
1995	247	62%	0.039	8%	0.024	5%	0.0001	0.25	1.73
1996	248	62%	0.042	8%	0.026	5%	0.00012	0.33	2.35
1997	252	63%	0.043	9%	0.027	5%	0.0001	0.35	2.83
1998	253	63%	0.041	8%	0.025	5%	0.0001	0.32	3.97
1999	248	62%	0.041	8%	0.025	5%	0.0001	0.36	4.72
2000	260	65%	0.042	8%	0.027	5%	0.0001	0.28	2.92
2001	249	62%	0.040	8%	0.025	5%	0.0001	0.30	1.32
2002	269	67%	0.037	7%	0.024	5%	0.0001	0.30	1.73
2003	276	69%	0.040	8%	0.027	5%	0.0001	0.37	1.50
2004	279	70%	0.039	8%	0.027	5%	0.0001	0.38	1.80
2005	287	72%	0.037	7%	0.026	5%	0.0001	0.35	1.87
2006	305	76%	0.036	7%	0.027	5%	0.0001	0.38	1.22
2007	319	80%	0.036	7%	0.028	6%	0.0001	0.33	2.92
2008	325	81%	0.033	7%	0.026	5%	0.0001	0.38	1.87

Sample = Designates replicate of the experiment; Sample size = number of animals with pedigree relationship to Line 1;Freq = Frequency of animals in sample having non-zero relationship to Line 1; Fx_r = Mean of maximum inbreeding coefficient of a "progeny" resulting from the pseudo-mating of sampled animal to Line 1 sires, for the subset of sampled animals that were related to Line 1; $R_r = (2*Fx_r)*100$, i.e. the percentage relationship between Line 1 and those sampled animals that were related to Line 1.; Fx_a = Mean of maximum inbreeding coefficient of a "progeny" resulting from the pseudo-mating of all sampled animal to Line 1 sires; R_a = the percentage relationship between Line 1 and all sampled animals; Min and Max = minimum and maximum of distribution of Fx_r, respectively; SD = standard deviation of relationship.

4.3.2 Geographic distribution of Hereford cattle in the U.S. and their relationship to Line 1

Hereford cattle were found in every state except Alaska and Rhode Island. More Hereford cattle were found in the Midwestern and Eastern United States than in the West and Southwest. This observation may simply reflect differences in stocking rates that are appropriate across the U.S (USDA, 1997). The location, in the United States, of Hereford cattle registered with the American Hereford Association is illustrated in Figure 4.2.

The 10 states having the greatest and fewest numbers of registered Hereford cattle are shown in Table 4.4.

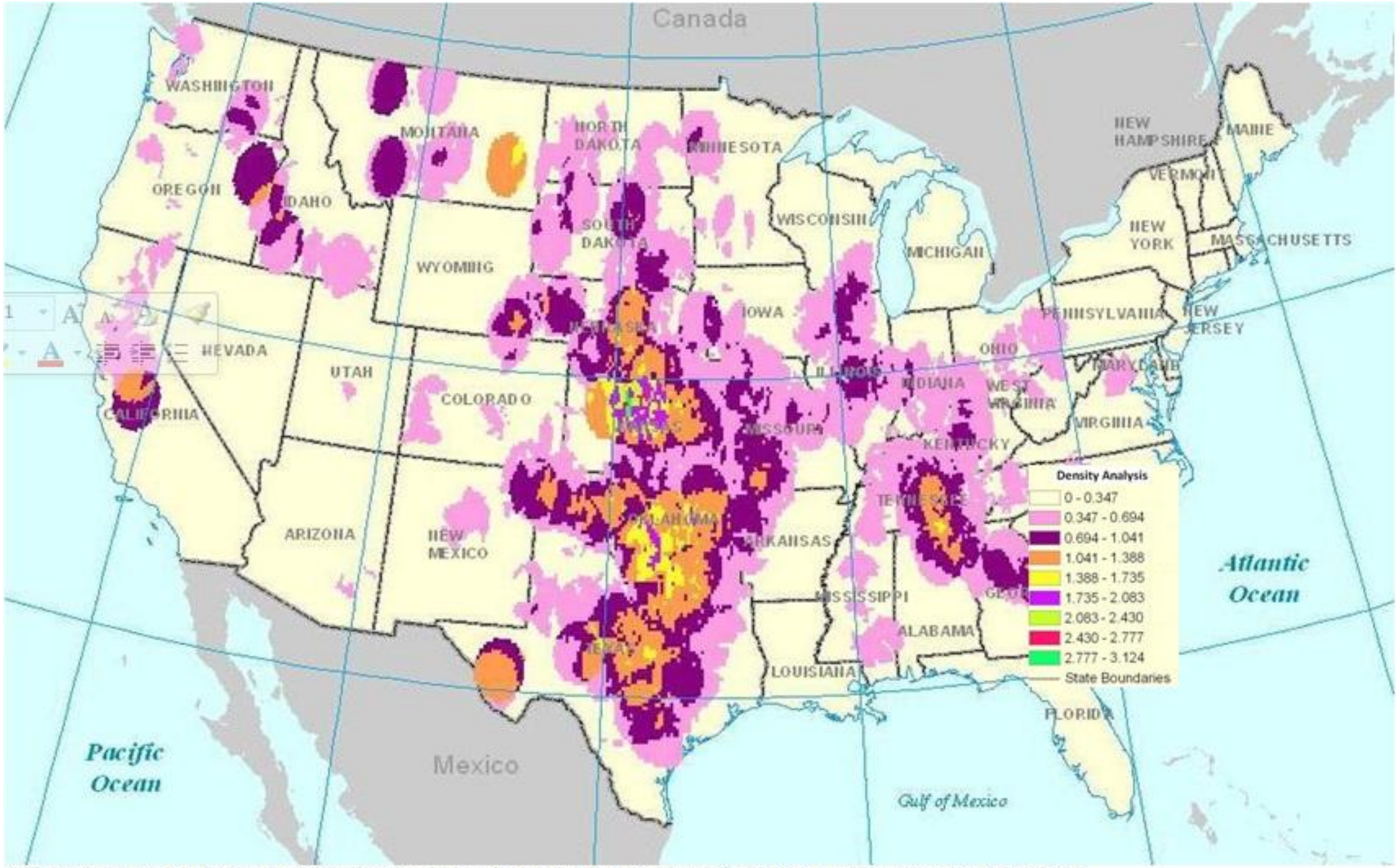
Table 4.4 Rank of States in the U.S. with the most Hereford registrations

Rank	States with most Hereford cattle	States with fewest Hereford cattle
{1}	Texas	Alaska
{2}	Nebraska	Rhode Island
{3}	Kansas	Hawaii
{4}	Oklahoma	New Hampshire
{5}	Missouri	Delaware
{6}	Montana	Maine
{7}	South Dakota	Vermont
{8}	Idaho	Connecticut
{9}	California	New Jersey
{10}	North Dakota	Massachusetts

Tracking the location of registered Hereford cattle allowed for geographical spatial density representation of Hereford concentrations. These spatial densities were then optimized with the inclusion of Hereford cattle related to the Line 1, enabling detection of how animals related to Line 1 are dispersed through the general concentrations of Hereford locations. It should be noted that animals related to the Line 1 Hereford herd can be located in every region and almost every state. The annual bull sale at Fort Keogh that took place every year since 1948 has led to the sale and distribution of Line 1 Hereford cattle to 34 states. Thus, the data indicate that people around the United States are buying and transporting descendants to additional states where no one has personally purchased a Line 1 Hereford via the production sale at Fort Keogh. Based upon analysis of the original 14 million records received from the American Hereford Association, all animals with information pertaining to their geographic location were mapped, among those samples Hereford cattle are registered in every state except, Alaska and Rhode Island.

Mapping the density of the Hereford cattle in the United States indicates where points or Hereford herds are concentrated. There is a point value for registered Hereford cattle that corresponds to their zip code, but with a density analysis the representation of Hereford cattle can be seen throughout the region. Density maps allow for a distribution of Hereford populations throughout the landscape. Along with these density maps is the reference that can be inferred with regard to relationships to Line 1 Hereford cattle. These density maps identify where Hereford cattle are concentrated as related to their registration information. While a point represents each one, these graphs show the spread of the population over a region. Not all Hereford cattle reside in one single spot, so these are the predicted distributions of population throughout the landscape.

Figures 4.1 through 4.4 represent the initial spatial point density of all Herefords and with an overlay of the highest levels of relationship to Line 1. ArcGIS Spatial Analyst was utilized to analyze point densities or measure the quantities of the input layers; in these scenarios the Hereford cattle, throughout the landscape or country to produce a continuous surface. Figure 4.1 identifies the overall densities or concentrations of registered Hereford cattle, the largest densities are in the central United States as well as portions of the southeast. On a state by state basis, the largest density of Hereford cattle is in northern Kansas and southern Oklahoma and into Texas. This location of Hereford cattle corresponds to historical data stating the Hereford breed gained strong footholds in this area throughout the 1870's (Miller, 1902).

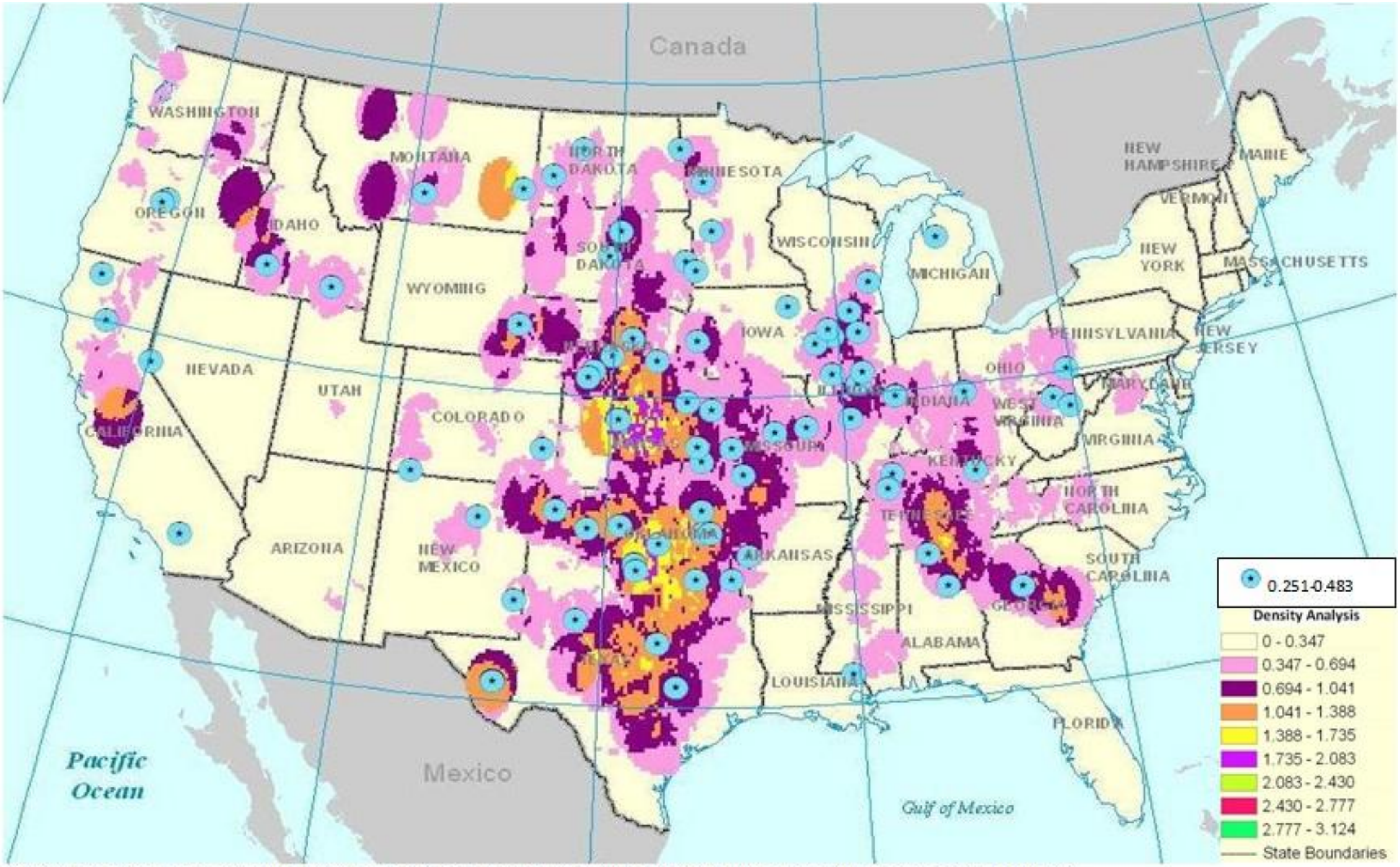


^^Point density is a calculated magnitude per unit area from point features that fall within a specific region around each cell.

Figure 4.1 Density of Hereford cattle recorded by the American Hereford Association in the United States.

Hereford cattle related to Line 1 with a relationship of 0.25 or greater are distributed all over the United States, with notable concentrations in the central United States and central east around Illinois and edges of Iowa and Wisconsin. These relationships are shown in Figure 4.2. The distributions of cattle related to Line 1 and the general distribution of all Hereford cattle are not different.

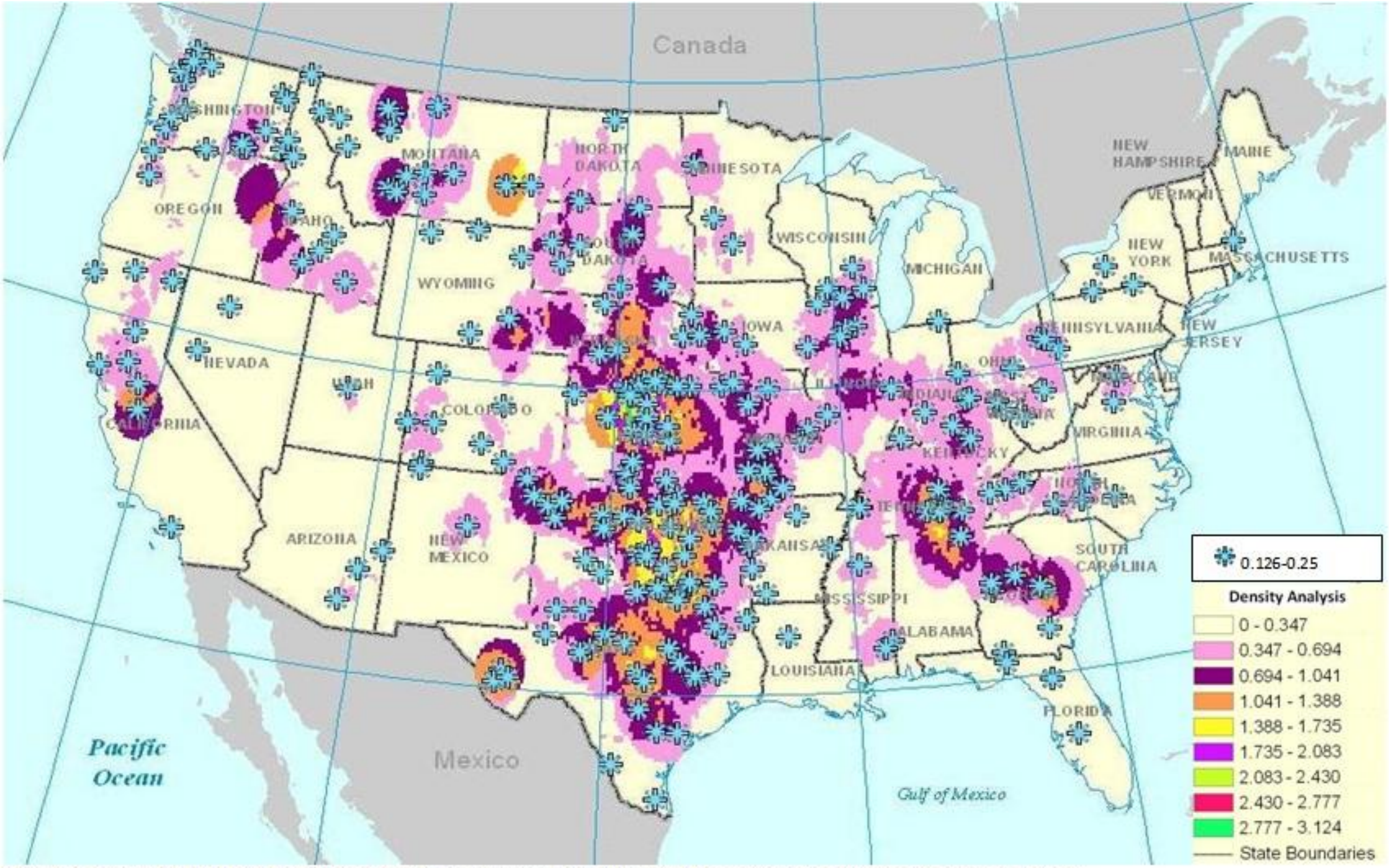
The breeders of these cattle with higher relationship to Line 1 can be identified as buyers at the Fort Keogh Line 1 Bull sale in the past 30 years. There are very few animals with this type of close relationship to Line 1. In many cases these animals are direct descendants of Line 1 Hereford, via a parent or grandparent.



^^Point density is a calculated magnitude per unit area from point features that fall within a specific region around each cell.

Figure 4.2 Density of Hereford cattle recorded by the American Hereford Association that are 25.1% to 48% related to Line 1.

Figures 4.3 and 4.4 summarize the relationship to Line 1 at levels of 0.126-0.25 and 0.063-0.125. In both figures the animals related to Line 1 has increased in distribution across the country. Notable concentrations for both groups related to Line 1 are in areas already catering to higher densities of Hereford cattle. These areas are northern Kansas and southern Oklahoma and into Texas, areas long known for Hereford cattle utilizing the abundance of grass, and ease of transportation to central markets (Miller, 1902). Figure 4.4 indicates a possible great-grand parent relationship, and it’s clear that animals more closely related to Line 1 are not distributed differently than those more distantly related or not related at all.

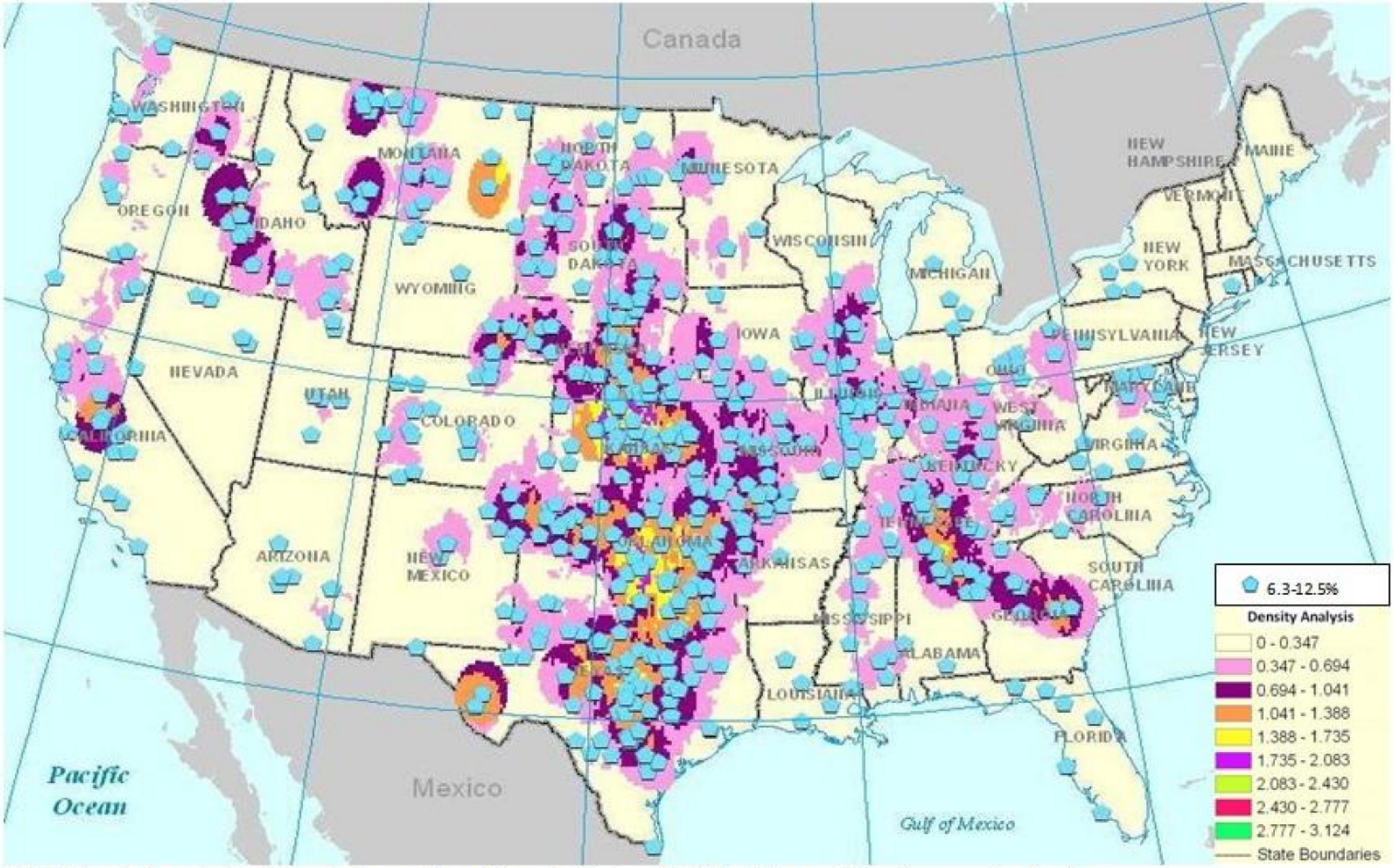


^^Point density is a calculated magnitude per unit area from point features that fall within a specific region around each cell.

Figure 4.3 Density of Hereford cattle recorded by the American Hereford Association that are 12.6% and 25% related to Line 1.

Additionally, the number of Hereford cattle potentially related to Line 1 is gaining across areas where there aren't large Hereford densities. Thereby further encompassing the country with animals that can spread the genetic contribution of the Line 1 Hereford herd.

In summary, nature does not assume organisms are distributed naturally or at random, forming some sort of spatial pattern (Legendre and Fortin, 1989). This is due to energy inputs, interaction and disturbances. This spatial variance is what creates diversity. The type of spatial arrangement of Hereford cattle around the country indicates interactions within and between their own breed and breeders and various management practices; such as abundance of feed or grass, interaction due to cattle sales and trades and disturbances which could be predatory or large scale dispersal of genetics. Human or breeder activities have the greatest impact on the spatial density and patterns of Hereford cattle largely due to historical and to smaller extent emotional ties. Many breeders associated with Hereford cattle closely related to Line 1 are known to perpetuate the breed within the industry. They are typically one of many generations of Hereford breeders, are well established and through continued sales contribute to the distribution of Line 1 genetics throughout the country; thereby aiding spatial diversity.



^^Point density is a calculated magnitude per unit area from point features that fall within a specific region around each cell.

<u>**Figure 4.4 Density of Hereford cattle recorded by the American Hereford Association that are 6.3% to 12.5% related to Line 1.**</u>

CHAPTER 5

INFLUENCE OF LINE 1 HEREFORD CATTLE ON HEREFORD CATTLE IN CANADA

5.1 INTRODUCTION

The Hereford breed has been credited with building the cattle industry in Canada (Canadian Hereford Association, 2010). In 1860, Frederick William Stone, a Warwickshire Englishman, arranged to purchase eight Hereford heifers and a young Hereford bull, Lord Bateman; in England. His intention was to show these cattle at a provincial exhibition in Ontario to attract some attention to the breed. An editorial in an agriculture publication noted these Hereford cattle from Lord Bateman stood “unequalled in purity, size, and symmetry in England” and Stone was congratulated for his purchase of these animals (Canadian Hereford Association, 2010). The Canadian Hereford Association was formed in 1890 with its primary objective being maintaining purity of the Hereford breed. In 2011, it was estimated there were 120,000 purebred Hereford females in production in Canada, with up to 350,000 straight-bred commercial Hereford females as well. They also estimate well over 30% of the beef cattle population in Canada has Hereford influence (Canadian Hereford Association, 2010).

What is the continuing impact of Line 1 on purebred Hereford cattle in Canada? Simply querying “L1 Domino” against the registration name field in the Canadian

Hereford Association website returned over 380 entries. The earliest recorded reference to L1 Dominette and L1 Domino occurs in 1948 and 1949 respectively. The objective of this study was to quantify the number of animals recorded in the Canadian Hereford registry that are descendants of Line 1 and the degree to which they are related to Line 1 Hereford cattle from Fort Keogh. A second objective was to examine the geographic distribution of Line 1 germplasm across Canada.

5.2 MATERIALS AND METHODS

5.2.1 Canadian Hereford Pedigree Records

Over two million pedigree records were obtained from the Canadian Hereford Association covering the period from 1951-2008. The intent was to estimate the relationship of Line 1 Hereford cattle among cattle recorded in the Canadian Hereford databases. However, records from the Canadian Hereford Association were not well connected to records of the American Hereford Association. The lack of cross-referencing between cattle recorded by the Canadian Hereford Association versus those recorded by the American Hereford Association compromised use of the Canadian Hereford Association database in calculating pedigree relationship to Line 1 (N = 7,912).

Table 5.1 itemizes the number of calves recorded by the Canadian Hereford Association from 1980 to 2008. Additionally, the numbers of calves registered by the

Canadian Hereford Association that have cross reference identification numbers to the American Hereford Association are included.

Table 5.1 Numbers of calves recorded by Canadian Hereford Association (CHA) for the years 1980 to 2008.

Year	Number of calves recorded by the Canadian Hereford Association	Number of calves recorded by the CHA and cross-referenced to the AHA.
1980	71021	348
1981	64470	243
1982	58603	122
1983	54362	187
1984	47257	204
1985	43820	228
1986	43157	200
1987	43253	193
1988	42355	170
1989	40244	139
1990	38450	121
1991	36562	125
1992	35614	100
1993	34992	90
1994	35133	125
1995	32194	96
1996	29154	67
1997	27465	66
1998	26317	69
1999	24693	74
2000	24594	77
2001	23868	69
2002	21801	46
2003	19209	30
2004	17991	17
2005	17036	32
2006	16166	40
2007	15371	41
2008	14754	25

AHA – American Hereford Association

5.2.2 Geographic distribution of Canadian Hereford cattle related to Line 1

Of the 2,265,631 animals in the Canadian Hereford Association database 1,056,623 (47%) had no listed owner and therefore their geographic location was unknown. This lack of postal code information, combined with the lack of cross referencing of animals between the Canadian Hereford Association and American Hereford Association databases, necessitated the use of all viable records in assessing the geographic distribution across Canada of animals that were related to Line 1. For these reasons the data are not a random sample of all animals recorded by the Canadian Hereford Association. The location (latitude and longitude) of each of the chosen calves was mapped using ArcGIS[2] software (ESRI, 2009). Canadian postal codes of Hereford breeders were used as input for Google Earth (Google, 2010) to obtain latitude and longitude of their location. Figure 5.1 is a reference map of the Canadian Postal Districts, summarized alphabetically right to left across the country.

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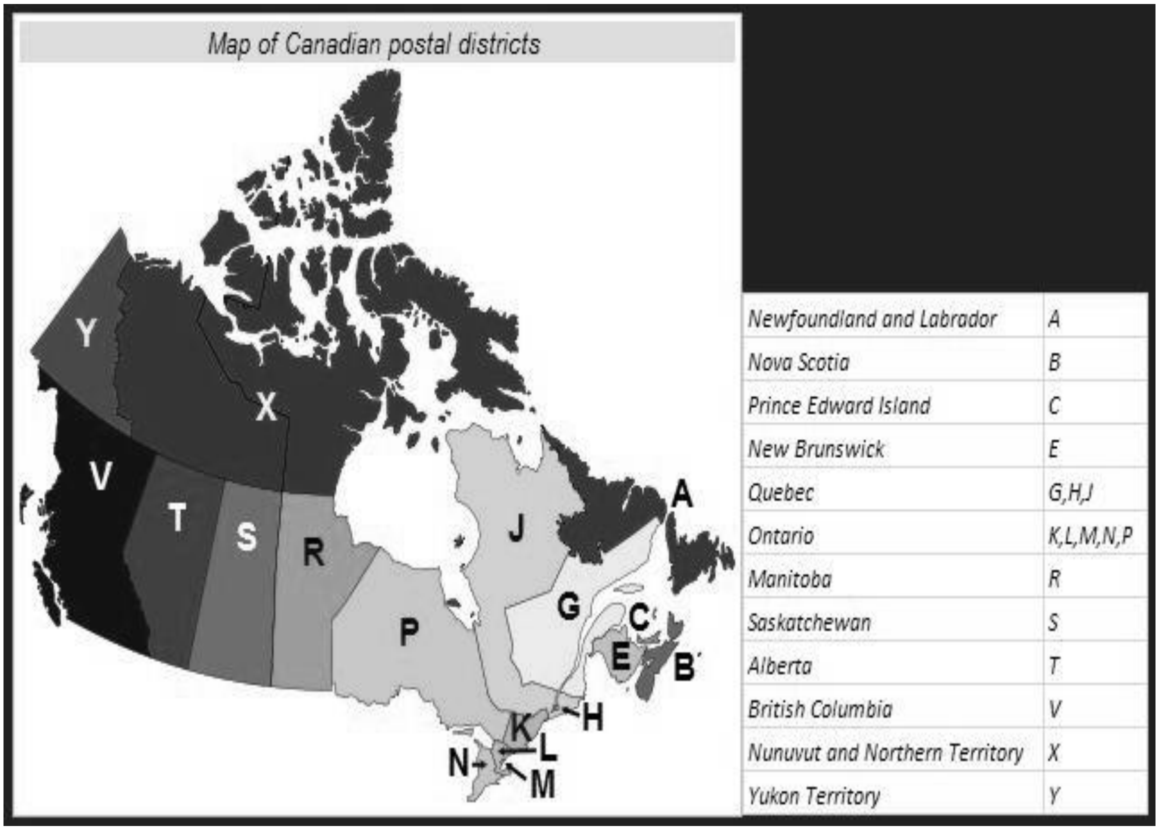
[2] ArcGis, ESRI Headquarters, Redlands, California



Newfoundland and Labrador	A
Nova Scotia	B
Prince Edward Island	C
New Brunswick	E
Quebec	G,H,J
Ontario	K,L,M,N,P
Manitoba	R
Saskatchewan	S
Alberta	T
British Columbia	V
Nunuvut and Northern Territory	X
Yukon Territory	Y

Figure 5.1 Canadian postal districts reference map

5.3 RESULTS AND DISCUSSION

5.3.1 Relationship of Canadian Hereford population to Line 1

The data received from Canadian Hereford Association can be described as follows: 317,478 animals in the dataset had a known breeder and postal code information. Of these animals, 6 are from 2 locations in the United Kingdom, 4,020 are from 120 locations in the United States, and the remaining 313,398 are from 158 locations in

Canada. There were a total of 7,912 animals with an American Hereford Association reference registration number with 3,348 of them falling into the 1980-2008 birth year guidelines for this study. Of the animals with known reference to the American Hereford Association, 2,247 were related to Line 1, and 1,130 of them were born between 1980 and 2008. Of these animals only 766 of them have a known breeder and/or postal code information in which to be mapped.

Analysis of data from Canada was based solely on those animals with American Hereford Association reference numbers (Table 5.2). Note the number of cattle that have American Hereford Association reference numbers decreased over time. The number of cattle related to Line 1 Hereford increased from 26% to 68% from 1980 to 2007, this is an increase of 42% or an increase at the rate of 1.6% per year. There is a significant decrease in 2008 where the percent of animals related is only 8%. This could be due to animals simply not being registered at the time the data were extracted from the database or American Hereford Association reference numbers having not yet been assigned (Schmid, personal communication). If sample sizes were adequate and using the data from 1980-2007, extrapolation into the future indicates that in 20 years’ time all Hereford cattle in Canada could have some relationship to Line 1.

Table 5.2 Relationship of calves recorded by the Canadian Hereford Association and cross-referenced to the American Hereford Association database with Line 1.

Sample	Sample Size	Freq	Fx_r	R_r, %	Fx_a	R_a, %	Min	Max	SD
1980	348	90	26%	0.064	13%	0.017	3%	0.0024	0.34
1981	243	52	21%	0.083	17%	0.018	4%	0.0068	0.31
1982	122	28	23%	0.081	16%	0.019	4%	0.0050	0.29
1983	187	56	30%	0.090	18%	0.027	5%	0.0023	0.32
1984	204	74	36%	0.062	12%	0.021	4%	0.0018	0.30
1985	228	48	21%	0.060	12%	0.013	3%	0.0022	0.18
1986	200	64	32%	0.069	14%	0.022	4%	0.0018	0.22
1987	193	58	30%	0.077	15%	0.023	5%	0.0011	0.30
1988	170	50	29%	0.043	9%	0.013	3%	0.0012	0.33
1989	139	48	35%	0.036	7%	0.013	3%	0.0004	0.19
1990	121	43	36%	0.028	6%	0.010	2%	0.0004	0.14
1991	125	38	30%	0.036	7%	0.011	2%	0.0003	0.23
1992	100	34	34%	0.032	6%	0.011	2%	0.0004	0.17
1993	90	36	40%	0.049	10%	0.020	4%	0.0006	0.15
1994	125	59	47%	0.035	7%	0.016	3%	0.0002	0.17
1995	96	32	33%	0.047	9%	0.016	3%	0.0001	0.24
1996	67	32	48%	0.028	6%	0.014	3%	0.0004	0.15
1997	66	31	47%	0.025	5%	0.012	2%	0.0002	0.10
1998	69	30	43%	0.034	7%	0.015	3%	0.0003	0.15
1999	74	23	31%	0.027	5%	0.008	2%	0.0001	0.11
2000	77	36	47%	0.029	6%	0.014	3%	0.0001	0.12
2001	69	34	49%	0.023	5%	0.011	2%	0.0002	0.12
2002	46	33	72%	0.019	4%	0.014	3%	0.0001	0.09
2003	30	15	50%	0.015	3%	0.008	2%	0.0002	0.06
2004	17	6	35%	0.051	10%	0.018	4%	0.0011	0.22
2005	32	22	69%	0.016	3%	0.011	2%	0.0001	0.08
2006	40	25	63%	0.021	4%	0.013	3%	0.0003	0.06
2007	47	32	68%	0.018	4%	0.012	2%	0.0002	0.10
2008	25	2	8%	0.037	7%	0.003	1%	0.0149	0.06

Sample = Designates replicate of the experiment; Sample size = number of animals with pedigree relationship to Line 1;Freq = Frequency of animals in sample having non-zero relationship to Line 1; Fx_r = Mean of maximum inbreeding coefficient of a "progeny" resulting from the pseudo-mating of sampled animal to Line 1 sires, for the subset of sampled animals that were related to Line 1; $R_r = (2*Fx_r)*100$, i.e. the percentage relationship between Line 1 and those sampled animals that were related to Line 1.; Fx_a = Mean of maximum inbreeding coefficient of a "progeny" resulting from the pseudo-mating of all sampled animal to Line 1 sires; R_a = the percentage relationship between Line 1 and all sampled animals; Min and Max = minimum and maximum of distribution of Fx_r, respectively; SD = standard deviation of relationship.

5.3.2 Geographic distribution of Hereford cattle in Canada and their relationship to Line 1

Shown in Figure 5.2 is the annual mean relationship to Line 1 Hereford from 1980-2008 for Hereford cattle registered with the Canadian Hereford Association. The level of relationship seen in Canadian Hereford cattle to Line 1 has remained fairly constant with few large deviations outside of the mean at 0.0145. However, the level of relationship for those animals directly related to the Line 1 Hereford has seen an overall drop from 0.064 to 0.037, this could simply be the result of fewer relational ties between the American Hereford Association and Canadian Hereford Association databases over time; though the levels are relatively small it can be more easily termed that the level of relationship went from being traced to a great-grandparent to a great-great or even a great-great-great grandparent in more recent years.

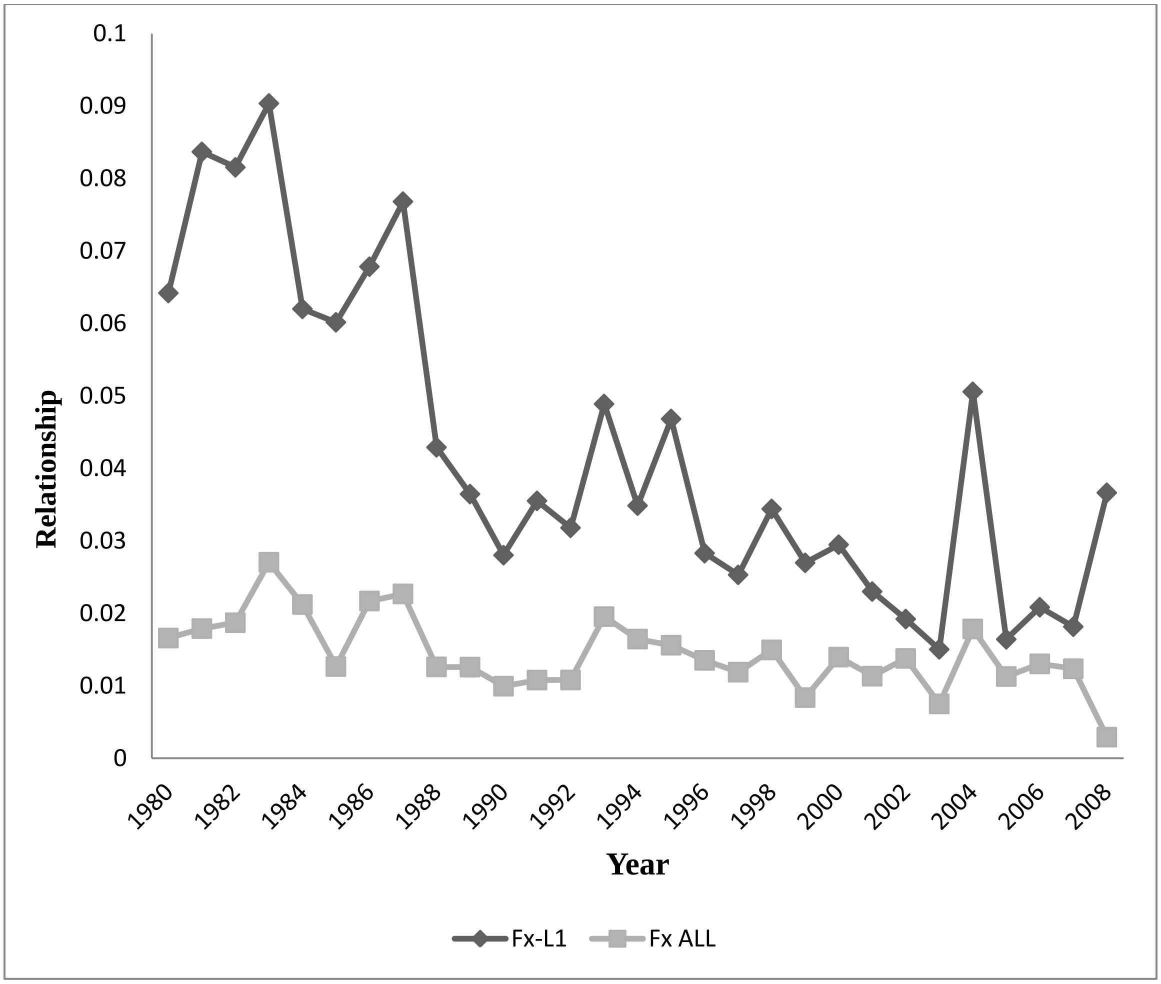


Figure 5.2 Annual mean relationship between Line 1 Herefords and Canadian Hereford cattle

Figure 5.3 provide information on the number of animals with known postal codes, province of registration and also the location and density of these Hereford cattle in Canada based upon the information for the 313,398 animals with their 158 known locations. The density of Hereford cattle in Canada is clearly in the southern portion of the country, with Hereford cattle breeders in 7 provinces and stretching from coast to coast. The largest concentration of Hereford cattle registered is in the province of Alberta and the fewest in New Brunswick.

Table 5.3 Number of Canadian Hereford cattle by province based upon known postal code information

New Brunswick	Quebec	Ontario	Manitoba	Saskatchewan	Alberta	British Columbia
2953	9667	17111	26827	107982	144421	4443

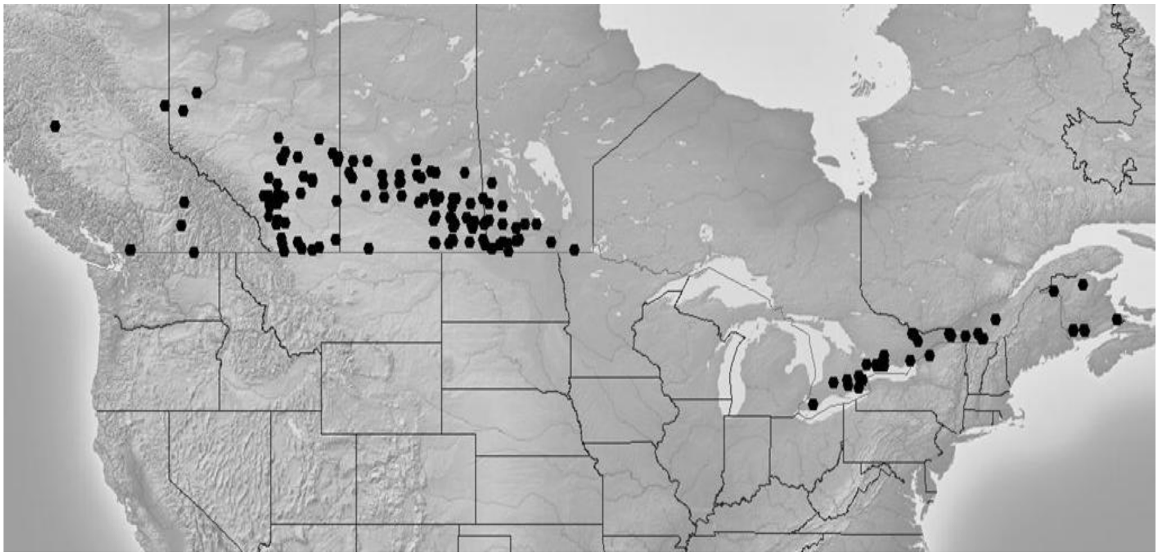
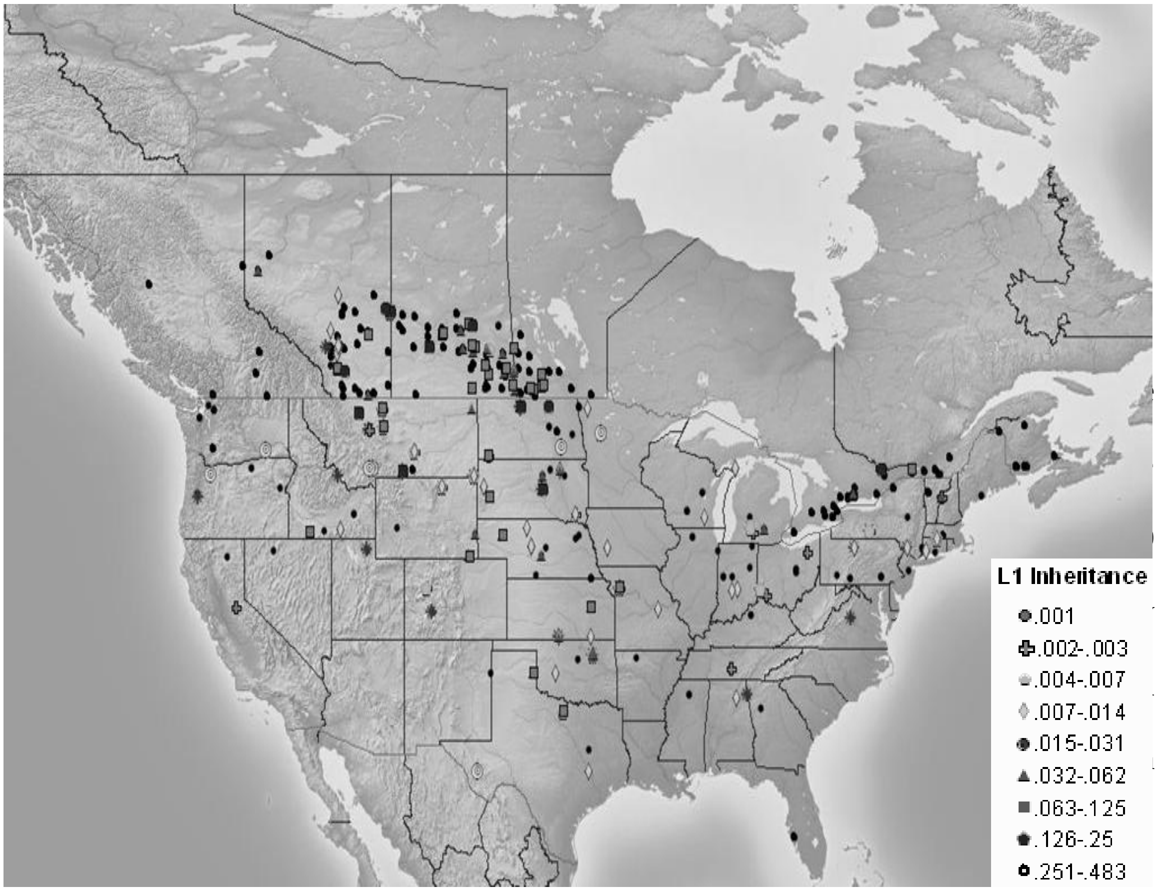


Figure 5.3 Density of Hereford Cattle Breeders in Canada with known postal code Information

In Figure 5.4 the relationships of Hereford cattle related to Line 1 are mapped according to the postal code that was received from the Canadian Hereford Association dataset. The animals while now owned by persons in Canada still show their origin from the United States.



*Bulleted points within the United States area of the map indicate animals were originally purchased in the United States and taken to Canada.

Figure 5.4 Density of Hereford cattle in Canada with relationship to Line 1 Hereford

These animals originating in the United States were purchased in the United States and taken to Canada; however Canadian Hereford Association rules states every animal used for breeding purposes needs to have a Canadian Hereford Association registration number if the intent is to register future offspring (Schmid, personal communication). All other information remains true to origin. The relationships are summarized in Table 5.4.

Table 5.4 Breakdown of inbreeding levels as compared to animals with known postal codes and country of origin.

Fx Levels	# w/ L1 Fx	# w/ PostCode	USA Origin	Canada Origin
0.251-0.50	27	9	9	0
0.126-0.25	190	50	42	8
0.063-0.125	536	157	123	34
0.032-0.062	571	167	122	45
0.015-0.031	373	119	94	25
0.007-0.014	227	98	92	6
0.004-0.006	102	34	31	3
0.002-0.003	97	53	52	1
0.001	126	79	76	3

Calculating the relationship of Hereford cattle in Canada using only the animals selected from 1980-2008 yields 67% of these animals with a relationship to the Line 1. However, only 34% could actually be mapped according to their postal codes, and of this 34% only 125 or 16% originated directly from Canada.

The proportion of Hereford cattle directly from Canada with at least a great-grandparent traceable to Line 1 is 90%. The number of animals imported into or born in Canada with Line 1 influence has decreased at a rate of 4.45% per year since 1980 with an overall decrease in reference to all Hereford cattle from the United States at a rate of 9.28% per year. This relationship is shown in Figure 5.6. Bear in mind all these numbers, figures and calculations are based upon incomplete data. While Canadian Hereford Association works hard to maintain a complete dataset much is still left up to the producers and breeders who are part of the Canadian Hereford Association. It is estimated that Hereford cattle makes up 30% of the total cattle population in Canada, many of these animals are not purebred, or may be purebred but not registered with the Canadian Hereford Association (Schmid, personal communication).

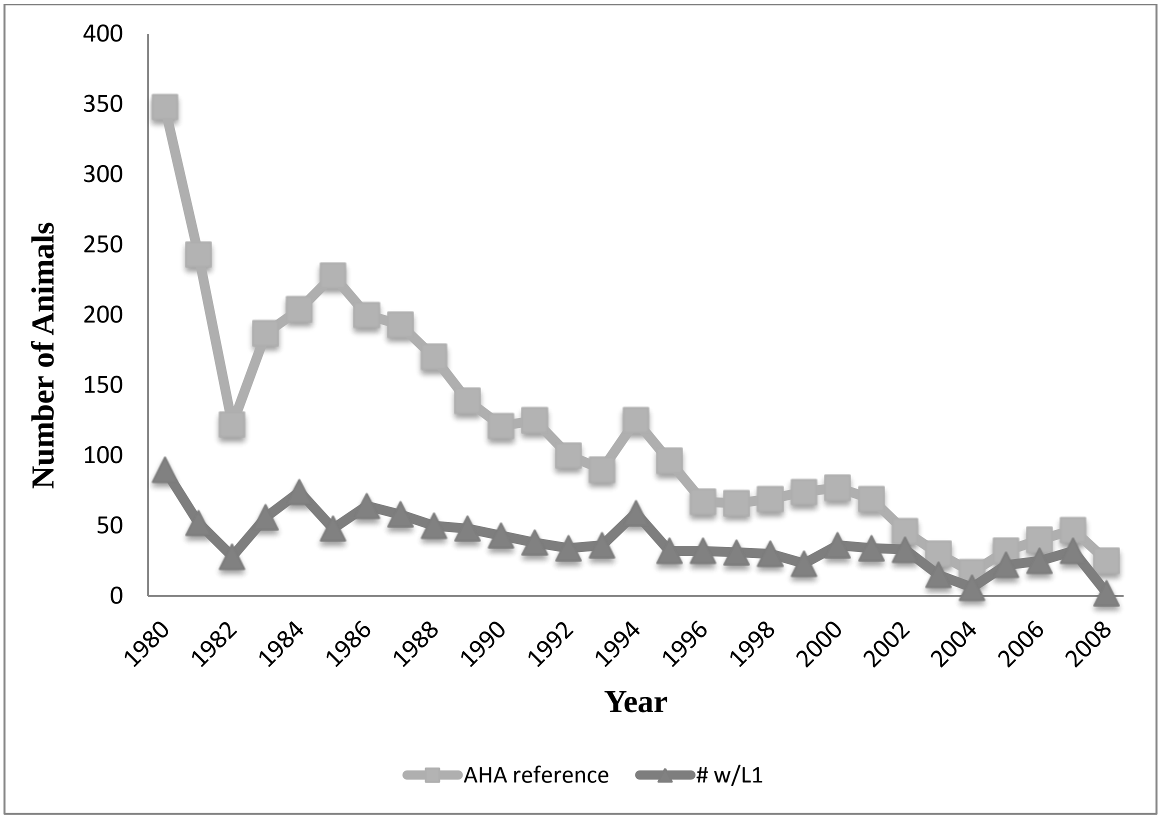


Figure 5.6 Decrease in reference of Hereford cattle from USA to Canada.

Of note; Fort Keogh's annual sale of cattle sent Line 1 cattle or cattle of Line 1 breeding to 5 Canadian provinces, namely Alberta (1956, 1959, 1980, 1985, 2010), Manitoba (1958, 1981), Saskatchewan (1956, 1960-61), Ontario (1957), and Nova Scotia (1964). Line 1 Hereford cattle maintain a presence in Hereford cattle in Alberta, Manitoba, Saskatchewan, and Quebec; yet there are no apparent registrations of any Hereford cattle in Nova Scotia at this present date. Additionally, while there are

Hereford cattle in British Columbia, Ontario and New Brunswick there is no Line 1 Hereford influence in any of these cattle, and based upon the records given dating back to 1951 there has never been any in either British Columbia or New Brunswick. By deduction, Line 1 Hereford cattle; while well established in the industry, their use and influence is perpetuated by breeders most familiar with their performance within a given region.

5.4 Summary

Overall, the analysis of the influence of the Line 1 Hereford on cattle in the United States to Hereford cattle in Canada needs careful thought. There is a considerable deficiency in information that could link the Hereford cattle from each country due to the lack of corresponding reference numbers. The completed analysis was simply based upon the available data with no assumptions made. Arguments can be made that the cattle that indicated a relationship to Hereford cattle in the United States and Fort Keogh was simply a representative sample and thus those relationships calculated are adequate. Alternatively, the assumption can also be made that cattle without an American Hereford Association reference number are completely unrelated to Hereford cattle in the United States and Fort Keogh.

A future analysis could be conducted like that described in Chapter 7 with a pedigree analysis of influential sires in Canada. An evaluation such as this could then document the flow of genetic material from Line 1 Hereford cattle to the Hereford cattle in Canada. Alternatively, when registered cattle are sold their registration names are not typically changed like that of their registration numbers. A representative sample could be chosen from the Canadian data within a time frame that corresponds with these previous analyses. Cattle then could be individually searched according to registration name within the American Hereford Association database. This process is extremely time consuming, but the search could potentially yield a registration number that corresponds with the registered name and pedigree analysis could move forward in much the same way as described in this, previous, and future chapters.

CHAPTER 6

USE OF MOLECULAR GENETICS AND PEDIGREE ANALYSIS TO DISCERN RELATIONSHIPS OF LINE 1 HEREFORD ON HEREFORD CATTLE IN THE UNITED STATES AND SOUTH AFRICA

6.1 INTRODUCTION

Studying the use of Line 1 Hereford cattle provides insight into dissemination of research results to an industry where those results are applied. Previously (Chapter 4), pedigree data were used to accomplish this end. However, pedigree, as reported by breeders, may contain errors or be otherwise unavailable due to concerns over ownership of intellectual property (Sanders, personal communication; Schmid, personal communication). Use of genotypic data may overcome these issues provided appropriate samples can be obtained. Research conducted by USDA-ARS has resulted in both Hereford sires representative of the U.S. industry and Line 1 being genotyped with a common set of SNP markers, referred to as the MARC 2,000 Bull project (Thallman, 2009).

The first Hereford bulls were imported into South Africa in 1890. Since that time, a substantial number of Hereford cattle have been imported into South Africa with the goal of improving the national herd (South African Hereford Breeders Society, 2010).

Furthermore, Hereford semen and embryos are frequently exported from the United States to South Africa (Coe, personal communication). Hereford cattle adapted well to conditions in southern Africa and were often compared to the native cattle and touted as healthy, hardy, and prolific (South African Hereford Breeders Society, 2010). Dr. Jan Bonsma, considered the father of the Bonsmara breed, once wrote that “the Hereford is the best grazing animal of the British Beef Breeds; it has a wonderful temperament and utilizes sour pasture well” (South African Hereford Breeders Society, 2010). In 2007, the South African Hereford Breeders Society marked its 90th anniversary. As of 2008, there was no online database of pedigree information for South African Hereford cattle which can be queried for the terms L1 Domino or L1 Dominette and the herdbook was viewed as proprietary. However, research collaboration between 1) the Agricultural Research Council (ARC) and the South African Hereford Breeders Society provided material for genotyping, and 2) the ARC and USDA-ARS assured common microsatellite markers were used in genotyping South African Hereford cattle and Line 1 data with resulting data shared between the two organizations.

Objectives of this study were to: 1) estimate relationships of the Line 1 Hereford cattle produced in research conducted at the Fort Keogh research facility, Miles City Montana with Hereford cattle in the United States and in South Africa; and 2) compare relationships derived from molecular markers with those estimated from recorded pedigrees.

6.2 MATERIALS AND METHODS

6.2.1 U.S.A. intra-country analysis

For comparison to the U.S. Hereford population, Line 1 was represented by 57 heifer and 63 bull calves born in 2008, and by 120 sires born between 1953 and 2006 for which semen was available from which to extract DNA. The U.S. Hereford population was represented by 311 bulls. These samples were obtained from 56 bulls used in the germplasm evaluation program at U.S. Meat Animal Research Center in Clay Center, NE (Matukumalli *et al.*, 2009) and 255 bulls that were nominated by members of the American Hereford Association.

Single nucleotide polymorphism (SNP) genotypes were produced in the Geneseek[3] laboratory from DNA applied to the Illumina BovineSNP50 BeadChip[4] (Matukumalli *et al.* 2009). Nine thousand one hundred and three of the 52,156 SNP were from the genome sequence of L1 Dominette 01449, American Hereford Association registration number 42190680.

The Line 1 pedigree was traced to the earliest of registration numbers in the American Hereford Association 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 from the pedigree records of the American Hereford Association. To compute the needed relationships, all

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[3] Geneseek, a registered trademark of Neogen Corp. Lincoln, Nebraska, U.S.A.
[4] Illumina Inc., San Diego, California, U.S.A.

possible matings between the Line 1 and industry animals were simulated. The inbreeding coefficient of the progeny from such a mating estimates one half the relationships between the two pseudo-mated individuals. The maximum of the 240 relationship coefficients for each industry bull, calculated thusly, was taken as a measure of that bull's relationship to Line 1.

6.2.2 Relationship to South Africa

Members of the South African Hereford Breeders Society provided hair samples from 36 domestically produced bulls that were important in South Africa. These samples were transferred to the ARC Genetics Laboratory in Irene, South Africa where DNA extraction, subsequent PCR, and genotyping were performed. A selection of Line 1 cattle used previously in other studies (Kealey *et al.*, 2006; Mapholi-Tshipuliso, 2007) was used for the purpose of comparison with these animals.

A set of 34 microsatellite markers covering the 29 bovine autosomes were chosen from http://www.marc.usda.gov/genome/cattle/cattle.html based on marker position, suitability for multiplex reactions and ease of scoring. These markers are presented in Table 6.1. At Fort Keogh, touchdown PCR was performed in MJ Research[5] thermocyclers as described in http://biolibrary.licor.com/htdocs/RnP/LabPrim.jsp. All genotypes were collected on a LiCor 4200 DNA Analysis System[6]. Genotypes were

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[5] MJ Research Thermocyclers, Waltham, Massachusetts, USA
[6] LiCor 4200 DNA Anaysis System, Lincoln, Nebraska, USA

independently scored by two individuals using the 4300 System Saga^{GT}[7]. Saga^{GT} automates electrophoresis, lane finding, location of standards, calibration of band sizes, and allele scoring. The independently scored genotypes were later compared, and discrepancies resolved if possible.

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[7] 4300 System Saga^{GT}[7], Lincoln, Nebraska, USA

Table 6.1 Microsatellite markers used to assess molecular genetic relationships of South African Hereford cattle to Line 1.

Marker	**BTA**	**Primer sequences**	
		Forward	**Reverse**
BMS574	1	ATGTTCTTTGACCACATGGATT	GAACAAGCATTCTGACCATAGC
URB014	1	CATTGGTAGGTGGGTTCTTTCC	GCAACCTAAGTGTCCATCAACAG
IDVGA-2	2	GTAGACAAGGAAGCCGCTGAGG	GAGAAAAGCCAAGAGCCAGACC
BMC5227	3	TGTGCGCTGTACAGTGAGTG	ATGTCAAGGTCAGGGAGGAA
AGLA227	4	TTAGAGCATAGTTGATTTAAAATG	CACAGGAAACTCTACTCAATATTC
BM8126	5	TCTTCCTCCGCAGACTGG	GAACCTGTGGATGAGCGG
BMS1315	5	AAGCCATTGATTGTAGATTGGG	GAGTTTCCTTTTTCCCCCAC
BL1038	6	GGCAAGCTAGAGTCAGACACG	GCAAAAGTCTAGGTGAAATGCC
BMS1247	7	TCAGCTCTCAGCAGCCTGTA	GGGGTTAATGGTGATCTGCA
BMS713	7	CCAAGGGAGGAAAAATAAGTTAA	ACCAGCAGTAGGTTGAGGTTAA
BMS836	8	GAAACTCTTTTCACTCTGCGC	GCTCTTAGGGATTGCTTCACC
RM321	8	CTATATTGTGTGCTTGAAATTTGC	TCTCACCTAGATGTCTCTGTATGTG
BMS1967	9	GGGCAGATGTGAGTAATTTTCC	AACTGAGCTGTATGGTGGACG
BMS2177	9	TTGCTAATGCAAATGTGTATGTG	GATCATGTCATCTGTGAAAAAAGA
BMS2614	10	ACTTTCTTTTCCTGTGGCTCG	CAGAGCTGGCACCAGAGG
CSSM038	10	TTCATATAAGCAGTTTATAAACGC	ATAGGATCTGGTAACTTACAGATG
BM827	11	GGGCTGGTCGTATGCTGAG	GTTGGACTTGCTGAAGTGACC
ILSTS028	11	TCCAGATTTTGTACCAGACC	GTCATGTCATACCTTTGAGC
BMS1316	12	CCTTCATGGAAGAAATTTTGTG	GGAGTTACAGTCCATGGGTTC
ILSTS059	13	AGTATGGTAAGGCCAAAGGG	CGACTTGTGTTGTTCAAAGC
BL1029	14	CAAATCAGCCTCTCCTCTTCC	GTGCTTCCAGAGACAATAAAGG
BMS2533	15	TGAAGTAAGTAAGCACACAAGCA	TTGATCATCTTTAGGTCCATCC
BM719	16	TTCTGCAAATGGGCTAGAGG	CACACCCTAGTTTGTAAGCAGC
ILSTS023	17	TCTAGAAGGCTGGGACTTGG	AGATTTCTGAAGTAGGGACC
INRA063	18	ATTTGCACAAGCTAAATCTAACC	AAACCACAGAAATGCTTGGAAG
BMC1013	19	AAAAATGATGCCAACCAAATT	TAGGTAGTGTTCCTTATTTCTCTGG
BMS745	19	TAGGGACTTGTTACCCGTGG	TGCAAGCTGTGAGGAGGAG
BMS1282	20	ACTCTTCCACAGTTGGCCTG	CCTCCTTCCTCCAGAGCC
IDVGA-45	21	GTGGTGGCAAAGAGTCAGA	AACAGCCCTGATTTCCATA
BM2613	22	AAGGAGAACCTCCATCCCTG	ATGGACAGAGGAACCCAGTG
BMS468	23	GTTAAGCAGAGGGTTTCCCC	TATTCCCAGGTGCTCTGAGG
BP28	25	AGGTGACAGGTGAGAGGGC	CCTCCACAACACCATCCTTC
CSSM036	27	GGATAACTCAACCACACGTCTCTG	AAGAAGTACTGGTTGCCAATCGTG
BMS510	28	TGCTGCATGATTCTCATTCC	AGCCTTCCTGTTCTCTGCTG
RM044	29	AAAGTGTTGGACATGACTGAAT	TTAACAATTAGCAACAGGAATAGG

Semen samples from three Hereford bulls (Huth Enhancer 2D, Gerber Killarney 058K, and LCG Master Duty 51J) were purchased from ABS Global. These three bulls were chosen simply because they have been approved for export to South Africa. The DNA from these bulls was genotyped with other samples at both the ARC and Fort Keogh to provide a basis for uniform scoring of genotypes in both laboratories.

6.2.3 Statistical Analysis

The program STRUCTURE (version 2.3.2; Pritchard *et al.*, 2010) was used to analyze the genotypic data. STRUCTURE is a software package developed to investigate population structure using multi-locus data. This was done separately for the two different countries, comparison of Line 1 Hereford bulls to the U.S.A. Hereford population and the comparison of Line 1 Hereford to the South African population. STRUCTURE can infer the presence of distinct populations; probabilistically assign individuals to populations while studying hybrid zones, identify migrants and admixed individuals and estimate population specific allele frequencies when many individuals are migrants or admixed.

STRUCTURE analyses of the U.S. Hereford cattle contained 551 individuals, with 33,154 polymorphic loci, a burn-in period of 10,000, and data sampled from run lengths of 20,000 to 100,000. These analyses were conducted using SNP from combined loci for samples from Line 1 and the U.S. Hereford cattle. Of these individuals Line 1 Hereford represented 240 animals. The standard STRUCTURE release for 32-bit machines was not able to properly analyze the extremely large dataset. Source code was downloaded and recompiled to run on a 64-bit machine and the command-line version of STRUCTURE was used. Individual animals were identified *a priori* as being in two clusters: Line 1 Hereford or rest of the United States Hereford population. Later the STRUCTURE parameters were set to assume a specific number of populations (k=2) so as to assign animals to membership groups. The program attempts to define each animal's probability of membership in a population, which may vary across independent samples (Pritchard and Cox, 2002). Following a burn-in of 10,000 samples, the run length was set at 100,000 samples. Pritchard *et al.* (2000a) and Pritchard *et al*. (2010) suggested that a great number of burn-in samples prior to collection of data minimized the effect of starting configuration and increasing the number of rounds of data collection improved accuracy of the parameter estimates. Resulting correspondance between genomic and pedigree relationship was assessed by linear regression.

STRUCTURE analysis of Line 1 and South African Hereford consisted of individual animals being identified *a priori* as being in two clusters: Line 1 and South African Hereford cattle. The program attempts to define each animal's probability of membership in both clusters, which may vary across independent samples (Pritchard and Cox, 2002). Following a burn-in of 10,000 samples, the run length was set at 200,000 samples. For samples from South Africa, the average probability of their membership in the Line 1 cluster was interpreted as a measure of their genetic relationship of these animals to Line 1 Hereford.

STRUCTURE implements a Bayesian model-based clustering method for inferring population structure using genotype data consisting of unlinked markers (Prichard *et al.*, 2000b; Falush et al., 2003, 2007; Pritchard *et al.*, 2010). STRUCTURE has several models to choose from in which to analyze data and for this project an independent allele frequency model was used. This model assumes allele frequencies are independent draws from a population-specific distribution. This is the original model used by Pritchard *et al*. (2000a). It works well for many data sets in that allele frequencies in the different populations are expected to be reasonably divergent from each other (Pritchard *et al*., 2010).

6.2.4 Pedigree Analysis

A similar approach was taken here relative to that used previously (Chapter 4) to assess the relationship between the U.S. Hereford population and Line 1 Hereford cattle from Fort Keogh. Pedigree data of 4,491 animals born since 1938 were obtained from the South African Hereford Society. The intent was to estimate the relationship of Line 1 Hereford cattle among cattle recorded in South African databases. However, records from the South African Hereford Society were not well connected to records of the American Hereford Association. The lack of cross-referencing between cattle recorded by the South African Hereford Society versus those recorded by the American Hereford Association compromised use of the South African Hereford Society database in calculating pedigree relationship to Line 1.

Individual animals from South Africa were each checked for membership in the American Hereford Association database by searching for their registered name, and if registered by the American Hereford Association their corresponding registration number was recorded. These registration numbers are important and provided a basis for comparison against the United States Hereford population. The number of animals resulting from the cross reference check was 1,972 animals with known American Hereford Association numbers.

In the event these extended pedigrees did not have data available through 1960, yet the animal was descended from the Hereford population in the United States and additional records were obtainable to this point, then these extended pedigrees were completed as best as possible. The resulting pedigrees generated from the Hereford cattle from South Africa contained 9,877 records.

The resulting datasets with American Hereford Association registration numbers were then pseudo-mated to Line 1 Hereford sires used at Fort Keogh from 1958 to present. Inbreeding coefficients were then calculated for the "offspring" resulting from these "matings" using the algorithm developed by Henderson and Quaas (1976). The relationship of Line 1 to each animal sampled from these countries was taken to be twice the maximum inbreeding coefficient for the set of Line 1 sires used in the pseudo-matings.

6.3 RESULTS AND DISCUSSION

6.3.1 Line 1 Hereford to U.S.A. Hereford cattle population

Each sample from the Line 1 Hereford and U.S. industry Hereford cattle was genotyped for 52,156 SNPs, 17% of the SNPs can be attributed to Line 1 Dominette 01449 and her sire. Ninety-six percent of the SNPs had < 0.1% missing genotypes and

SNPs that were missing for more than 3% of the samples were not used. All animals had <0.5% missing genotypes. SNPs that didn't have chromosomal or position information in UMD3.1[8] map also were not used. Twenty-two percent of the SNP were fixed in these samples.

Animals identified *a priori* as belonging to Line 1 were grouped in cluster 1 with an average probability of membership >0.98, standard deviation of 0.053 and standard error of 0.0034. The U.S. industry Hereford cattle had varying probabilities of membership in the Line 1 cluster and the non-Line 1 cluster. The average probability of their membership in the Line 1 cluster was distributed on the interval from 0.00 to 1.00 with mean = 0.20 and median = 0.14, with standard deviation of 0.25 and standard error of 0.0144. For the five bulls having greatest probability (> 0.89) of membership in Line 1, nine of their ten collective parents were from the Line 1 Hereford herd at Fort Keogh. The tenth parent was linebred to members of the Line 1 Hereford herd.

Pedigree relationship of the 311 Hereford bulls sampled from the U.S. industry with Line 1 was distributed on the interval 0.00 to 0.50 with mean = 0.08 and median = 0.04. Shown in Figure 6.1 is the relationship between probability of membership in the Line 1 cluster that was inferred using STRUCTURE and the pedigree relationship of the animals that were assumed to represent the U.S. industry with Line 1 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 Line 1 on pedigree relationship for 311 observations was 0.65 with a standard error of 0.19. The trend-line suggests general agreement between relationships indicated based on genomic

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[8] Available in GenBank; http://www.ncbi.nlm.nih.gov/projects/genome/guide/cow/

and pedigree data. However, the scattering of points along the x-axis indicating relatively high degrees of pedigree relationship without support from the genomic data are problematic.

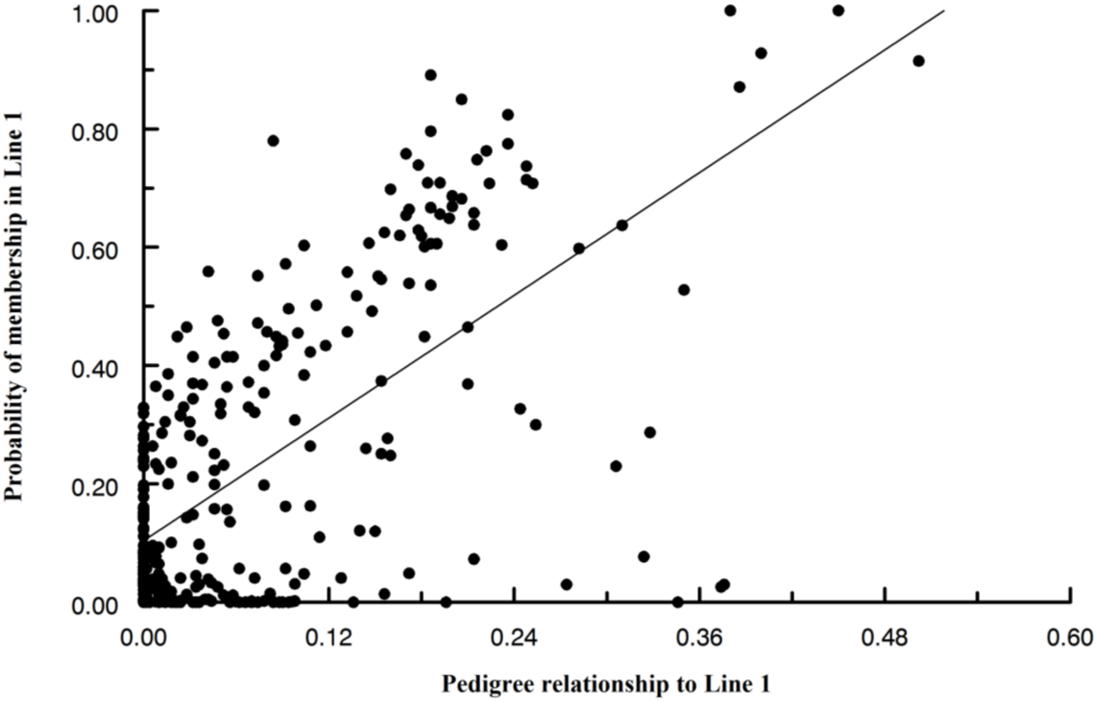

Figure 6.1 Correspondence of pedigree relationship and probability of membership in Line 1 Hereford population at Fort Keogh, Miles City, Montana, U.S.A.

Individuals that depart from the general relationship may be interesting case studies. In particular, individuals having disparate pedigree relationship and probability of membership may reflect error in pedigree recording or less than adequate sampling of the population for pedigree analysis. This could suggest that the extended pedigree data available do not contain or contain few ancestral animals for disparate animals. The readily available dataset from the American Hereford Association contains most recently registered animals and their contingent of extended pedigree and ancestral animals that are of specific interest and demand to the general populace. Ancestral animals that do not have much influence within the current population are archived so that space is available for servers to maintain data of animals of most interest and value to breeders.

6.3.2 Line 1 Hereford to South African Hereford genetic population

The probability of membership in Line 1 was calculated for Hereford cattle sampled from South Africa (Figure 6.2). This probability was distributed on the interval 0.23 to 0.58, with mean and median = 0.38 and standard deviation = 0.08.

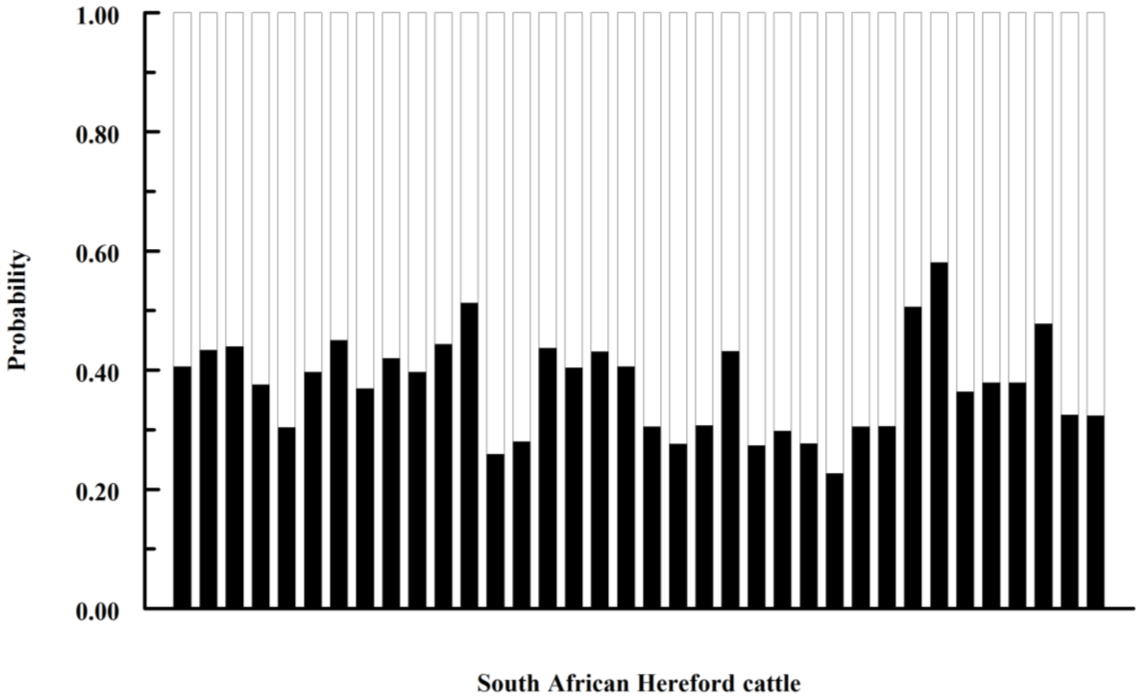

Figure 6.2 Probability of Hereford cattle sampled from South Africa being members of the Line 1 Hereford population from Fort Keogh.

These results are consistent with the method developed and tested by Pritchard *et al.* (2000b) that demonstrates animals can be accurately clustered in their appropriate populations and subpopulations with a modest number of loci. However, problems arise where breed associations do not have strong ties to breeders and vice versa. Samples for genotyping can be collected quickly and relatively easily at any stage of an animal's life; however, breeders may lack the necessary skills or resources to do so.

In interpreting these results, it is important to bear in mind that the probability of membership in Line 1 is not assessed on the same scale as a pedigree derived relationship, nor are the two statistics strictly proportional to each other. Probability of membership has to deal with the measure of how likely an animal could belong to a particular population, in this case based upon the molecular genetics SNP data. Pedigree data on the other hand actually refers to a lineage or genealogical descent. These two statistics can be compared but are not products of each other. This agrees with Rosenberg *et al.* (2002) that suggests an overall similarity of populations is evident given the geographically widespread nature of most alleles. Given these results it leads us to suggest that while understanding alleles are widespread around the world, it could be common that breeds of cattle could all contain a certain subset of similar genes and alleles. Numerous studies have used microsatellite markers to describe the relationships between breeds and if possible their history as well (MacHugh *et al.*, 1994; 1998; Ciampolini *et al.*, 1995; Moazami –Goudarzi *et al.*, 1997; Kantanen *et al.*, 2000; Beja-Pereira *et al.*, 2003). The ability to conduct molecular genetic analyses around the globe can identify these differences and similarities. However, the ability to predict or present lineage data and pedigree relationship that can be compared to this molecular data is much more difficult due to proprietary beliefs held by breeders, breed associations, etc.

6.3.3 Line 1 Hereford to South African Hereford pedigree population

The initial file of 4,491 animals from South Africa contained 1,972 animals with a known American Hereford Association registration number. This equates to 44% of the South African population having direct pedigree ties to American Hereford cattle. The extended pedigree of these 1,972 animals contained an additional 9,877 records, with 14,647 unique animals. Of these 14,647 animals 1,990 have a non-zero inbreeding coefficient for their pseudo-progeny resulting from matings to Line 1 Hereford, thus indicating some relationship. Thus, it may be concluded that approximately 14% of Hereford cattle in South Africa have pedigree relationships to the Line 1 Hereford cattle. This result agrees with a statement by a semen sales representative who exports Hereford genetics to South Africa, U.S. Hereford cattle genetics are consistently being exported to South Africa every year as has also been the case for at least the past 25-30 years (Cox, personal communication).

Many large scale genetic evaluations involve animals with incomplete pedigrees (Lutaaya *et al.*, 1999). Regular inbreeding algorithms based on the definition by Wright (1922) and Quaas (1976) calculate the relationship of animals with at least one parent missing as zero. Even if both parents are known, inbreeding could be underestimated if some of their ancestors are unidentified. If the proportion of missing ancestors or parents is large the relationship trend could be seriously underestimated for a population (Lutaaya *et al.*, 1999). This could lead to losses in relationship estimation, thereby underestimating animals that are more or less related to a general or specific population. Much of the pedigree information gathered from these animals resulted in some incomplete or missing ancestral information. The database used for comparison from the American Hereford Association is practically complete through 1960 with millions of records. The corresponding pedigree from South Africa is much smaller, although comprehensive and highly informational.

Yet, the sheer volume of the American Hereford database as compared to the South African database leads to interesting concerns. Essentially this was a pedigree analysis of the entire South African Hereford population, given the entire recorded history of the Hereford bred in South Africa in 4,491 animals. These records are not published online and the South African Hereford association recognizes 81 animals as being original to the American Hereford Association. If this were the analysis used then only 2% of the population would have any connection to the Hereford cattle in the U.S. By searching each individual animal to cross reference the two databases allowed for a larger, more complete, extended pedigree and substantially more informative results.

Analysis for South Africa showed the greatest relationship to Line 1 of all other analyses conducted so far. The average relationship between the South African Hereford population and the Line 1 herd at Miles City, MT USA was 10.6%. The level of inbreeding of pseudo-progeny of those animals related to Line 1 Hereford cattle was 0.12 or their relationship was 24%; which is approximately equivalent to having a grandparent from Line 1. Inbreeding of the pseudo-progeny resulting from mating Line 1 Hereford cattle to South African Hereford cattle was distributed on the interval 0.00 to 0.41; with 139 South African Hereford cattle having a relationship to Line 1 greater than 70%.

6.4 Summary of South African analysis

Pedigree relationship of South African Hereford cattle returned a 24% relationship to Line 1 Hereford while the association of genotyped data was 38%. A pedigree is a convention by way to track genetic traits to derive genotypes. If 24% of the 38% of the genotyped traits are directly related to the pedigree relationship of Line 1 Hereford cattle then the remaining difference may highlight more common traits among the Hereford breed as a whole rather than segregating them for or against the Line 1 Hereford cattle. Zhang *et al.* (2007) quantified genomic relationships from single nucleotide polymorphisms (SNP) with genomic prediction of breeding values. The availability of these SNP, being very dense molecular markers, has created opportunity for genomic selection (Meuwissen *et al.*, 2001). A SNP analysis of the South African sires used to generate the genetic distance molecular traits compared to the previous SNP analysis of U.S. Hereford sires could prove much more informative and definitive for this analysis.

CHAPTER 7

PEDIGREE ANALYSIS OF INFLUENTIAL SIRES IN THE UNITED KINGDOM, AUSTRALIA, AND URUGUAY

7.1 INTRODUCTION

More than 5 million pedigree Hereford cattle currently exist in over 50 countries. The export of Hereford cattle from Great Britian began in 1817, spreading throughout the United States and Canada, and then through Mexico to the beef raising areas of South America. Today, Hereford cattle are found around the world in Australasia to Russia, Israel, Japan, and throughout Scandinavia and continental Europe (Figure 7.1). The growth and spread of the breed led to the formation of the World Hereford Council in 1951, they deal globally with concerns of common interest to pedigree Hereford breeders (Hereford Cattle Society, 2011).

Hereford genetics from the United States have been shipped all over the world. There is also an increased interest in across country genetic evaluation of beef cattle in order to increase accuracy of prediction and to enhance the worldwide marketing of germplasm (de Mattos *et al.*, 2000). Thus, due to the influence of Line 1 Hereford cattle from Fort Keogh on the U.S. Hereford population, the spread and scope of the Line 1 could be far reaching and provide genetic connectedness in international evaluation. Their impact and effect is important to research and it has surely been felt. What has been the international influence and impact of Line 1? Documenting the flow of genetic material from Line 1 Hereford cattle to the United Kingdom, Australia and Uruguay will provide some insight in addressing this question. Thus, the objective of this chapter was to estimate the relationship between influential sires in the herd books of Australia, the United Kingdom and Uruguay with the Line 1 Hereford cattle at Fort Keogh Livestock and Range Research Laboratory.

Figure 7.1 Geographic regions where Hereford cattle are used extensively.

7.2 MATERIALS AND METHODS

It was infeasible to obtain complete Hereford herdbooks from the United Kingdom, Australia, and Uruguay. Thus, a different approach was taken here relative to that used previously (Chapter 4) to assess the relationship between the Hereford populations in the United Kingdom, Australia, and Uruguay to the Line 1 Hereford cattle from Fort Keogh. Online Hereford databases maintained by The Hereford Cattle Society (United Kingdom), Herefords Australia, and American Hereford Association (Uruguay), respectively were queried for sires of calves born between 1984 and 2010 and whose weaning weight evaluation had high accuracy. High accuracy sires have more progeny than those sires with an EBV of lower accuracy and thus contribute more genetically to the respective population. Sires from the United Kingdom and Uruguay were selected for a minimum weaning weight accuracy of 82% resulting in 159 and 101 sires, respectively. Sires from Australia were selected for a minimum weaning weight accuracy of 92% resulting in 155 sires.

The extended pedigree (through 1960 if possible) for each of these sires was then collected from the appropriate online database so as to obtain a similar point of reference to the records used in the evaluation of the U.S. Hereford population to which they would be analyzed against. Individual animals were each checked for membership in the American Hereford Association by searching for their registered name, and if registered by the American Hereford Association their corresponding registration number was recorded. These registration numbers are important and provided a basis for comparison against the United States Hereford population.

In the event these extended pedigrees did not have data available through 1960, yet the animal was descended from the Hereford population in the United States and additional records were obtainable to this point, then these extended pedigrees were completed as best as possible. The resulting pedigrees generated from the country specific databases contained 3,751 animals from the United Kingdom, 7,076 animals from Australia, and 423 animals from Uruguay.

The resulting country-specific datasets with American Hereford Association registration numbers were then pseudo-mated to Line 1 Hereford sires used at Fort Keogh from 1958 to present. Inbreeding coefficients were then calculated for the “offspring” resulting from these “matings” using the algorithm developed by Henderson and Quaas (1976). The relationship of Line 1 to each animal sampled from these countries was taken to be twice the maximum inbreeding coefficient for the set of Line 1 sires used in the pseudo-matings.

7.3 RESULTS AND DISCUSSION

The initial pedigree for 159 genetically influential sires from the United Kingdom obtained 3,751 animals (Table 7.1). Individually verifying each animal’s presence in the American Hereford Association database resulted in 1,498 animals that were also registered in the United States. Consequently, 40% of the Hereford cattle in the pedigree of influential sires in the United Kingdom have a representative relationship to Hereford cattle in the United States. The pedigree of the 154 genetically influential sires in Australia returned 7,076 animals and 1,769 of them were registered by the American Hereford Association. Accordingly, approximately 25% of these animals were represented among the Hereford cattle in the United States. Finally, the 101 genetically influential sires from Uruguay had 423 animals in their pedigree, with 318 of them having an American Hereford Association registration number. Thus, 75% of them have some pedigree relationship to Hereford cattle in the United States. These data are summarized in the Table 7.1.

Table 7.1 Number of foreign sires with pedigree results

Country	Number Of Sires	Initial Pedigree Size	USA American Hereford Association Registration	% USA Hereford
United Kingdom	159	3751	1498	40%
Australia	155	7076	1769	25%
Uruguay	101	423	318	75%

Table 7.2 summarizes the analyses of the extended pedigrees of influential sires from each country and numbers of animals in these pedigrees that had some relationship to the Line 1 Hereford cattle from Fort Keogh. There is a potential for bias using the greater amount of information available from the American Hereford Association database as compared to online Hereford datasets from other countries. It may be that animals less related to the current United States Hereford population are less likely to be available in the online American Hereford Association dataset. This is due to the fact that the American Hereford Associations total archive contains over 26 million records (Sanders, personal communication). However, only 14 to 16 million records are available over the World Wide Web, these available records are related to most recent registrations and animals of greater influence to the current Hereford population in the United States. Animals that are not queried over periods of time are removed from the

online database, but are maintained in the greater historical archive, which is available to the general public per request.

Table 7.2 Foreign pedigree analyses as compared to American Hereford Association and Line 1 Hereford databases.

Country	USA American Hereford Association Registration	% USA Hereford	N of animals in American Hereford Association derived Pedigree	Line 1 Hereford	% Line 1 Fx
United Kingdom	1498	40%	3207	720	22%
Australia	1769	25%	3584	1070	30%
Uruguay	318	75%	3221	756	23%

The 1,498 animals from the pedigree of influential Hereford sires in the United Kingdom with known American Hereford Association registration numbers resulted in a complete pedigree of 3,207 animals registered through 1960. This completed the pedigrees as accurately as possible and of these 720 could be directly traced to the Line 1 Hereford cattle at Fort Keogh. Thus, it may be concluded that approximately 22% of Hereford cattle in the United Kingdom have pedigree relationship to the Line 1 Hereford cattle.

The 1,769 animals from the pedigree of influential Hereford sires in Australia with known American Hereford Association registration numbers resulted in a pedigree of 3,584 animals with 1,070 being traceable to the Line 1 Hereford cattle at Fort Keogh. As a result, 30% of the animals in the pedigree of influential sires in Australia have some pedigree relationship to the Line 1 Hereford cattle. This result agrees with a statement by a breeder and producer in Australia that there was a large influx of Line 1 genetics into

Australia in the early 1980’s by large groups of breeders working together to import some of the top genetics at the time (Neilson, personal communication).

The 318 animals from the pedigree of influential Hereford sires in Uruguay with known American Hereford Association registration numbers resulted in an extended pedigree of 3,221 animals with 756 traceable to the Line 1 Hereford cattle at Fort Keogh. Thus, 23% of Hereford cattle in Uruguay have some pedigree relationship to Line 1 Hereford cattle. Uruguay’s online sire summary is not very complete, in many cases pedigree information is missing in total or in part. Extended pedigrees are also sparsely populated in the online database. Because of the connection with the American Hereford association and the ability to cross reference the two databases it allows for a larger, more complete, extended pedigree. However, the large amount of missing data from the Uruguay Hereford sire summary could suggest a deeper pedigree could mean very different results.

Many large scale genetic evaluations involve animals with incomplete pedigrees (Lutaaya *et al.*, 1999). Regular inbreeding algorithms based on the definition by Wright (1922) and Quaas (1976) calculate the relationship of animals with at least one parent missing as zero. Even if both parents are known, inbreeding could be underestimated if some of their ancestors are unidentified. If the proportion of missing ancestors or parents is large the relationship trend could be seriously underestimated for a population (Lutaaya *et al.*, 1999). This could lead to losses in relationship estimation, thereby underestimating animals that are more or less related to a general or specific population. Much of the pedigree information gathered from these three countries resulted in incomplete or missing ancestral information. The database used for comparison from the

American Hereford Association is practically complete through 1960. The corresponding country databases would often return incomplete information 10 to 20 or even 40 years different from 1960. That amount of data loss could result in possibly generations of missing data, effectively altering the true relationship calculable. For these reasons the country-specific pedigrees that contained animals registered with the American Hereford Association were subjected to completing the pedigrees as best as possible through 1960 so that analyses would result in a fair and accurate representation of relationships.

Calculating the inbreeding coefficients was the final analyses conducted. These results are presented in Table 7.3.

Table 7.3 Pedigree analysis of Hereford cattle from three countries for relationship with Line 1 Hereford cattle

Country	Line 1 Hereford	% Line 1 Fx	Avg Fx %L1	Parent Relation	Avg FX ALL	Parent Relation	Low Fx L1	High Fx L1
United Kingdom	720	22%	0.106	21%	0.024	5%	0.0011	0.39
Australia	1070	30%	0.116	23%	0.035	7%	0.0006	0.43
Uruguay	756	23%	0.106	21%	0.025	5%	0.0021	0.43

Individual analysis for each country comparably showed similar high levels of inbreeding along with South Africa, versus all other analyses conducted so far as related to the Line 1 Hereford cattle. The level of inbreeding for those animals related to Line 1 Hereford cattle was 0.106 for the United Kingdom and Uruguay, and 0.116 for Australia, or conversely the parental relationship was 21% and 23% which is traceable to at least a great-grandparent. The level of inbreeding compared to all Hereford cattle in the United States was 0.024, 0.025, and 0.035 for the United Kingdom, Uruguay, and Australia, respectively. Parental relationship was 5%, 5%, and 7%, which is traceable to at least a great-great grandparent. The highest level of inbreeding noted for each country was 0.43 for Australia and Uruguay and 0.39 for the United Kingdom.

7.4 SUMMARY

These results indicate that through the transfer of genetic material, via live animals, semen, or embryos the Line 1 Hereford has been able to contribute genetically to cattle herds around the world. While most of these cattle are not direct descendants of Line 1, a relationship to the Line 1 genetics through pedigree evaluation is possible, thereby establishing their genetic contribution. While these results were based upon analysis of high accuracy sires in their respective countries, should larger datasets be acquired there is speculation that the relationships could be deeper and extend further into history as animals could conceivably be traced back to animals maintained in the first Hereford Herdbook.

CHAPTER 8

SUMMARY OF RESULTS, IMPLICATIONS

The Line 1 Hereford population was developed in isolation in Miles City, Montana with no outside genetic influence for a period of more than 75 years. However, due to annual production sales Line 1 Hereford genetics can be found the world over. The following is a summary of the results and interesting notations from the various chapters of this thesis.

1. Since the earliest recorded sale of cattle from Fort Keogh, it is noted that purchases of Line 1 and other lines of cattle have been to producers in 34 States and 5 Canadian provinces.
2. Hereford cattle that are related to Line 1 were found in nearly every state, except Alaska and Rhode Island.
3. Since 1955, adjusted for inflation, sales of Line 1 Bulls and Heifers have generated $12,670,253.76.
4. In 2010, an estimated 81% of Hereford cattle in the US were related to the Line 1 Hereford cattle at Fort Keogh; and the number of animals that are related to Line 1 is currently increasing at an annual rate of approximately 2%.
5. References to Line 1 Domino and Line 1 Dominette were found in most pedigrees of Hereford cattle from several countries where a Web-based database is available.

6. Proportion of Hereford cattle related to Line 1 as estimated using pedigree analysis, by country, is:
    - United States – 81%
    - Canada – 8%
    - South Africa – 24%
    - United Kingdom – 22%
    - Australia – 30%
    - Uruguay – 23%
7. Affiliation of molecular markers between Line 1 Hereford cattle and Hereford cattle in South Africa resulted in an estimated 38% relationship.

Through these results it is apparent the Line 1 Hereford cattle from Miles City, MT U.S.A. have influenced Hereford cattle around the world; as such, it is recommended that Line 1 provided genetic connectedness for international genetic evaluation systems. The apparently successful migration of Line 1 genetics from Montana provides an interesting counterpoint to the usual experience in exporting germplasm to regions where its adaptation is questionable. It is recommended that follow-up studies be conducted to determine mechanisms that underlie local adaptability; particularly since Line 1 Hereford cattle seemingly provide a model for these studies. Furthermore, research into breed development could prove insightful, considering Hereford cattle were developed in Great Britain and exported globally. In recent times it appeared Hereford cattle genetics in the United States were being driven by single herd or small groups of herds. Exportations back to Great Britain have seemingly changed Hereford cattle genetics at their origin.

CHAPTER 9

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APPENDIX A

Table A-1 Genetic analysis of Line 1 Hereford relationship to chosen calves utilizing effective sample size – RUN 1

Year	**Sample**	**Freq**	**Fx_r**	**R_r, %**	**Fx_a**	**R_a, %**	**Min**	**Max**
1980	87	22%	0.060	12%	0.013	3%	0.0015	0.38
1981	104	26%	0.050	11%	0.014	3%	0.0014	0.29
1982	138	35%	0.050	9%	0.016	3%	0.0014	0.35
1983	169	42%	0.052	11%	0.022	4%	0.0014	0.30
1984	154	39%	0.051	10%	0.019	4%	0.0014	0.03
1985	157	39%	0.053	11%	0.021	4%	0.0006	0.39
1986	181	45%	0.048	10%	0.022	4%	0.0007	0.38
1987	185	46%	0.055	11%	0.026	5%	0.0023	0.37
1988	193	48%	0.046	9%	0.022	4%	0.0006	0.37
1989	209	52%	0.050	10%	0.026	5%	0.0003	0.31
1990	203	51%	0.042	8%	0.021	4%	0.0006	0.33
1991	168	42%	0.025	5%	0.011	2%	0.0022	0.12
1992	239	60%	0.042	8%	0.025	5%	0.0002	0.40
1993	215	54%	0.038	8%	0.020	4%	0.0002	0.21
1994	231	58%	0.047	9%	0.027	5%	0.0001	0.39
1995	248	62%	0.038	8%	0.024	5%	0.0001	0.25
1996	243	61%	0.044	9%	0.026	5%	0.0001	0.34
1997	246	62%	0.046	9%	0.028	6%	0.0001	0.42
1998	249	62%	0.045	9%	0.028	6%	0.0001	0.34
1999	214	54%	0.034	7%	0.018	4%	0.0001	0.42
2000	264	66%	0.042	8%	0.028	6%	0.0001	0.24
2001	252	63%	0.042	8%	0.026	5%	0.0001	0.20
2002	259	65%	0.039	8%	0.026	5%	0.0001	0.32
2003	286	71%	0.042	8%	0.030	6%	0.0001	0.41
2004	271	68%	0.040	8%	0.027	5%	0.0001	0.39
2005	286	72%	0.040	8%	0.028	6%	0.0001	0.36
2006	309	77%	0.040	8%	0.031	6%	0.0001	0.40
2007	322	81%	0.039	8%	0.032	6%	0.0001	0.39
2008	313	78%	0.038	8%	0.029	6%	0.0001	0.41

Sample = Designates replicate of the experiment; Sample size = number of animals with pedigree relationship to Line 1;Freq = Frequency of animals in sample having non-zero relationship to Line 1; Fx_r = Mean of maximum inbreeding coefficient of a "progeny" resulting from the pseudo-mating of sampled animal to Line 1 sires, for the subset of sampled animals that were related to Line 1; $R_r = (2*Fx_r)*100$, i.e. the percentage relationship between Line 1 and those sampled animals that were related to Line 1.; Fx_a = Mean of maximum inbreeding coefficient of a "progeny" resulting from the pseudo-mating of all sampled animal to Line 1 sires; R_a = the percentage relationship between Line 1 and all sampled animals; Min and Max = minimum and maximum of distribution of Fx_r, respectively.

Table A-2 Genetic analysis of Line 1 Hereford relationship to chosen calves utilizing effective sample size – RUN 2

Year	Sample	Freq	Fx_r	R_r, %	Fx_a	R_a, %	Min	Max
1980	85	21%	0.045	9%	0.010	2%	0.0015	0.30
1981	130	33%	0.054	11%	0.018	4%	0.0011	0.29
1982	135	34%	0.052	11%	0.018	4%	0.0028	0.30
1983	133	33%	0.048	10%	0.016	3%	0.0007	0.29
1984	155	39%	0.050	10%	0.019	4%	0.0024	0.37
1985	174	44%	0.052	10%	0.023	5%	0.0012	0.31
1986	168	42%	0.056	11%	0.023	5%	0.0006	0.30
1987	187	47%	0.050	10%	0.023	5%	0.0023	0.40
1988	173	43%	0.046	9%	0.020	4%	0.0012	0.21
1989	209	52%	0.046	9%	0.024	5%	0.0005	0.38
1990	209	52%	0.043	9%	0.022	4%	0.0003	0.24
1991	207	52%	0.044	9%	0.023	5%	0.0002	0.31
1992	211	53%	0.040	8%	0.021	4%	0.0002	0.37
1993	231	58%	0.042	8%	0.024	5%	0.0004	0.24
1994	228	57%	0.050	10%	0.027	5%	0.0001	0.38
1995	251	63%	0.044	9%	0.027	5%	0.0001	0.25
1996	255	64%	0.048	10%	0.031	6%	0.0002	0.41
1997	258	65%	0.040	8%	0.026	5%	0.0001	0.19
1998	253	63%	0.042	8%	0.026	5%	0.0001	0.24
1999	262	66%	0.047	9%	0.031	6%	0.0001	0.42
2000	244	61%	0.047	9%	0.029	6%	0.0001	0.25
2001	241	60%	0.044	9%	0.027	5%	0.0001	0.35
2002	272	68%	0.042	8%	0.028	6%	0.0001	0.34
2003	277	69%	0.044	9%	0.030	6%	0.0001	0.40
2004	287	72%	0.041	8%	0.030	6%	0.0001	0.42
2005	287	72%	0.037	7%	0.026	5%	0.0001	0.41
2006	305	76%	0.037	7%	0.028	6%	0.0001	0.40
2007	300	75%	0.035	7%	0.026	5%	0.0001	0.35
2008	326	82%	0.032	6%	0.026	5%	0.0001	0.37

Sample = Designates replicate of the experiment; Sample size = number of animals with pedigree relationship to Line 1;Freq = Frequency of animals in sample having non-zero relationship to Line 1; Fx_r = Mean of maximum inbreeding coefficient of a “progeny” resulting from the pseudo-mating of sampled animal to Line 1 sires, for the subset of sampled animals that were related to Line 1; $R_r = (2*Fx_r)*100$, i.e. the percentage relationship between Line 1 and those sampled animals that were related to Line 1.; Fx_a = Mean of maximum inbreeding coefficient of a “progeny” resulting from the pseudo-mating of all sampled animal to Line 1 sires; R_a = the percentage relationship between Line 1 and all sampled animals; Min and Max = minimum and maximum of distribution of Fx_r, respectively.

Table A-3 Genetic analysis of Line 1 Hereford relationship to chosen calves utilizing effective sample size – RUN 3

Year	Sample	Freq	Fx_r	R_r, %	Fx_a	R_a, %	Min	Max
1980	111	28%	0.062	12%	0.017	3%	0.0011	0.31
1981	112	28%	0.062	12%	0.017	3%	0.0028	0.39
1982	154	39%	0.056	11%	0.022	4%	0.0028	0.28
1983	152	38%	0.063	13%	0.024	5%	0.0028	0.32
1984	166	42%	0.071	14%	0.030	6%	0.0022	0.34
1985	177	44%	0.057	11%	0.025	5%	0.0012	0.34
1986	175	44%	0.049	10%	0.022	4%	0.0012	0.20
1987	194	49%	0.045	9%	0.022	4%	0.0012	0.39
1988	188	47%	0.047	9%	0.022	4%	0.0006	0.34
1989	193	48%	0.042	8%	0.020	4%	0.0003	0.23
1990	221	55%	0.047	9%	0.026	5%	0.0009	0.41
1991	219	55%	0.045	9%	0.025	5%	0.0006	0.42
1992	219	55%	0.042	8%	0.023	5%	0.0002	0.35
1993	250	63%	0.039	8%	0.025	5%	0.0002	0.36
1994	249	62%	0.043	9%	0.027	5%	0.0001	0.23
1995	233	58%	0.042	8%	0.024	5%	0.0001	0.035
1996	239	60%	0.044	9%	0.026	5%	0.0001	0.24
1997	250	63%	0.050	10%	0.031	6%	0.0001	0.38
1998	273	68%	0.043	9%	0.029	6%	0.0001	0.34
1999	257	64%	0.041	8%	0.026	5%	0.0001	0.22
2000	261	65%	0.041	8%	0.027	5%	0.0001	0.23
2001	249	62%	0.045	9%	0.028	6%	0.0001	0.39
2002	274	69%	0.039	8%	0.026	5%	0.0001	0.32
2003	270	67%	0.044	9%	0.030	6%	0.0001	0.42
2004	285	71%	0.045	9%	0.032	6%	0.0001	0.39
2005	281	70%	0.044	9%	0.031	6%	0.0001	0.41
2006	308	77%	0.035	7%	0.027	5%	0.0001	0.33
2007	320	80%	0.038	8%	0.030	6%	0.0001	0.20
2008	324	81%	0.026	5%	0.021	4%	0.0001	0.35

Sample = Designates replicate of the experiment; Sample size = number of animals with pedigree relationship to Line 1;Freq = Frequency of animals in sample having non-zero relationship to Line 1; Fx_r = Mean of maximum inbreeding coefficient of a "progeny" resulting from the pseudo-mating of sampled animal to Line 1 sires, for the subset of sampled animals that were related to Line 1; $R_r = (2*Fx_r)*100$, i.e. the percentage relationship between Line 1 and those sampled animals that were related to Line 1.; Fx_a = Mean of maximum inbreeding coefficient of a "progeny" resulting from the pseudo-mating of all sampled animal to Line 1 sires; R_a = the percentage relationship between Line 1 and all sampled animals; Min and Max = minimum and maximum of distribution of Fx_r, respectively.

Table A-4 Genetic analysis of Line 1 Hereford relationship to chosen calves utilizing effective sample size – RUN 4

Year	Sample	Freq	Fx_r	R_r, %	Fx_a	R_a, %	Min	Max
1980	87	22%	0.043	9%	0.010	2%	0.0012	0.25
1981	123	31%	0.055	11%	0.017	3%	0.0021	0.41
1982	123	31%	0.039	8%	0.012	2%	0.0012	0.29
1983	136	34%	0.042	8%	0.014	3%	0.0003	0.28
1984	144	36%	0.044	9%	0.016	3%	0.0018	0.22
1985	167	42%	0.043	9%	0.018	4%	0.0009	0.31
1986	165	41%	0.042	8%	0.017	3%	0.0009	0.20
1987	167	42%	0.040	8%	0.017	3%	0.0002	0.30
1988	193	48%	0.039	8%	0.019	3%	0.0002	0.29
1989	187	47%	0.039	8%	0.018	4%	0.0004	0.20
1990	224	56%	0.037	7%	0.020	4%	0.0009	0.31
1991	207	52%	0.038	8%	0.020	4%	0.0002	0.41
1992	207	52%	0.036	7%	0.019	4%	0.0002	0.36
1993	221	55%	0.034	7%	0.019	4%	0.0002	0.36
1994	245	61%	0.037	7%	0.023	5%	0.0001	0.34
1995	251	63%	0.035	7%	0.022	4%	0.0001	0.36
1996	261	65%	0.036	7%	0.024	5%	0.0001	0.33
1997	266	67%	0.039	8%	0.026	5%	0.0001	0.40
1998	259	65%	0.036	7%	0.023	5%	0.0001	0.30
1999	255	64%	0.039	8%	0.025	5%	0.0001	0.38
2000	254	64%	0.040	8%	0.025	5%	0.0001	0.33
2001	252	63%	0.037	7%	0.023	5%	0.0001	0.36
2002	272	68%	0.033	7%	0.022	4%	0.0001	0.29
2003	277	69%	0.033	7%	0.023	5%	0.0001	0.39
2004	274	68%	0.034	7%	0.023	5%	0.0001	0.38
2005	298	75%	0.030	6%	0.022	4%	0.0001	0.21
2006	304	76%	0.035	7%	0.027	5%	0.0001	0.38
2007	326	82%	0.029	6%	0.023	5%	0.0001	0.35
2008	334	84%	0.034	7%	0.028	6%	0.0001	0.39

Sample = Designates replicate of the experiment; Sample size = number of animals with pedigree relationship to Line 1;Freq = Frequency of animals in sample having non-zero relationship to Line 1; Fx_r = Mean of maximum inbreeding coefficient of a "progeny" resulting from the pseudo-mating of sampled animal to Line 1 sires, for the subset of sampled animals that were related to Line 1; $R_r = (2*Fx_r)*100$, i.e. the percentage relationship between Line 1 and those sampled animals that were related to Line 1.; Fx_a = Mean of maximum inbreeding coefficient of a "progeny" resulting from the pseudo-mating of all sampled animal to Line 1 sires; R_a = the percentage relationship between Line 1 and all sampled animals; Min and Max = minimum and maximum of distribution of Fx_r, respectively.

Table A-5 Genetic analysis of Line 1 Hereford relationship to chosen calves utilizing effective sample size – RUN 5

Year	Sample	Freq	Fx_r	R_r, %	Fx_a	R_a, %	Min	Max
1980	90	23%	0.052	10%	0.012	2%	0.0024	0.37
1981	139	35%	0.043	9%	0.015	3%	0.0013	0.26
1982	147	37%	0.045	9%	0.017	3%	0.0012	0.31
1983	167	42%	0.047	9%	0.020	4%	0.0012	0.31
1984	170	43%	0.054	11%	0.023	5%	0.0005	0.30
1985	174	44%	0.056	11%	0.024	5%	0.0009	0.30
1986	176	44%	0.043	9%	0.019	4%	0.0007	0.21
1987	186	47%	0.044	9%	0.020	4%	0.0008	0.32
1988	205	51%	0.038	8%	0.019	4%	0.0002	0.31
1989	212	53%	0.034	7%	0.018	4%	0.0009	0.36
1990	197	49%	0.035	7%	0.017	3%	0.0004	0.30
1991	201	50%	0.040	8%	0.020	4%	0.0002	0.35
1992	243	61%	0.037	7%	0.022	4%	0.0002	0.36
1993	222	56%	0.037	7%	0.020	4%	0.0002	0.19
1994	270	68%	0.035	7%	0.023	5%	0.0001	0.29
1995	251	63%	0.037	7%	0.023	5%	0.0001	0.37
1996	240	60%	0.041	8%	0.025	5%	0.0001	0.33
1997	240	60%	0.038	8%	0.023	5%	0.0001	0.37
1998	231	58%	0.039	8%	0.022	4%	0.0001	0.37
1999	251	63%	0.041	8%	0.026	5%	0.0001	0.37
2000	275	69%	0.038	8%	0.026	5%	0.0001	0.35
2001	253	63%	0.032	6%	0.020	4%	0.0001	0.21
2002	268	67%	0.030	6%	0.020	4%	0.0001	0.24
2003	271	68%	0.035	7%	0.023	5%	0.0001	0.23
2004	277	69%	0.033	7%	0.023	5%	0.0001	0.33
2005	285	71%	0.033	7%	0.023	5%	0.0001	0.37
2006	297	74%	0.034	7%	0.025	5%	0.0001	0.38
2007	326	82%	0.037	7%	0.030	6%	0.0001	0.38
2008	328	82%	0.033	7%	0.027	5%	0.0001	0.39

Sample = Designates replicate of the experiment; Sample size = number of animals with pedigree relationship to Line 1;Freq = Frequency of animals in sample having non-zero relationship to Line 1; Fx_r = Mean of maximum inbreeding coefficient of a "progeny" resulting from the pseudo-mating of sampled animal to Line 1 sires, for the subset of sampled animals that were related to Line 1; $R_r = (2*Fx_r)*100$, i.e. the percentage relationship between Line 1 and those sampled animals that were related to Line 1.; Fx_a = Mean of maximum inbreeding coefficient of a "progeny" resulting from the pseudo-mating of all sampled animal to Line 1 sires; R_a = the percentage relationship between Line 1 and all sampled animals; Min and Max = minimum and maximum of distribution of Fx_r, respectively.

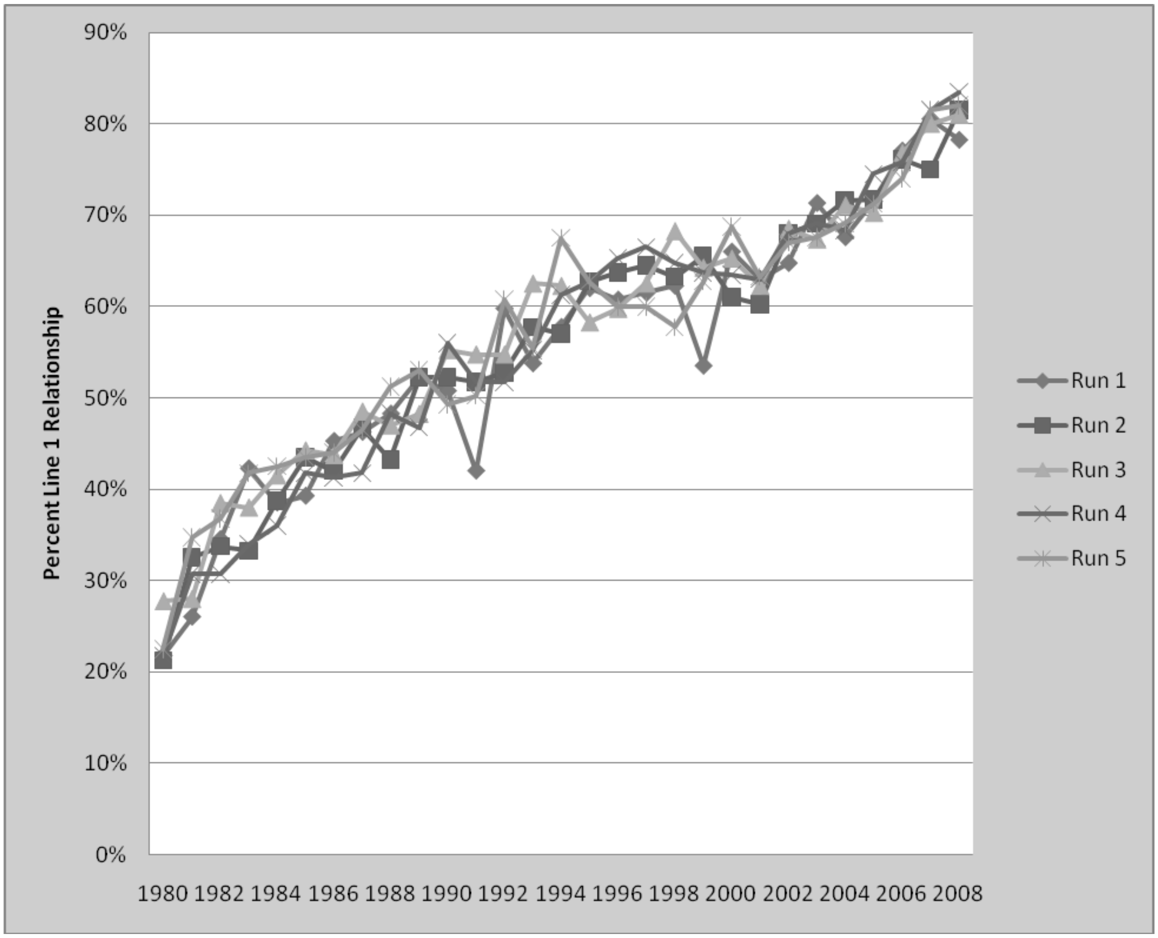

Figure A-1 Increasing genetic influences of Line 1 Hereford cattle 1980-2007 to entire population of Hereford cattle registered in the USA.

This figure is a graphical representation of the increasing genetic relationship Hereford cattle in the United States have with the Line 1 population. This graph is merger of all 5 of the individual runs. It is clear that the relationship has increased over these past 28 years. All the trend lines appear tangled up together, which indicates there is little deviation in the multiple runs. Every run produced a comparable result to earlier or additional analyses.