ABSTRACT

A GENETIC CHARACTERIZATION OF THE HAYS CONVERTER

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This thesis gives a genetic overview of the Hays Converter, a beef breed developed in Canada in the 1950s. Pedigree records were examined to determine genetic diversity and inbreeding. A positive rate of inbreeding and a decrease in the amount of genetic diversity was found. Single trait and bivariate animal models were used to determine genetic parameters and trends for growth, ultrasound, and carcass traits. An increasing genetic trend was found for growth traits which the breed was selected for. The accuracy of imputation from 6k to 50k marker panels using a reference group of 100 animals was determined. Imputation was performed with a high accuracy (>0.93) for pure Hays Converter animals, but was found to be unsuccessful when individuals had large contributions from additional breeds. This work forms the foundation for future management and advance of the breed while outlining its history and progress.
ACKNOWLEDGEMENTS

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CHAPTER 1

GENERAL INTRODUCTION

The Hays Converter breed of beef cattle, developed by Harry Hays, was the first breed of livestock developed in Canada by private interests to be recognized under the Livestock Pedigree Act. The ideas of Harry Hays were innovative and an example of an effort to transform the Canadian beef industry and improve beef cattle genetics to better fit the unique Canadian production environment. The breed is a noteworthy part of Canadian animal agricultural history due to its distinct formation, composition, and selection practices. There has been no previous examination of the Hays Converter breed’s genetic progression and current status. A genetic characterization of the breed is necessary to observe the progress the breed has made in the past, and to generate and advise potential selection strategies for the future.

The Hays Converter was developed at a time when animal movement into Canada was restricted due to concerns over animal health. Without the ability to import animals and breeds to meet market demands and improve Canadian beef cattle, Hays crossed specific individuals available in North America representing Hereford, Holstein, and Brown Swiss breeds. A composite, or synthetic breed, was formed which presents a practical alternative to crossbreeding production systems since after development, it can be managed as a purebred while still taking advantage of additive breed differences and breed complementarity (Dickerson, 1973). Breeds are said to be complementary to each other when they excel in different traits and their crossbred progeny have desirable levels of performance in a larger number of traits than either of the parent breeds alone (Weaber, 2009). The qualities of Hereford, Holstein, and Brown Swiss breeds were combined to produce a superior animal optimized to perform in the environment and markets of Western Canada.
The addition of dairy genetics into beef herds may present numerous advantages to beef producers for both maternal and growth traits. Dairy breeds have genetic potential for body size, milk yield, maturing rate, growth rate, leanness, fertility, calving ease, and gastrointestinal capacity (Cartwright, 1983). Large-bodied dairy breeds such as Holstein and Brown Swiss have been reported as having greater growth potential than the small-bodied British beef breeds (Cole et al., 1963). A study by Garcia-de-Siles et al. (1977) found Holstein steers were significantly heavier than the Hereford steers artificially raised in identical production environments at 280 and 365 days of age and exhibited greater growth rates. Dairy-beef crossbred and synthetic dams have been found to produce calves with greater pre-weaning growth rates and weaning weights (Butson and Berg, 1984; Basarab et al., 1986). These differences were largely attributed to increased milk production and persistency.

The level of genetic diversity present in the breed can have major implications on the selection strategies and the potential for further genetic improvement. A small number of foundation animals were used to create the Hays Converter. Three key individuals were the basis of a group methodically mated to a herd of foundation beef cows and their progeny. The small number of foundation animals and breeding animals throughout the breed’s history suggests the relationship between Hays Converter animals may be high and genetic diversity in the breed may be low. Knowledge of the amount of inbreeding and rate of inbreeding in the population is necessary for consideration in future selection strategies and management of the breed.

Key traits in the development of the Hays Converter were weaning and yearling weights, with the purpose of creating a fast and efficient growing animal. Carcass quality traits are becoming more important in the marketing of fed cattle. As a result, the genetic improvement of both growth and carcass quality traits is important for the future of the Hays Converter breed.
Genetic parameters for the Hays Converter have never been estimated prior to this study and are required to estimate genetic progress observed in the breed and determine the genetic worth of individuals.

The possible low level of genetic diversity and high relatedness of the Hays Converter population may become beneficial when genomic data are examined. Untyped markers on a high density marker panel can be determined for individuals genotyped using less expensive, low density marker panels through the method of genotype imputation using a reference population with high density genotypes (Weigel et al., 2010a). Genotype imputation has been found to be more accurate for animals with a high degree of relatedness to the reference population (Druet, 2010). Determination of imputation accuracy in the Hays Converter population with the use of a small reference population is required to conclude its value for future use in the breed.

This thesis provides a genetic overview of the Hays Converter breed. Chapter 2 describes the background and process of the breed’s creation and subsequent development. The pedigree was examined in Chapter 3 to determine the level of genetic diversity present in the breed and trends in inbreeding. Chapter 4 aims to estimate genetic parameters for traits of interest for the breed to compute estimated breeding values (EBV) for individuals and genetic trends. Genotypic data is studied in Chapter 5 to establish the potential of genotype imputation in Hays Converter cattle as well as the breed composition of individuals for possible future use in selection.
CHAPTER 2

HISTORY OF THE HAYS CONVERTER

The Hays Converter was the first beef breed developed in Canada to be recognized pursuant to the Canadian Livestock Pedigree Act and combines the genetics of the Hereford, Holstein, and Brown Swiss breeds. It was developed by the late Canadian Senator Harry Hays, a livestock producer, former Mayor of Calgary, AB, and Minister of Agriculture of Canada, to address a divide he believed existed between cattle breeders and the market demands. The Hays Converter was created to convert feed to gain as efficiently as possible in the rangelands of Western Canada.

The idea for a new breed of beef cattle had long been considered in the mind of Hays. Through decades of work as a livestock auctioneer, he observed the slow evolution of beef cattle in a direction opposite to what he felt consumers demanded. Hays believed that for a long time, beef breeders were regressing. At a time when hog producers had started breeding leaner animals, many beef breeders aimed to create fatter animals. In the 1930s and into the 1950s there was a trend toward breeding animals that were of an ultra-thick, deep type, which was mainly done by selecting for shortness of leg and body, resulting in lower body weights (Warwick, 1958). The winnings of the “comprest” Herefords and “compact” Shorthorns in the major steer shows furthered their selection, and forms of dwarfism started to appear (Stonaker and Tom, 1944; Stringam, 1958). A lot of purebred beef breeders were selecting largely on the way the cattle looked, and not on performance or carcass quality. Cattle were not able to be imported from Europe into Canada in the 1940s to 1960s because of fears of spreading disease, in particular foot and mouth disease. As a result, Hays was unable to bring in the Continental European breeds he admired and other cattle genetics to obtain animals he felt the Canadian market needed.
Hays wanted to create a breed that would be more like the cattle of the past and circumvent the period’s breeding tendencies using genetics then available in North America.

With little formal education, Hays relied on his vast personal experiences to come up with a plan for what would become his new beef breed. Not only had he spent his life thus far as a dairy farmer, rancher, cattle exhibitor, cattle exporter, and livestock auctioneer, he had also been president of the Canadian Swine Breeders, a founding member and president of the Alberta Poultry Breeders’ Association, and president of the Alberta Holstein Breeders’ Association. He drew ideas from his own observations and what he had learned from others.

Hays wanted to develop a breed of cattle that would have a higher percentage of lean meat, but most importantly, he wanted one that would be able to convert feed to gain as efficiently as possible. In order to develop the most efficient animal he could, Hays wanted to create a breed that would reach market weight at the earliest possible age. His reasoning for this came from his observations of human babies. He observed that in the first year of life, the human baby converts its food more efficiently than any other time of its life (Hays, 1980). Hays had also taken notice of the work of Donald Shaver. Shaver, a chicken producer and renowned breeder from Galt, ON, used the fact that chicks, like humans, converted their feed to growth most efficiently at the earliest stages of their lives. He noted that more meat from less feed was created in the first third of the chick’s twelve-week maturation period than at any other period of its life. Shaver mated two enormous birds with hopes to develop a line that would achieve a conversion rate of two pounds of feed to one pound of meat (Peacock, 1986). The thought for Hays’ cattle was that the greater the genetic background for size of the animal, the more weight it would gain during the most efficient first year of its life. Hays’ goal was therefore to breed an animal that
would convert feed to lean meat efficiently and reach the then desirable market weight of 1,100 lbs at the earliest age possible.

In Hays’ opinion, Shaver was able to break the purebred registration myth with his lines of chickens (Peacock, 1986). Shaver did not believe in using identified breeds where bad qualities could be locked in, and instead combined several breeds of chickens to create the bird he wanted. His lines of chickens were sold strictly on their performance. Hays relished this idea as he did not like what was happening with purebred cattle at the time. Purebred breeders concentrated too much on appearance in his opinion. Hays thought most beef producers were too concerned with colour, width between the eyes, tail settings, and depth of flank, while he believed that an animal’s ability to convert feed to meat should be the principal criteria for selection (The New Breed, 1969). By not confining himself to using a single breed, Hays would be able to get the positive characteristics he wanted from different breeds. He did not care what his beef cattle looked like; he would develop his breed guided by the objective measure of performance.

Another animal breeder and great Canadian geneticist Hays admired was Quebec Holstein breeder Thomas Bassett “T. B.” Macaulay (Hays, 1980). In the early 1930s, Hays had spent a lot of time with Macaulay listening to his views on cattle breeding. In addition to his work with Shetland ponies and soybeans, Macaulay completely made over the Holstein breed according to Hays, and essentially developed a breed within a breed (Hays, 1980). Macaulay taught Hays that if you wanted to change an animal and do it with the little time that you had on this earth, you would have to line breed and inbreed (Hays, 1980). Hays knew he would have to use line breeding, a type of inbreeding, to achieve his goals, and he was not afraid to do so. He noted that many wild animals and grains such as rye were products of brother-sister matings.
(Hays, 1980). When discussing the biblical adjurations against inbreeding Hays commented to reporters:

> These precautions might have been good guidelines for the preservation of nomadic peoples who wrote the Bible, but in cattle genetics they have no place. I mated the best families, father to daughter, son to mother, and other such incestuous combinations to bring out the best meat-producing characteristics possible. Look at Cleopatra – she was the result of four brother-sister matings and an uncle and a niece, and we’re still talking about her two thousand years later.

(Peacock, 1986)

To get the results he desired in the shortest time, Hays would plan on using line breeding and not concern himself with trying to maintain heterosis.

The plan for a new breed of beef cattle was soon set. Hays would develop a new breed of range cow with the hardiness to survive the harsh Canadian conditions like those encountered on his ranch in the foothills of the Rocky Mountains. The breed would have to combine quick, efficient gains with a large, rugged frame and good reproductive performance. Important characteristics were growth, fertility, calving ease, well-attached udders, abundant milk, sound feet and legs, and pigmentation. The goal was an animal that would efficiently convert feed to lean meat and reach market weight at approximately 12 months of age. Selection would be based only on performance, not on appearance or fads. He would call his new beef breed the Hays Converter for its ability to convert feed to gain.

Hays first began work planning the breeding procedures for the breed in 1952. The first step was to find the breeds and individual animals that exhibited the characteristics he wished to combine to form his new breed. The choice of foundation breeds is a fundamental part of
creating a composite. Large differences exist between breeds for most major economically important traits (Gregory et al., 1993). The selection of the foundation parental breeds should optimize the additive genetic composition to the production and climatic environment consistent with the production environment and market requirements of the composite (Gregory and Cundiff, 1980). Hays started by selecting a group of commercial Hereford cows from a neighbouring rancher, the then owner of the Bar U Ranch near Pekisko in southern Alberta, James “Allen” Baker. The Baker Herefords were a herd of smallish, very tough and fecund, “survival” Herefords well adapted to the western Canada rangelands (Jacobs, 1993). They were said to have been flourishing under a system of benign neglect and Baker himself often boasted that he had not fed his herd for 20 years while consistently achieving an 85% calf crop (Evans, 2004). He rid his herd of troublesome cows, and his bulls were selected with trouble-free calving in mind (Evans, 2004).

In 1954, Hays began looking for a big Holstein bull that would consistently sire big, rugged daughters with good udders. Hays knew the Holstein breed extremely well, as he was a top exporter of Canadian Holsteins and had previously run a dairy for 30 years, milking as many as 200 cows. At one point, it was one of the largest milking herds in North America and held numerous world records. He had always been impressed with the growth potential of the Holstein. In addition, Holstein genes would give greater milk production that a calf needs from its mother to permit maximum growth. Experience had shown Hays that the average beef cow did not produce a sustained supply of milk after the initial peak at the beginning of lactation (Peacock, 1986).

The Holstein bull he decided on was Spring Farm Fond Hope, specifically chosen for his unique structure within the Holstein breed. He was classified “Excellent” for conformation, yet
displayed unusual thickness within the breed. Fond Hope had a well-fleshed hindquarter and tended to be more of the type of the European Friesian than the Canadian Holstein (Ritchie, 2009). Fond Hope was champion at several shows in Canada and the United States, weighing approximately 3,000 lbs in good condition (Bailey, 1971). Fond Hope progeny were known for their large size, strong constitution, excellent feet, and outstanding udders (Ritchie, 2009). More than 1,100 of his daughters averaged over 4% butterfat on R.O.P. tests, and had an average milk production of approximately 12,000 lbs. More than 80% of all his daughters were in the three top brackets of Holstein classification.

Hays wanted greater milk production to increase weaning weights so he began by crossing beef and dairy. The Holstein blood would add gainability and milk production, while the Hereford blood would give better carcass characteristics, rapid maturity and ruggedness. In the fall of 1957, Hays mated eight Fond Hope sons to Baker’s herd of 700 Hereford females. An unknown number of polled Hereford and Angus females were also included in the foundation female herd. From this and a subsequent year of matings, Hays selected the best Holstein x Hereford heifers to be backcrossed to a Hereford bull. The 159 selected heifers were bred by artificial insemination to the big Canadian Hereford bull, Silver Prince 7P. Bred by legendary Hereford breeder Jim Hole of Airdrie, AB, Silver Prince added more size potential and early maturity to the herd. The Hole Herefords were widely respected as one of the best in Canada. Hole bred what he liked and his animals were never exposed to the numerous changes and fads that affected other breeding herds. He bred big, thick, heavy boned cattle. Silver Prince was a Certified Meat Sire, a classification given to bulls at the time with a minimum of ten progeny meeting or exceeding growth and carcass trait standards set by Performance Registry International in Joplin, MO. He weighed approximately 2,640 lbs in breeding condition and was
known to transmit size, length, bone and fleshing ability to his offspring. Silver Prince was the biggest Hereford bull Hays could find around at the time, and the better breeders for the most part called him a horse (Hays, 1980). Hays would have liked to have used a larger bull, but had to settle with what was available. From the resulting progeny of these matings, the top five fastest gaining bulls were saved and bred back to the 159 Holstein x Hereford females. All other progeny were sold.

The final addition to the breed occurred in 1959 when Hays mated four young Brown Swiss bulls with 100 cows selected from the original Baker Herefords. The bulls had heavy bone structure and weighed about 2,400 lbs each, but were out of 1,900 to 2,000-lb cows. They were all sired by Colonel Harry of Judge Bridge, a son of Jane of Vernon. Jane of Vernon was a 1,600-lb Brown Swiss cow bred by Orbec Sherry of Viroqua, WI and lived from 1929 to 1945. Almost all Brown Swiss today trace back to this cow, which was judged as having the world’s most perfect udder (Briggs, 1980). Jane of Vernon was a four-time Grand Champion Female and dam of International Grand Champion sons and daughters. In 1933 at four years, seven months, she produced 23,569 lbs of milk, and 4.65% (1,075.58 lbs) butterfat in 365 days to establish a new world record in the four-year-old class. On May 15, 1943 at the age of 15 years and 3 months, Jane of Vernon became one of the first cows to be scored “Excellent” under the classification program in the United States. Being from a dairy background, Hays was particularly aware of a cow’s udder and considered it a major weakness of most range cows (Bailey, 1971). With the Brown Swiss genetics, he hoped to get the exceptionally strong udders he was after. In addition to her udder, Hays chose Jane of Vernon for the fact that she never needed her feet trimmed, her milk production held up until the end of lactation, her progeny excelled in growth, and she had excellent feet and legs. Hays also wanted to add Brown Swiss
into his breed because they brought skin pigmentation, which would reduce to some degree, the problems with eyes and udder chapping seen in range cattle. For several years, the best females from this Brown Swiss x Hereford cross were selected and placed in the foundation herd.

By 1963, the foundation herd contained the progeny of the Silver Prince sons, the Holstein x Hereford crosses and the Brown Swiss x Hereford crosses. At this time the herd was closed to all outside blood and the top performing males and females were mated to one another. For about the next decade, Hays selected intensely for the characteristics most important to him and culled mercilessly. Only animals with the qualities desired by Hays were kept for breeding. Selection strategies emphasized weaning weight, yearling weight and the udders on replacement heifers. Cows were initially selected for their growth performance, but once in the brood herd, their ability to remain in the herd depended on their ability to produce offspring and survive. Each female had to calve between the age of 23 and 25 months of age and wean a calf every year after. She had to become pregnant on the bull’s first service, and the calf had to be born unassisted in the open pasture. If the cow failed to meet these criteria, had any problems nursing her calf, or if she needed help in any other way, such as hoof trimming or milking out, she was sent to slaughter in the fall. Males retained for service duties always came from second or more generation Converter dams. Bulls had to weigh 1,100 lbs at one year of age, the goal of the Hays Converter, to qualify for service. The number of a bull’s progeny that remained in the herd was also considered when looking at a bull’s worth. Mainly yearling bulls were used in the foundation years, and only rarely were herd sires retained for several years of service. Hays’ theory was that even though a yearling bull may be highly superior in performance and structure, he must produce one or more sons as good as himself, and if so, those then become their sire’s replacements. Performance was always the main focus of selection with maximum economic
benefit in mind. Colour was never a trait Hays cared about because he felt that it had little connection with profitability. In the beginning, the colour of the Hays Converters varied greatly, “with all the colours of Joseph’s coat,” as Hays once said (Bailey, 1971). They ranged from the traditional black and white of the Holstein, to brown, grey, and red, most with white faces and some white underneath but solids were not uncommon.

The intense selection practices seemed to be paying off for Hays. In a 1967-1968 government supervised feeding test of 537 yearling bulls, the Hays Converters out-gained its competitors putting on an average of 3.68 pounds per day, compared to the next highest rate of 3.41 pounds per day (Bailey, 1971). The Converters had an average 365-day weight of 1,135 lbs while the runners-up had a 365-day weight of 1,079 lbs (Bailey, 1971). The following year, Hays put five of his Hays Converter bulls into the government beef testing station in Bassano, AB where they were measured against conventional British-based beef breeds and the recently imported French Charolais breed. The Converter bulls had an average feed conversion ratio of 5.98 and had on average one-third more daily gain than the British breeds (Peacock, 1986). Only three of the Charolais bulls had better conversion rates than Hays’ bulls, but it was still a Hays Converter bull that topped the list, gaining 3.96 pounds per day (Peacock, 1986). At the test station in Bassano during 1969 feeding trials, the Hays Converters showed how well they could handle the harsh Alberta winters. During one 40-day period, 34 of those days averaged temperatures of -17°C and the Hays Converters still gained 3.25 pounds per day, while some animals failed to gain or even lost weight (Bailey, 1986).

The Hays Converters had started gaining interest and Hays declared that in the beginning he would not sell any of the offspring of his Hays Converters for breeding purposes, but he would sell semen and lease bulls. In June 1969 it was announced that Hays would give American
Breeders Service, a worldwide distributor of livestock semen based in DeForest, WI, exclusive rights to the marketing of Hays Converter semen. Semen would at first be available from three bulls named Tom, Dick and Harry. An official unveiling of the breed occurred on Oct. 23, 1969 at a field day organized by Hays and American Breeders Service. The crowd of 750 people was composed of reporters and cattlemen from every province in Canada, 13 American states, England, Scotland, France, and the Caribbean. The publicity aided in spreading interest in the Hays Converter internationally.

The Hays Converter did not appeal to everyone. To anyone attached to the traditional British breeds, the Converters were easy to criticize. In the opinion of many, the crossbred Holsteins, as they referred to them, were the ugliest cattle they had ever laid eyes on (Peacock, 1986). They were very rugged and lacked the smooth finish seen on high-quality beef cattle at the time. The brood cows looked a lot thinner then people were used to, but this was because Hays had purposely developed the Hays Converter to be lean. The thinness of his cattle was also likely due to the fact that Hays strongly believed in not over-feeding his cattle. He favoured grazing his cows on minimal pasture to keep them lean (Peacock, 1986). However, Hays did not care about the opinions of his critics as long as the packer liked his cattle. Many cattle producers did like the Hays’ cattle and in 1970 he sold 15,000 ampules of semen from his top bulls. Although the Converters were bred specifically with western Canada range conditions in mind, semen from foundation bulls was sold all across Canada, the USA, USSR, Cuba, New Zealand, Australia, Europe, and Central and South America.

The next step for Hays was to get the Hays Converter recognized as an official breed. In 1974, an advisory committee was appointed by the Canadian Department of Agriculture to establish criteria for the eligibility of new breeds of livestock in Canada and inspect the
foundation herd at the Hays’ ranch. The committee included Dr. C. M. “Red” Williams from the Animal Science Department, University of Saskatchewan, Jack Stothart, Director of the Dominion Research Station, Lacombe, AB, Ed Noad, former President of the Canadian Hereford Association, and John Willmott, former President of the Canadian Aberdeen-Angus Association. The committee suggested that new breeds be accepted according to the following criteria:

A population of animals propagated within a pedigree barrier which produces progeny possessing both a good degree of genetic stability as evidenced by phenotypic uniformity and performance levels for one or more economically important traits that offers a meaningful advance over breeds already recognized and/or established. (AAFC, 1999)

The Livestock Pedigree Act required that in order for a new breed to be eligible for registration in Canada, the first animals had to be from identified parents from a foundation population that had been closed to outside breeding for at least three generations. In order for the Hays Converter to become a recognized breed, it had to be proven to the Agriculture Canada committee that it could provide benefit over and above the existing breeds and it would breed true. The committee reviewed the breeding program, and inspected and nominated foundation animals. Under the Animal Pedigree Act (1985, s 2), "foundation stock" are defined as "in relation to a distinct breed, means such animals as are recognized by the Minister as constituting the breed's original stock", although this definition did not exist under the Livestock Pedigree Act at the time of the incorporation of the Hays Converter. The 300 females and 25 bulls of the foundation herd would become the parents of the first registered Hays Converters. On Dec. 4, 1975, the first purebred Certificate of Registration was issued for the Hays Converter by the Canadian National Livestock Records under the provisions of the Livestock Pedigree Act. The
Canadian Hays Converter Association was incorporated under the Livestock Pedigree Act on Dec. 17, 1975, with Harry Hays as president, his son Dan Hays as vice-president, and Sid Williams, former Deputy Minister of Agriculture and partner in Hays & Williams Enterprises, as the secretary-treasurer. The first by-laws of the association were approved on Apr. 26, 1976, establishing the legal authority to register Hays Converter cattle. The approved rules of eligibility for the association included that "a foundation animal shall be one so identified by the Canada Department of Agriculture." Foundation animals were reported to the Canadian National Livestock Records and the rules of eligibility required all other registered or recorded animals to relate back to the foundation animals. Furthermore, the association required that corrected 200-day and 365-day weights be submitted by the owners for entry on certificates of registration.

Harry Hays continued to maintain and improve the Hays Converter breed under commercial conditions with steers fed out alongside purchased feeders so performance could be measured in comparison to other breeds and crosses. By this time, the breed had much more uniformity, and performance was still the main criteria for selection. All stages of development were closely monitored particularly weaning and yearling weights. Only R.O.P. tested animals were used as replacements and all AI bulls had to have an adjusted 365-day weight of at least the generation interval as short as possible, Hays would artificially inseminate the top 125 to 150 yearling heifers with semen from the top performing four or five yearling bulls. In the rest of the herd, the selected mature bulls with top performing progeny were mated to cows with superior traits. Almost without exception, no cow was kept who did not calve to a first or second service or did not wean a calf each year. With fertility having been a main focus in the development of the herd, very few cows at this point were culled for not conceiving and most were still calving when they were voluntarily culled at 10 to 11 years of age. Cows still had to have trouble-free
calving, excellent udders and feet, and strong legs to remain in the herd. These qualities were important in making sure the Hays Converter would continue to perform well on the range. These were major weaknesses, Hays thought, of many eastern and European cattle, who frequently needed help calving and with their feet, and who had trouble surviving under range conditions. Converter cows spent all year on pasture with supplemental feeding only in the most severe weather and for 50 to 100 days at calving.

The breed as it is today is described as large, growthy, rugged, well fleshed, and long-bodied cattle with strong legs, good hoofs, and excellent udders on the cows. They are usually black bodied with white markings although there are some red with white markings. Cows provide ample milk, peaking in production when the calf can use it and lasts until weaning but they do not need to be milked out. They are fertile, do not need their feet trimmed, and are used to wintering under western Canada range conditions. In breeding condition, mature cows weigh around 1,400 lbs and mature bulls can weigh up to 2,800 lbs. Steers under typical feedlot conditions reach 1,100 lbs at 12 to 14 months of age and have a high degree of performance uniformity.

Work on the Hays Converter breed was undertaken by Hays until his death in 1982, at which time the duties were taken over by Dan Hays. Dan Hays continued the work of his father on the Hays Converter and ran the almost 800-cow-calf operation on the Hays Ranch. In 2000, Dan Hays sold the ranch and the Converters were moved to another operation near High River, AB. The breeding herd decreased during this move and the Hays Ranch herd now includes approximately 200 cows with 120 breeding females expected to calve in 2013.

Harry Hays developed the Hays Converter breed of beef cattle in an effort to create a breed that would progress the Canadian beef industry and provide cattle that would benefit the
producer and consumer. By combining the best animals from different breeds, Hays wished to produce an animal that could excel in the rangeland, feedlots, and packing plants of Canada. Hays believed “Had the Hays Converters been on the scene before the Charolais importations in the mid-60s, I think they would have taken over the Canadian cattle industry” (Schmidt, 1980). Although the Hays Converter exists in small numbers today, its distinctive history, selection practice, and genetic composition make it unique in the cattle industry and a significant part of Canadian agriculture history.
CHAPTER 3

PEDIGREE ANALYSIS AND INBREEDING ESTIMATION FOR HAYS CONVERTER CATTLE

3.1. Abstract

A pedigree file containing 13,673 purebred and percentage beef cattle of the Hays Converters breed born between 1960 and 2011 was analyzed to assess the genetic diversity and level of inbreeding. The completeness and quality of the pedigree was examined. Pedigree completeness index values were greater than 0.6 for 49% of animals in the pedigree. For animals born between 1995 and 1999 the effective number of founders, effective number of ancestors, and effective number of founder genomes were 63.7, 25.6, and 13.2, respectively. These values decreased to 61.3, 13.5, and 7.4 when animals born from 2006 to 2011 were used as a reference population. The ratio of the effective number of founders to the effective number of ancestors was 4.5 for animals born between 2006 and 2011. The top 10 ancestors with the largest marginal contribution to animals born from 2006 to 2011 explained approximately 65% of the gene pool with the top 5 ancestors explaining over 50%. Animals born in 2011 had an average inbreeding level of 3.4%. This value increased to 5.4% when only animals with pedigree completeness index values greater than 0.6 were examined. When missing pedigree information was accounted for in determining inbreeding the average level was approximately 9%. Expected inbreeding for animals born in 2011 was found to be 7.8% using a simulated pedigree. The current effective population size was found to be small at 26.5 and as a result genetic diversity is expected to continue to decrease. Proper management of the Hays Converter population to maintain genetic diversity is needed.
3.2. Introduction

The Hays Converter breed of beef cattle was developed from a small number of animals representing three different breeds. The initial group of animals that creator Harry Hays used to construct the breed consisted of 700 Hereford cows, 1 Hereford bull, 8 half-sibling Holstein bulls, and 4 half-sibling Brown Swiss bulls. The breeding scheme used to combine the genetics of the chosen animals made close inbreeding a very likely reality. Hays did not attempt to avoid inbreeding and wittingly used inbreeding and line breeding as a breeding strategy. Hays explained that he “mated the best families, father to daughter, son to mother, and other such incestuous combinations to bring out the best meat-producing characteristics possible,” (Peacock, 1986). The herd was closed in 1963 and many generations of inter se mating followed. In closed populations, inbreeding may be difficult to avoid. In 1975, 300 cows and 25 bulls were appointed to be foundation animals for the Hays Converter breed. All future Hays Converter cattle had to descend from these named foundation animals. The breed has always existed in relatively small numbers. Between the official recognition of the breed in December 1975 and December 2011 there have been 4,797 purebred and 628 percentage registrations. The small number of animals used to form the breed, the low population size throughout its history, and the high prevalence of matings between relatives make genetic diversity a probable concern in the Hays Converter.

The preservation of genetic diversity is central in maintaining the full adaptive potential of a species and allowing for a level of productivity to be maintained or increased (Notter, 1999; Barker, 2001). In any population some loss in genetic variation is inevitable over time due to genetic drift, but this depletion will be more rapid for small populations and those under selection (Lacy, 1987). Inbreeding leads to a loss of genetic diversity in a population and is the cause of inbreeding depression that can negatively affect production and fitness traits (MacNeil
et al., 1989; Miglior et al., 1992). Pedigree analysis is an important tool to evaluate genetic diversity and its change over time. Measures of gene origin including effective number of founders ($f_e$), effective number of ancestors ($f_a$), and effective number of founder genomes ($f_g$) are useful measures of genetic diversity calculated from pedigree information (Lacy, 1989; Boichard et al., 1997; Caballero and Toro, 2000). Inbreeding and effective population size ($N_e$) calculations from the pedigree are important measures of genetic variation for consideration in genetic conservation strategies. The rate of inbreeding is more informative than the actual level of inbreeding, because the actual level is relative to a base population that is assumed to be unrelated (FAO, 1998).

Inbreeding depression occurs in many production and fitness traits, although estimates are not very precise and vary greatly. The effects of inbreeding in beef cattle have been extensively reviewed by Burrow (1993). Inbreeding had adverse effects on most traits of economic importance to beef cattle, though the impact was generally minor and there was large variation in the reported effects. Inbreeding depression is a function of allele frequencies at loci that affect the traits of interest and is dependent on the different ancestors contributing to inbreeding. Therefore, inbreeding depression is expected to be different between breeds, populations, and families (Miglior et al., 1994; Carolino and Gama, 2008).

Inbreeding in cattle has been shown to have a negative effect on birth weight, weaning weight, postweaning weight, and mature weight (Burrow, 1993; MacNeil et al., 1998; Carrillo and Siewerdt, 2010; Santana et al., 2010). McCurely et al. (1984) found that each 1% increase in an individual’s inbreeding was associated with an approximately 2-kg decrease in mature weight. In Limousin cattle, Gengler et al. (1998) found a decrease in total postweaning gain of 0.24 kg per percentage of inbreeding. Milk production traits in dairy cows decline as a result of
inbreeding. In Jersey cows, a 0.27, 0.30, and 0.05% reduction for milk yield, fat yield, and fat percentage, respectively, was observed on average for each 1% increase in inbreeding (Miglior et al., 1992). Smith et al. (1998) estimated a lifetime profit decrease of $24 per cow with a 1% increase in inbreeding.

For traits influenced by maternal effects, individual and maternal inbreeding coefficients are both expected to have unfavourable results on animal performance (Falconer and Mackay, 1996). Carolino and Gama (2008) found a significant effect of maternal inbreeding for calf weight at three and seven months of age but not for birth weight. However, Pariacote et al., (1998) found significant maternal inbreeding effects for birth weight as well as daily gain and weaning weight.

Female fertility traits are of economic importance for cattle producers. In Herefords, MacNeil et al. (1989) found a decrease in calving rate and weaning rate as inbreeding increased. González-Recio et al. (2007) found pregnancy rate decreased by an average of 1.68%, 2%, and 6.37% for Spanish dairy cows with an inbreeding coefficient between 6.25 and 12.5%, 12.5 and 25%, and greater than 25%, respectively, compared to cows with an inbreeding coefficient less than 3.125%. The effect of inbreeding is lower for animals with small inbreeding coefficients and increased for animals with high inbreeding levels (Burrows, 1993; Santana et al., 2010). Burrows (1993) concluded the rate of inbreeding had an importance in the amount of inbreeding depression observed for production traits in beef cattle, as the most severe effects of inbreeding were reported for animals bred at a rapid rate.

The objective of this study was to analyse the pedigree of Hays Converter cattle to assess the current level of genetic diversity and inbreeding in the breed and predict the future rates of inbreeding for the population.
3.3. Materials & Methods

3.3.1. Pedigree data

A pedigree of 13,673 animals was obtained from Hays Ranches in Calgary, AB and the Canadian Livestock Records Corporation (CLRC) electronic herdbook. The pedigree files included purebred and percentage animals of the Hays Converter breed born between 1960 and 2011. Animals included in the pedigree consisted of those owned by Hays Ranches as well as Hays Converters from other herds registered with the Hays Converter Association before 2000. When conflicting parentage information was found between the two pedigree sources, it was assumed the CLRC records were correct. Figure 3.1 illustrates the number of animals born per year included in the pedigree data. The birth year of 57 animals were unknown. Only a small number of animals born in the 1960s were recorded. These animals were predominantly females that were listed as ancestors of later progeny. The number of animals born each year and recorded in the pedigree file increased throughout the 1970s. Animals selected for breeding purposes were more likely to be recorded, and therefore females appear in the pedigree more often than males. The greatest number of calves born and recorded in a year was 646 occurring in 1993. In 2000, the herd experienced a downsizing and the number of births recorded decreased correspondingly. Prior to 1975, individual sires were not recorded because sire groups were exclusively used. Sire groups were also employed on occasion in later years on select cows. A total of 22 sire groups appeared in the pedigree and listed as a sire in the pedigree a total of 1,330 times. Bull groups recorded as sires were switched to unknown for analysis. Animals with duplicate identification names (IDs) were renamed so all animals had unique IDs. Dam and sire IDs were changed to reflect these altered IDs by selecting the proper dam or sire according to recorded birth years. Animals originating from outside the Hays Ranches’ herd were
distinguished using the prefix of the herd with which they were registered, and had some degree of relatedness to the Hays Ranches’ herd.

Pedigree information was edited before analysis. The final revisions to the pedigree used in the analysis occurred in November 2011 and does not include corrections to any errors discovered after this date. The pedigree was first checked for validity. Sires and dams with recorded birth years the same as or more recent than their listed progeny were removed. Progeny that had a parent that appeared in the pedigree as both a sire and dam had the parent replaced with unknown where the sex of the listed parent could not be confirmed by the CLRC records. Dams listed in the pedigree with multiple calves in a single year that were known to not be twins or the product of embryo transfer were switched to unknown unless parentage was verified by the CLRC pedigree.

Bulls identified in the pedigree file with no connection to the Hays Converter breed appeared as sires between 2006 and 2011. These sire IDs were retained in the pedigree for all calculations with the exception of inbreeding estimation as only inbreeding resulting from Hays Converter breeding was of interest.

3.3.2. Measures of pedigree completeness

The quality and completeness of the pedigree are important factors that may affect the accuracy and conclusions of inbreeding estimates and relationships among animals. Percentage of animals with known parents, discrete generation equivalents \( (g_e) \), and pedigree completeness index \( (PCI) \) were calculated for each individual to evaluate the quality of the pedigree. The average number of complete generation equivalents \( (g_c) \) is equal to the number of generations in a pedigree with no overlapping generations (Woolliams and Mäntysaari, 1995). It was calculated using the equation:
where, \( n_j \) is the total number of ancestors of animal \( j \), and \( g_{ij} \) is the number of generations between \( j \) and its ancestor \( i \) (Sölkner et al., 1998).

The pedigree completeness index (PCI), proposed by MacCluer et al. (1983), describes the proportion of known ancestors in each ascending generation. Pedigree completeness index (PCI) was calculated for five (5G) and ten generations (10G) as:

\[
PCI = \frac{4C_{sire} \cdot C_{dam}}{C_{sire} + C_{dam}}
\]

where, \( C_{sire} \) and \( C_{dam} \) are the paternal and maternal line contributions, respectively:

\[
C = \frac{1}{d} \sum_{i=1}^{d} a_i
\]

where \( d \) is the total number of generations taken into account (here: \( d=5 \) or \( d=10 \)), and \( a_i \) is the proportion of ancestors known in generation \( i \). PCI is a good indicator of the ability to detect inbreeding in the pedigree (Sørensen et al., 2005). Being a harmonic mean of parental contributions, PCI is equal to zero if one parent is unknown regardless of how complete the pedigree is for the other parent.

3.3.3. Measures of genetic diversity

Measures of genetic diversity were calculated for animals with both parents known that were born between 1995 and 1999 and for animals born between 2006 and 2011. A founder in the pedigree was defined as an ancestor with unknown parents. The unknown parent of an animal with only one known parent was also considered a founder. Relationships between the founders and their descendants in the reference population were calculated, and each founder’s
contribution is equal to the sum of that founder’s relationship with each individual in the reference population. Proportional contributions ($q_i$) are calculated by dividing the founder’s contribution by the number of individuals in the reference population. The effective number of founders ($f_e$), represents the number of equally contributing founders that would be expected to produce the same genetic diversity as the reference population (Lacy, 1989). It was calculated as:

$$f_e = \frac{1}{\sum_{i=1}^{f} q_i^2}$$

where $q_i$ is the proportion of alleles in the reference population contributed by the founder $i$.

The effective number of ancestors ($f_a$) proposed by Boichard et al. (1997) represents the minimum number of ancestors (founder or not) required to explain the complete genetic diversity in the reference population. An ancestor may not be a founder and may be related to other ancestors. As a result their expected genetic contribution ($q_k$) could be redundant, and consequently, the expected contributions may sum to more than one. Marginal contributions ($p_k$), the contribution not yet explained by other ancestors, removes these redundancies and are used to calculate the effective number of ancestors ($f_a$):

$$f_a = 1/\sum_{i=1}^{f} p_i^2$$

where $p_i$ is the marginal contribution of ancestor $i$ of the reference population, and $f$ is the number of ancestors.

The effective number of founder genomes ($f_g$) is related to the expected loss of genetic diversity resulting from genetic drift (Lacy, 1989). It is equal to the number of equally
contributing founders with no random loss of founder alleles that would provide the same genetic diversity as in the reference population (Lacy, 1995). It is calculated as:

\[ f_g = \frac{1}{2\bar{f}_g} \]

where \( \bar{f}_g \) is the average coancestry in the group \( g \) (Caballero and Toro, 2000).

### 3.3.4. Calculation of inbreeding coefficients

An algorithm described by Sargolzaei et al. (2005) based on the indirect method proposed by Colleau (2002) was used to calculate inbreeding coefficients (F) for all individuals. Inbreeding coefficients were examined considering PCI (5G) categories (PCI < 0.24; 0.24 ≤ PCI > 0.4; 0.4 ≤ PCI > 0.6; 0.6 ≤ PCI > 0.8; PCI > 0.8). Average levels of inbreeding were examined for all animals and for animals with PCI values ≥0.6.

The inbreeding coefficients of all animals born between 2006 and 2011 were decomposed into ancestral components (Sargolzaei and Colleau, 2006).

The accuracy of inbreeding estimates is dependent on the quality and completeness of the pedigree. The pedigree of the Hays Converter herd contained many unknown parents and is not complete back to the formation of the breed. In closely related populations such as the Hays Converter population, on average, unknown parents may not differ genetically from known parents. The real average inbreeding in animals with unknown parents may be comparative to that of their contemporaries with known parents. VanRaden (1992) proposed an algorithm (VRA) that assigns animals whose parent(s) are unknown an inbreeding coefficient equal to the mean inbreeding of their contemporaries with both parents known. Inbreeding was calculated using VRA to account for missing pedigree information. Animals with an unknown sire and/or dam
which were known not to be a breed other than Hays Converter were assigned foundation groups as parents.

The Hays Converter pedigree records do not contain information going back to the conception of the breed. The founder animals of the available pedigree are not those involved in the original breeding that formed the group that ultimately became the Hays Converter breed. Calculations performed with the original pedigree file assume the pedigree foundation animals are unrelated although they derive from a herd that had been closed for several generations. The Hays Converter breed provides a unique opportunity in that the process used for the creation of the breed is mostly known. A pedigree based on the breed’s formation history was simulated to consider inbreeding in the herd since its initiation. The founding animals included 700 Hereford cows assumed to be unrelated, one Hereford bull, eight Holstein bulls from the same sire, and four Brown Swiss bulls from the same sire. Matings based on the known history were simulated with mating pairs randomly selected. The eight Holstein bulls were mated to the Hereford cows for two years. One hundred fifty-nine females were selected to be mated to the Hereford bull. Five bulls from these matings were selected to mate back to the 159 females. The four Brown Swiss bulls were mated with the 100 of the original Hereford cows. Selected progeny from all parts of the breeding scheme were combined into a breeding group. For the years following the herd closure in 1963, recorded information on the breeding scheme was used to simulate breeding practices and make assumptions. The simulation assumed that out of the progeny produced each year, 100 heifer and 25 bull calves were assigned to the breeding groups. The maximum age for last breeding was ten years of age for cows and four years of age for bulls. Five percent of cows, independent of age, were removed from the cow herd each year to account for non-age related culling. A maximum cow herd size of 700 animals was imposed. Ten non-
yearling bulls were used for breeding each year. These bulls were selected based on the number of their progeny who entered the breeding groups. In 1975, 300 cows and 25 bulls were selected to be the breed foundation and the pedigree of all future Hays Converters had to trace back to these animals. In 2000, the herd experienced a down size and the maximum number of cows calving each year was lowered in the simulation to 125 and the number of bulls decreased to 5. The simulation was repeated 10 times and the average inbreeding coefficient by year of birth was calculated along with estimated breed composition.

The simulated pedigree was combined with the original pedigree file. Animals in the original pedigree with an unknown parent that was known not to be a percentage Hays Converter or from a non-Hays Converter breed had their unknown parent replaced by a simulated parent active in the same year as the animal’s birth. Inbreeding coefficients were calculated for animals appearing in the original pedigree file only.

Wright (1931) defined the effective population size \( N_e \) as the size of an ideal population whose genetic composition is influenced by random processes in the same way as the real population. It is regarded as a good indicator of the risk of genetic erosion (FAO, 1998). The effective population size \( N_e \) was calculated from the anticipated number of sires and dams used in the current Hays Converter breeding program using the equation:

\[
N_e = \frac{4N_mN_f}{N_m + N_f}
\]

where, \( N_e \) is the effective population size, \( N_m \) is the number of males, and \( N_f \) is the number of females.

The future rate of inbreeding per generation was estimated from the calculated \( N_e \) using the formula:
\[ \Delta F = \frac{1}{2N_e} \]

where, \( \Delta F \) is the change in inbreeding per generation, and \( N_e \) is the effective population size.

3.3.5. Software used

The software package Pedig (Boichard, 2002) was used to calculate effective number of founders \( (f_e) \), effective number of ancestors \( (f_a) \), effective number of founder genomes \( (f_g) \), and marginal contributions of ancestors. The VANRAD program in Pedig was used to calculate average inbreeding by year using VRA accounting for missing pedigree information. Pedigree completeness, inbreeding coefficients, and the ancestral decomposition of inbreeding were calculated using CFC (Sargolzaei et al., 2006).

3.4. Results

3.4.1. Pedigree completeness

The Hays Converter pedigree is relatively incomplete and does not cover the entire depth of the breed’s formation. For all animals in the pedigree 67% have both parents known, while 22% have only their dam known, 2% have only their sire known, and 9% have no known parent. The percent of known parents by year of birth are displayed in Figure 3.2. Prior to 1968 no parentage data was recorded. Dam information was listed for select animals starting in 1968. There was no sire information available for any animal born before 1975. Approximately 99% of animals born between 1975 and 1978 had both parents identified. The percent of animals with both parents identified gradually declined after 1978 until 1995. The percent of known parents was variable depending on the year following 1995. The longest ancestral path covered was 15 ancestral paths and the average longest ancestral path was 6.0 ancestral paths. Figure 3.3 depicts the average
discrete generation equivalents ($g_e$) by year of birth. The average discrete generation equivalents ($g_e$) for all animals born in 2011 was 5.46 generations.

The average PCI for all animals was 0.487 for 5 generations and 0.27 for 10 generations. Figure 3.4 displays the distribution of PCI (5G) values by category. For all animals in the pedigree 33.8% had a PCI (5G) value less than 0.24, 7.0% were greater than or equal to 0.24 and less than 0.4, 10.3% were greater than or equal to 0.4 and less than 0.6, 17.5% were greater than or equal to 0.6 and less than 0.8, and 31.4% were greater than 0.8. Figure 3.5 shows the PCI for 5 and 10 generations by year of birth. The average PCI (5G) for animals born between 2006 and 2011 was 0.50.

3.4.2. Genetic diversity

There were 1,601 and 365 individuals in the 1995-1999 and 2006-2011 reference populations, respectively. The average PCI (5G) was similar for both reference populations, each equalling approximately 0.85. The number of founders, effective number of founders ($f_e$), effective number of ancestors ($f_a$), and founder genome equivalents ($f_g$) are displayed in Table 3.1. The number of founders, effective number of founders ($f_e$), effective number of ancestors ($f_a$), and founder genome equivalents ($f_g$) were all lower for the 2006-2011 population. The effective number of founders ($f_e$) was greater than the effective number of ancestors ($f_a$) for both reference groups. The $f_e/f_a$ ratio was approximately 2.5 for animals born from 1995 to 1999 and 4.5 for animals born from 2006 to 2011.

The top ten marginal genetic contributing animals explained approximately 65% of the genetic pool for reference animals born between 2006 and 2011 and are presented in Table 3.2. The top contributing animal (HAY305J99) was a bull born in 1999 and exhibited the greatest number of progeny recorded with 155. The birth year of the ancestors ranged from 1972 to 2002.
The four ancestors with the greatest contribution were all born after 1997. The number of animals that explain 25%, 50%, 75%, 90%, 95%, and 99% of the genetic pool of animals born in 1995-1999 and 2006-2011 are displayed in Table 3.3. Fewer animals are needed to explain the genetic pool for animals born in 2006 to 2011 then for those born in 1995 to 1999. For 1995-1999 born animals, 99% is explained by 307 ancestors while 2006-2011 born animals require only 108 ancestors. The reference populations both had a low number of ancestors needed to represent 25% of the genetic pool with 3 and 2 ancestors for 1995-1999 and 2006-2011 reference populations, respectively.

The average inbreeding was decomposed into ancestral components and the ten ancestors who explained the largest amount of inbreeding are shown in Table 3.4. Five of the ancestors also appear in the list of the top ten genetic contributors (Table 3.3). The average birth year of these animals is approximately 1987, and a larger number of early ancestors are represented compared to the top genetic contributing animals. The number of ancestors contributing 99% of the average inbreeding in the 2006-2011 born animals was 52 (Table 3.5).

3.4.3. Inbreeding

The lack of pedigree information before 1975 resulted in inbreeding to be inestimable before this time. The base year of inbreeding coefficients calculated is for that reason 1975, the year the breed was officially recognized. The percent of animals with some degree of inbreeding in the pedigree was approximately 43%. The mean inbreeding for all inbred animals was 4.3%. The presence and degree of inbreeding depended on the completeness of an individual’s pedigree. The mean level of inbreeding and percent of inbred animals by pedigree completeness is displayed in Table 3.6. No inbreeding was found in animals with a PCI (5G) value less than 0.24 as there is known ancestors beyond the parents of the animal. The percent of inbred animals
increased with each increment in PCI category. The percent of animals with a PCI (5G) ≥ 0.8 that were inbred was 97.8%, and the mean level of inbreeding for animals in this category was about 4.1%. The maximum level of inbreeding discovered was 32.47%. The maximum inbreeding for the categories 0.24 ≤ PCI > 0.4 and 0.4 ≤ PCI > 0.6 were both 25%, representing episodes of recent and close inbreeding.

Apart from inbreeding coefficients of all animals in the pedigree, inbreeding of animals with a PCI (5G) ≥ 0.6 were examined. This group represented 48.9% (n=6,689) of animals in the pedigree. Figure 3.6 shows the distribution of inbreeding coefficients for all animals, and animals with a PCI ≥ 0.6. The majority of the animals in the pedigree (57%) had inbreeding coefficients of zero. Most of the animals with a more complete pedigree displayed low levels of inbreeding. The average inbreeding coefficient by year of birth is presented in Figure 3.7. The level of inbreeding shows an increasing trend over time. On average, inbreeding was 1.5% higher per year when only animals with more complete pedigrees were considered. After 2000, the average level of inbreeding by year of birth was variable with large increases and declines. Animals with a PCI ≥ 0.6 born in 2003 had the greatest average inbreeding at 6.2%. Animals born in 2011 had an average level of inbreeding of 3.5% when all animals were considered and 5.4% for animals with a more complete pedigree.

Average inbreeding estimates using VRA were greater than those calculated without taking missing pedigree information into account. The average inbreeding by year of birth with inbreeding coefficients calculated using VRA is shown in Figure 3.8. For animals born in 2011 the average inbreeding was estimated to be approximately 9.1%. This is 3.7% higher than the average level calculated using the incomplete pedigree for animals born in 2011.
The base year for calculating inbreeding coefficients for the simulated pedigree was the year the breeding scheme originated, 1958. The simulated, and simulated and pedigree combined average inbreeding coefficient by year of birth are displayed in Figure 3.9. The simulated inbreeding coefficients showed a spike for animals born in 1962 followed by a constant increase each year. In 2000, the rate of increase was accelerated. The average level of inbreeding for simulated animals born in 2011 was 7.8%, 2.4% higher than that of 2011 animals with a PCI ≥ 0.6 from the pedigree file. When the simulated and original pedigrees were combined, 2011 born animals had an average inbreeding of 7.2%. The combined average inbreeding estimates by year of birth were greater than those of the simulated pedigree until 2005. The combined pedigree did not exhibit the same increase in the rate of inbreeding after 2000 as the simulated pedigree.

The current Ne for the Hays Converter herd is 26.5 animals. This corresponds to an inbreeding rate of 1.89% per generation. If a generation interval of 6 years is assumed, the rate of inbreeding would equate to 0.315% per year.

3.5. Discussion

An incomplete pedigree can be problematic in the estimation of genetic diversity and the genetic management of a population. Boichard et al. (1997) found in a simulation study that inbreeding trends were only well estimated when the pedigree was complete, and were underestimated when there was some degree of incompleteness. Inbreeding coefficients based on the definition of Wright (1922) are calculated as zero if at least one of an animal’s parents is unknown, and inbreeding coefficients of future descendants could therefore be underestimated because of the incomplete pedigree and unidentified ancestors. Parameters derived from the probability of gene origin are also sensitive to an incomplete pedigree but to a lesser degree than inbreeding. The effective number of ancestors (fa) is the most robust against incomplete
pedigrees out of the genetic diversity parameters calculated because it relies on shorter relationship pathways (Boichard et al., 1997). Inbreeding calculations depend on long relationship pathways and therefore are more influenced by pedigree incompleteness. The completeness of the Hays Converter pedigree is poor and varied depending on the year. No parentage information was available for animals born before 1968 which represented 1% of animals listed in the pedigree file. Sire groups were exclusively used in the Hays Converter breeding program prior to 1975 and as a result no individual sires were recorded. In 1975, the Hays Converter was recognized as an official breed under the Livestock Pedigree Act and descendants of a named foundation group were able to be registered. Parentage information was necessary for registration and both parents were identified and recorded for animals at this time at a greater frequency. The decline in the percent of animals with known parents after 1978 may have resulted from the genetics of other breeds being brought in, sire groups being used again to some degree, changes in management practices, or a combination.

Founders are animals that contribute to the population but have no pedigree information. The number of founders may be overestimated when limited pedigree information is available. Many of the unidentified parents were likely animals that appear in the pedigree file. The Hays Converter pedigree is relatively incomplete and does not date back to the creation of the breed. Many animals were considered founders only because information on their parents was not recorded. Bull groups were used extensively in the Hays Converter’s history and progeny of these groups had their sires recorded as unknown for the analysis. As a result each of the unknown sires of these animals was considered separate founders of the population if the animal’s dam was known. If no dam information was available, the animal was considered a founder although it was known its sire was one of the bulls in the sire group. Consequently many
more founders are acknowledged than there may be in actuality. The number of founders of this population would decrease if the pedigree was more complete. The number of founders of the 2006-2011 reference population was 345 but $f_e$ was only 61.3. This signifies that some founders were used more frequently, whereas others contributed little to the population (Lacy, 1989). A low effective number of founders suggest that genetic drift has been occurring since the founder generation (Sørensen et al., 2005).

The 1995-1999 reference population had a greater number of individuals and a greater number of founders than the 2006-2011 reference population. The average PCI (5G) value was equal for the two reference populations (0.85). The effective number of founders ($f_e$) was similar for both populations, despite the large decrease in the number of breeding Hays Converter animals which occurred between the births of the two reference populations ($f_e$=63.7 for 1995-1999; $f_e$=61.3 for 2006-2011). Estimation of $f_e$ is dependent on the size of the reference population and the number of actual founders. A smaller population would be expected to have a smaller effective number of founders. Therefore, a greater $f_e$ value was expected for the 1995-1999 population compared to the 2006-2011 population. The use of artificial insemination and a small number of families represented in the breeding herd may have resulted in the low $f_e$. This suggests the 1995-1999 reference group had a large number of founders with little genetic contribution and fewer founders were used extensively. The effective number of founders ($f_e$) only considered founder contributions and thus did not decrease at as great a rate as the other parameters. The decrease in the breed population size created a small decrease in the number of equally contributing founders required to produce the level of genetic diversity observed in the reference population.
The genetic contribution of ancestors of the Hays Converter population gives a better estimate of genetic losses and diversity. The most important ancestor was HAY305J99, a bull used extensively as an AI sire from 2004 to present, showing a marginal genetic contribution of 18.39%. HAY305J99 had 155 progeny recorded in the pedigree, the third greatest for all Hays Converter animals. HAY305J99 was the sire of many females retained for breeding purposes and an AI sire included in the reference population. The pedigree completeness index (5G) value for HAY305J99 was very high (0.99), but the genetic contribution of the close ancestors to the reference population was primarily through HAY305J99. The four ancestors with the greatest marginal contribution were all recent ancestors and were all AI sires used considerably in recent years. The top two contributors explained approximately 32% of the genetic pool while 50% was able to be explained by only five ancestors. These results are similar to those found in Canadian Holstein cattle where the top two ancestors explained about 30% and six ancestors were able to explain 50% (Stachowicz et al., 2011). The information on the contribution of ancestors points toward heavy use of some specific animals in the Hays Converter breed. The use of artificial insemination as a breeding tool in the Hays Converter breed may explain the low number of animals explaining the genetics of the reference population. In addition, the reference population contains animals born between 2006 and 2011 that have both parents known. A sire group was regularly used as clean-up bulls on cows that did not conceive through artificial insemination. Progeny born between 2006 and 2011 that were a result of a natural mating were less likely to have their sire recorded and as a result, were not largely represented in the reference population. This may have resulted in higher marginal genetic contributions of some AI sires. The number of ancestors needed to explain the genetics of all animals born during the reference period may be
greater, as more bulls were used but not recorded. However, the animals with unknown sires were not as likely to be selected to remain in the herd for breeding purposes.

The effective number of ancestors \( (f_a) \) is useful in comparison with the effective number of founders. The effective number of founders \( (f_e) \) is expected to be larger than \( f_a \) (Boichard et al., 1997). The effective number of ancestors \( (f_a) \) for the Hays Converter population was as expected, lower than the effective number of founders \( (f_e) \) indicating a bottleneck has occurred in the past. The ratio of the effective number of founders to the effective number of ancestors \( (f_e/f_a) \) is a meter of the importance of bottlenecks in the development of the population (Sørensen et al., 2005). Both reference populations had a ratio greater than one. The greater the value of the \( f_e/f_a \) ratio is, the greater the bottleneck effect resulting from the decrease in the number of breeding animals over time (Oliveira et al., 2012). The \( f_e/f_a \) ratio was greater for the 2006-2011 reference population than for the 1995-1999 reference population. This shows a bottleneck has occurred between these two time periods. In 2000, the Hays Converter herd experienced a major downsizing. In the 1990s there were 570.3 animals born per year on average while in the 2000s there were only 136.6 born each year on average. The sizable decrease in the number of breeding Hays Converter animals at this time was the primary cause of the increase in the \( f_e/f_a \) ratio. The effective number of founder genome equivalents accounts for all possibilities of founder genome losses and is calculated using the average co-ancestry of the population. The Hays Converter population is highly related and a low \( f_g \) value was expected. The decrease in the number of breeding individuals likely resulted in the decrease in \( f_g \). The effective number of founders, ancestors, and founder genomes are all expected to further decrease overtime at varying degrees (Boichard et al., 1997).
Data were selected based on PCI in an attempt to make the average inbreeding more reliable. Animals with a PCI \((5G) < 0.6\) largely had inbreeding coefficients of zero which brought the average inbreeding coefficient toward zero. Removing the animals with a less complete pedigree also inadvertently removed percentage animals and therefore determined an average inbreeding level more representative of the Hays Converter breed. Additionally, animals with a more complete pedigree are expected to be selected as replacement breeding animals more frequently than animals with little known pedigrees and thus the estimates are depictive of the proper breed trends.

The average inbreeding by year of birth for the pedigree generally increased until 2000. After 2000, the average inbreeding became variable depending on the year. A small number of animals were included in the pedigree at this time and management decisions may have had a large impact on the observed inbreeding level. The bulls selected to breed cows in a particular year could cause the large differences in inbreeding depending on the bull’s relationship to the cow herd. Because of the short period of time that has passed since the decrease in the number of breeding Hays Converter cattle in 2000, the consequences have likely not yet been observed in the current inbreeding level. In the next generations the extent of the increase in inbreeding from the herd’s downsize will be detected.

The greatest inbreeding estimates were obtained using VRA. This method may underestimate the inbreeding value for animals with parents that are more related than average or overestimate for animals with parents less related than average. Lutaaya et al. (1999) found the amount of inbreeding recovered using VRA is dependent on the completeness of the pedigree, with VRA recovering the most inbreeding with up to 20% of the pedigree missing. The large increase in the inbreeding estimate using VRA was expected because of the large amount of
missing pedigree records in the Hays Converter breed. In the Canadian Holstein breed, which had 90\% of animals having both parents known since the 1980s, Stachowicz et al. (2011) found the amount of inbreeding recovered using VRA was double the amount found when not accounting for missing pedigrees. The estimates using VanRaden’s method may be greater than the real values for the Hays Converter breed due to the unknown number of unrelated parents from other breeds. The unknown parents of some animals may have unknowingly been unrelated to the Hays Converter population.

The simulated pedigree estimated inbreeding level cannot be directly compared to the other estimates because a different base year was used. The simulated pedigree used a base year of 1958, when the breed originated. The real pedigree did not have information recorded on ancestors dating back to the formation and instead used a base year of 1975. It is assumed in the real pedigree that all founders are unrelated although this is only a result of incomplete pedigrees. The real pedigree does not take into account the 17 years previous that the herd was closed. Any two of these animals could be traced back to a common ancestor if their lineages were entirely obtainable. The rate of inbreeding per generation is not dependent on the base year and can be compared between pedigrees with different base years. The post-2000 inbreeding rate is greater for the simulated pedigree than that seen in the other estimates which are variable in this period. The simulated pedigree gives an estimate of the level and rate of inbreeding if the entire breed history is considered.

The simulated pedigree did not take into account several characteristics of the breeding scheme of the Hays Converter that could impact the inbreeding level estimated. The simulated pedigree assumed the herd was closed and the only founders were the original Hereford, Holstein, and Brown Swiss animals. The Hays Converter Association allows for upgrading and as a result,
genetics from outside animals have been brought in. The actual average inbreeding level may therefore be lower than estimated from the simulation. The true level of inbreeding may also be greater than the simulated estimate because the simulated pedigree assumed a population not under selection and random mating occurring. All sires had an equal probability of being mated to each of the dams. With the advent of artificial insemination in the Hays Converter breeding program, a small number of bulls were used on a large number of cows while others were used minimally. This would cause an increase in inbreeding. Additionally, all animals in the simulation had an equal chance of being selected to join the breeding herd. In reality certain families may have had a greater likelihood of being selected because of superior performance or bias of the herd manager. The real Hays Converter population likely represented fewer families and a greater rate of inbreeding. This is a possible reason why the average inbreeding of the real and simulated combined pedigree is greater than the average inbreeding in the simulated pedigree. Beginning around 1975, when the Hays Converter pedigree began to be more complete, the average inbreeding by year of birth was greater than that of the simulated pedigree. The difference was greatest in 1991 when the average inbreeding was 1.82% higher for the combined pedigree. During this period the true Hays Converter breeding strategy saw a small number of sires producing the majority of recorded progeny and many close matings performed. In the more recent years the inbreeding estimate is close to or less than the simulated pedigree’s because of fewer animals with a complete pedigree, together with an underestimation of the relationship between the inserted simulated parents and breeding animals of the time with known ancestors. Non-Hays Converter sires were also used at a greater frequency at this time. The combined pedigree inbreeding estimates account for the entire breed history, missing pedigree, and the actual recorded pedigree.
The effective population size ($N_e$) of the herd was low and suggests genetic erosion is very likely to occur in the breed. The estimate of $N_e$ does not factor in the addition of outside animals from other herds and other breeds. The estimated rate of inbreeding of 1.89% per generation is greater than recommended, as the FAO advises an inbreeding rate of greater than 1% per generation (corresponding to an $N_e$ of 50) be avoided to maintain fitness in a breed (FAO, 1998). Nicholas (1989) suggested a critical level of 0.5% inbreeding per year for animal breeding programs. Although the expected rate of inbreeding for the Hays Converter is lower than this critical level, a lower rate may be advisable for maintaining a population in need of conservation for a long time horizon.

The management of small populations should put an emphasis on maximizing the effective population size ($N_e$). The sex ratio has a significant effect on $N_e$ as each sex contributes half of the genetics to their progeny. A management program should be designed around the number of animals that can be sustained long term to avoid fluctuations in size and creation of bottlenecks (Fernandez, et al., 2011). Once the total number of individuals is set, the optimal policy for maximizing $N_e$ is to have an equal number of animals from each sex contributing to the next generation. In the Hays Converter breeding program a maximum number of males, the limiting sex, should be kept in each generation to maintain as low a female to male ratio as possible.

The current level of genetic diversity in the Hays Converter is important for consideration in future management and selection strategies. The completeness of the pedigree is a limiting factor in the accuracy of the estimation of the probability of gene origin parameters and inbreeding coefficients. The increase in the availability of genotyping technology will allow the identification of parents for all progeny especially those sired by bull groups. This will ensure a
more complete and accurate pedigree, and improved estimates of genetic diversity. A more complete pedigree will also result in an increase in the accuracy of relationships between individuals to assist in breeding decisions to maintain genetic diversity. Reliable and complete pedigree information is also necessary for proper management of inbreeding (Weigel, 2001).

The apparent relatively low level of genetic diversity in conjunction with a small population size warrants some genetic conservation strategies be employed in combination with genetic improvement in the future development of the breed. In the absence of policies to maintain genetic diversity it is likely that inbreeding in a small population will increase quickly. Several methods of controlling inbreeding in selection programs have been proposed, including imposing restrictions on family size, reducing selection intensity, limiting the use of family information, balancing estimated breeding values with relationships to other selected parents, and optimized mating programs (Toro and Perez-Enciso, 1990; Caballero et al., 1996; Sonesson et al., 2000). Traditional methods of selection to maximize genetic gain incorporate information on relatives which may result in more individuals from the best families being selected. Best linear unbiased prediction (BLUP; Henderson, 1975) increases the amount of genetic gain but also the rate of inbreeding (Belonsky and Kennedy, 1988). Frozen semen and embryos also provide an opportunity as a strategy for conservation as genetic drift and change will occur even with conservation measures and genetics from distant ancestors can be brought back in. Another option for the Hays Converter breed to increase genetic diversity would be to bring in new genetics from other breeds and subsequently upgrade animals to purebred Hays Converter status.

3.6. Conclusion

The Hays Converter breed was developed in a manner that readily endured and permitted inbreeding. A small number of animals formed the breed and contributed to the present
population. As a result a low amount of genetic diversity was discovered. The condition of the pedigree information resulted in some difficulty obtaining accurate estimates of the current level of genetic diversity and inbreeding in the population, and the results need to be considered with the incomplete pedigree in mind.

An increasing rate of inbreeding was observed for the population. A greater level of inbreeding was observed when missing pedigree information was accounted for suggesting inbreeding was underestimated using the available pedigree. A more complete and deeper pedigree would give a better understanding on the real inbreeding level currently in the breed.

The low number of Hays Converter animals maintained in the breeding population suggests the level of inbreeding could increase substantially and a rapid loss of genetic diversity could occur if measures to limit the rate are not exercised. Genetic progress and preservation of genetic diversity in the population need to be considered for future economic viability and to ensure long-term response to selection and survival. An increase in pedigree knowledge is essential in implementing genetic conservation strategies. An increase in \( N_e \) by raising the total number of breeding animals, or increasing the number of bulls utilized can reduce the rate of genetic diversity loss. The introduction of genetics from other beef cattle breeds followed by breeding back to the Hays Converter breed provides an opportunity to increase the genetic diversity observed in the breed. Selection strategies can be employed to make decisions to improve traits of interest while limiting inbreeding.
Table 3.1. Total number of animals, number of founders, effective number of founders ($f_e$), effective number of ancestors ($f_a$), and founder genome equivalents ($f_g$) for the reference populations.

<table>
<thead>
<tr>
<th></th>
<th></th>
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<tbody>
<tr>
<td>Total animals</td>
<td>1601</td>
<td>365</td>
</tr>
<tr>
<td>Founders</td>
<td>589</td>
<td>345</td>
</tr>
<tr>
<td>$f_e$</td>
<td>63.7</td>
<td>61.3</td>
</tr>
<tr>
<td>$f_a$</td>
<td>25.64</td>
<td>13.46</td>
</tr>
<tr>
<td>$f_g$</td>
<td>13.18</td>
<td>7.38</td>
</tr>
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</table>
### Table 3.2. Top ten marginal contributing ancestors to the 2006-2011 reference population.

<table>
<thead>
<tr>
<th>Ancestor</th>
<th>Sire</th>
<th>Dam</th>
<th>Year</th>
<th>Sex</th>
<th>Contributions</th>
<th>No. progeny</th>
<th>No. descendants</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>total</td>
<td>marginal</td>
<td>cumulated</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HAY305J99</td>
<td>HAY160C</td>
<td>HAY318C</td>
<td>1999</td>
<td>M</td>
<td>0.1839</td>
<td>0.1839</td>
<td>0.1839</td>
</tr>
<tr>
<td>GOC074G</td>
<td>HAY030E95</td>
<td>HAY055D94</td>
<td>1997</td>
<td>M</td>
<td>0.1315</td>
<td>0.1315</td>
<td>0.3154</td>
</tr>
<tr>
<td>HAY044L01</td>
<td>HAY101M</td>
<td>HAY044E95</td>
<td>2001</td>
<td>M</td>
<td>0.1110</td>
<td>0.1110</td>
<td>0.4264</td>
</tr>
<tr>
<td>KU001M</td>
<td>KU027H</td>
<td>KU009B</td>
<td>2002</td>
<td>M</td>
<td>0.0555</td>
<td>0.0555</td>
<td>0.4818</td>
</tr>
<tr>
<td>HAY143F</td>
<td>unknown</td>
<td>HAY044B</td>
<td>1974</td>
<td>M</td>
<td>0.0930</td>
<td>0.0436</td>
<td>0.5254</td>
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<tr>
<td>HAY107E</td>
<td>unknown</td>
<td>HAY081C</td>
<td>1973</td>
<td>M</td>
<td>0.1084</td>
<td>0.0356</td>
<td>0.5610</td>
</tr>
<tr>
<td>HAY009F</td>
<td>unknown</td>
<td>HAY094A</td>
<td>1974</td>
<td>M</td>
<td>0.0509</td>
<td>0.0310</td>
<td>0.5921</td>
</tr>
<tr>
<td>HAY179M</td>
<td>HAY126J</td>
<td>HAY031B</td>
<td>1980</td>
<td>M</td>
<td>0.0791</td>
<td>0.0246</td>
<td>0.6166</td>
</tr>
<tr>
<td>HAY115X</td>
<td>HAY059N</td>
<td>COZ040P</td>
<td>1988</td>
<td>M</td>
<td>0.0303</td>
<td>0.0227</td>
<td>0.6394</td>
</tr>
<tr>
<td>HAY394D</td>
<td>unknown</td>
<td>HAY070A</td>
<td>1972</td>
<td>M</td>
<td>0.0381</td>
<td>0.0202</td>
<td>0.6596</td>
</tr>
</tbody>
</table>


Table 3.3. Number of ancestors required to explain percent of the genetic pool of animals included in reference populations.

<table>
<thead>
<tr>
<th>Reference population</th>
<th>25%</th>
<th>50%</th>
<th>75%</th>
<th>90%</th>
<th>95%</th>
<th>99%</th>
</tr>
</thead>
<tbody>
<tr>
<td>1995-1999</td>
<td>3</td>
<td>9</td>
<td>30</td>
<td>110</td>
<td>184</td>
<td>307</td>
</tr>
<tr>
<td>2006-2011</td>
<td>2</td>
<td>5</td>
<td>18</td>
<td>47</td>
<td>70</td>
<td>108</td>
</tr>
</tbody>
</table>
Table 3.4. Ten Hays Converter ancestors with the largest ancestral contribution to the inbreeding found in animals born between 2006 and 2011.

<table>
<thead>
<tr>
<th>Ancestor</th>
<th>Sire</th>
<th>Dam</th>
<th>Year</th>
<th>Sex</th>
<th>Inbreeding contribution</th>
<th>percent of total</th>
<th>cumulated percent</th>
<th>No. progeny</th>
<th>No. descendants</th>
</tr>
</thead>
<tbody>
<tr>
<td>HAY305J99</td>
<td>HAY160C</td>
<td>HAY318C</td>
<td>1999</td>
<td>M</td>
<td>0.004795</td>
<td>13.1768</td>
<td>13.1768</td>
<td>155</td>
<td>286</td>
</tr>
<tr>
<td>HAY107E</td>
<td>unknown</td>
<td>HAY081C</td>
<td>1973</td>
<td>M</td>
<td>0.004461</td>
<td>12.2590</td>
<td>25.4358</td>
<td>140</td>
<td>8455</td>
</tr>
<tr>
<td>HAY143F</td>
<td>unknown</td>
<td>HAY044B</td>
<td>1974</td>
<td>M</td>
<td>0.003497</td>
<td>9.6108</td>
<td>35.0466</td>
<td>144</td>
<td>8514</td>
</tr>
<tr>
<td>HAY179M</td>
<td>HAY126J</td>
<td>HAY031B</td>
<td>1980</td>
<td>M</td>
<td>0.002303</td>
<td>6.3284</td>
<td>41.3750</td>
<td>118</td>
<td>4990</td>
</tr>
<tr>
<td>HAY101M</td>
<td>HAY229H</td>
<td>HAY127G</td>
<td>1980</td>
<td>M</td>
<td>0.001937</td>
<td>5.3223</td>
<td>46.6972</td>
<td>204</td>
<td>2960</td>
</tr>
<tr>
<td>HAY222Y</td>
<td>HAY255T</td>
<td>HAY245R</td>
<td>1989</td>
<td>M</td>
<td>0.001766</td>
<td>4.8531</td>
<td>51.5503</td>
<td>126</td>
<td>1076</td>
</tr>
<tr>
<td>GOC074G</td>
<td>HAY030E95</td>
<td>HAY055D94</td>
<td>1997</td>
<td>M</td>
<td>0.001370</td>
<td>3.7648</td>
<td>55.3151</td>
<td>129</td>
<td>209</td>
</tr>
<tr>
<td>HAY053H</td>
<td>HAY143F</td>
<td>HAY021E</td>
<td>1976</td>
<td>M</td>
<td>0.001255</td>
<td>3.4495</td>
<td>58.7646</td>
<td>79</td>
<td>4319</td>
</tr>
<tr>
<td>HAY255T</td>
<td>HAY179M</td>
<td>SMS025P</td>
<td>1985</td>
<td>M</td>
<td>0.001023</td>
<td>2.8126</td>
<td>61.5772</td>
<td>29</td>
<td>1419</td>
</tr>
<tr>
<td>HAY031F</td>
<td>unknown</td>
<td>HAY064B</td>
<td>1974</td>
<td>M</td>
<td>0.000953</td>
<td>2.6184</td>
<td>64.1956</td>
<td>75</td>
<td>5111</td>
</tr>
</tbody>
</table>
Table 3.5. Number of ancestors explaining percent of the inbreeding decomposed into ancestral components for animals born between 2006 and 2011.

<table>
<thead>
<tr>
<th>Percent explained</th>
<th>25%</th>
<th>50%</th>
<th>75%</th>
<th>90%</th>
<th>95%</th>
<th>99%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of animals</td>
<td>2</td>
<td>6</td>
<td>16</td>
<td>26</td>
<td>33</td>
<td>52</td>
</tr>
</tbody>
</table>
Table 3.6. Mean pedigree completeness index (PCI) for five generations (5G), mean level of inbreeding (F), range of inbreeding and percent of inbred animals by PCI (5G) category.

<table>
<thead>
<tr>
<th>PCI category</th>
<th>n animals</th>
<th>Percent animals</th>
<th>mean PCI</th>
<th>mean F</th>
<th>Range of F</th>
<th>n animals</th>
<th>Percent animals</th>
<th>Range of F</th>
<th>n animals</th>
<th>Percent animals</th>
<th>Range of F</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 ≤ PCI &lt; 0.24</td>
<td>4608</td>
<td>33.7</td>
<td>0</td>
<td>0</td>
<td>0 - 0.25</td>
<td>3</td>
<td>0.3</td>
<td>0.125</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>0.24 ≤ PCI &lt; 0.4</td>
<td>974</td>
<td>7.1</td>
<td>0.33</td>
<td>0.00064</td>
<td>0 - 0.25</td>
<td>3</td>
<td>0.3</td>
<td>0.125</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>0.4 ≤ PCI &lt; 0.6</td>
<td>1405</td>
<td>10.3</td>
<td>0.501</td>
<td>0.0146</td>
<td>0 - 0.25</td>
<td>221</td>
<td>15.7</td>
<td>0.00098</td>
<td>0.3</td>
<td>0.125</td>
<td>0.25</td>
</tr>
<tr>
<td>0.6 ≤ PCI &lt; 0.8</td>
<td>2395</td>
<td>17.5</td>
<td>0.701</td>
<td>0.0234</td>
<td>0 - 0.3125</td>
<td>1461</td>
<td>61.0</td>
<td>0.00098</td>
<td>0.6</td>
<td>0.3125</td>
<td>0.32</td>
</tr>
<tr>
<td>0.8 ≤ PCI ≤ 1</td>
<td>4294</td>
<td>31.4</td>
<td>0.920</td>
<td>0.0407</td>
<td>0 - 0.32</td>
<td>4199</td>
<td>97.8</td>
<td>0.0004</td>
<td>0.9</td>
<td>0.32</td>
<td>0.32</td>
</tr>
</tbody>
</table>
Figure 3.1. Number of female, male, and total recorded births per year included in the Hays Converter pedigree file.
Figure 3.2. Percent of animals born by year of birth in the Hays Converter pedigree with only sire known, only dam known, both parents known, and no parent known.
Figure 3.3. Average number of generation equivalents (ge) by year of birth.
Figure 3.4. Distribution of Pedigree completeness index (PCI) values for five generations (5G).
Figure 3.5. Average pedigree completeness index (PCI) for five generations (5G) and ten generations (10G) by year of birth.
Figure 3.6. Distribution of inbreeding coefficients (F) for all animals and animals with a pedigree completeness index (PCI) for five generations (5G) greater than or equal to 0.6 (PCI≥0.6).
Figure 3.7. Average inbreeding coefficient (F) by year of birth for all animals and animals with a pedigree completeness index (PCI) for five generations (5G) greater than or equal to 0.6.
Figure 3.8. Average inbreeding coefficient (F) by year of birth calculated using VRA accounting for missing pedigree information and average F calculated with the original pedigree for animals with a pedigree completeness index (PCI) greater than or equal to 0.6.
Figure 3.9. Average inbreeding coefficient (F) by year of birth calculated with the simulated pedigree and the combined original and simulated pedigree, and the average F from the original pedigree for animals with a pedigree completeness index (PCI) greater than or equal to 0.6.
CHAPTER 4
ESTIMATION OF GENETIC PARAMETERS AND TRENDS FOR HAYS CONVERTER CATTLE

4.1. Abstract

The estimation of genetic parameters and breeding values for Hays Converter would be valuable for the development of future breeding strategies for the breed. Records for birth weight, weaning weight, yearling weight, ultrasound lean meat yield, ribeye area, marbling, and back fat, and carcass fat cover, hot weight, marbling, ribeye area, and percent saleable meat were analyzed using a univariate and bivariate animal model. The Hays Converter breed has been selected primarily to increase weaning and yearling weights. The heritability of direct and maternal weaning weight effects and yearling weight were 0.30, 0.04, and 0.42, respectively. The genetic correlation between direct weaning weight and yearling weight was 0.81. Both weaning weight direct and yearling weight showed a positive trend in average estimated breeding value over time. Heritability estimates for ultrasound lean meat yield, ribeye area, and marbling were 0.21, 0.19, and 0.23, respectively. A low number of records available for ultrasound and carcass traits did not allow for the accurate estimation of genetic parameters and breeding values.

4.2. Introduction

Knowledge of genetic parameters is critical in the development of breeding strategies for genetic improvement. Tosh (1999) noted the necessity of genetic parameters in the implementation of breeding programs and the assessment of breeding strategies. Genetic parameters are needed in the determination of the genetic merit of animals which is important in selection and the optimization of genetic gain for traits of interest. In addition, an understanding
of genetic correlations among traits is required by many methods of genetic evaluation and to produce successful breeding selection programs. The accurate estimation of genetic parameters requires large across-generation data sets with reliable pedigree information. Genetic parameters for production traits in beef cattle have been widely reported in the literature and have been reviewed by Meyer (1992a), Koots et al. (1994a), and Marshall (1994). These estimates use a variety of methods and populations, and at times had conflicting results.

The Hays Converter breed of beef cattle was primarily developed and selected to excel in growth since its formation in the late 1950s. Weaning and yearling weight phenotypic measures were used to determine superior animals for growth and aid in selection decisions to further the breed. The Hays Converter Association (Calgary, AB) requires adjusted weaning and yearling weights to be included on the registration papers of all registered Hays Converters. Furthermore, in an effort to maintain the selection focus of the breed on growth, all bulls used for artificial insemination to produce registrable Hays Converter progeny must have a recorded adjusted yearling weight of at least 1,100 lbs (500 kg). Genetic improvement programs for beef cattle have traditionally focused on live animal growth traits because cattle were customarily priced based on average live or dressed weight. Value-based marketing has been adopted by a number of processors in the beef industry consisting of a base price with premiums and discounts applying to carcasses above and below base quality specifications. In addition to growth traits, carcass quality traits should also be considered in genetic improvement programs to increase economic worth. Real-time ultrasound in beef cattle provides a cost-effective method of evaluating an animal’s carcass merit without the animal having to be slaughtered (Wilson, 1992). Moser et al. (1998) concluded ultrasound measurements could be used to attain accurate estimates of genetic merit of carcass traits for potential breeding animals.
The objective of this study was to estimate genetic parameters and genetic trends for growth, ultrasound, and carcass data collected on Hays Converter cattle.

4.3. Materials & Methods

4.3.1. Phenotypic records

Data were recorded and provided by Hays Ranches (Calgary, AB) and combined with the pedigree information. The last updated data was received in November, 2011. Traits analyzed included birth weight (BW), weaning weight (WW), yearling weight (YW), ultrasound back fat (UBF), marbling (UMAR), ribeye area (UREA), lean meat yield (ULMY), carcass hot weight (CHW), fat cover (CFAT), ribeye area (CREA), marbling score (CMAR), and percent saleable meat (CSAL). Records for animals that were from embryo transfer (n=14), twins (n=126), or were fostered by another dam (n=41) were removed.

4.3.2. Weight trait data

Weight trait records available for select animals born between 1969 and 2011 included birth weight (BW; n=5,564), weaning weight (WW; n=9,523), and yearling weight (YW; n=6,601). Weaning and yearling weight data were available in the form of raw weights at time of weaning and/or as adjusted weights calculated by two sources, Hays Ranches and the Canadian Livestock Records Corporation (CLRC). Calculated adjusted weights by the two sources were not equal as different, unknown adjustments were used. If the raw weights were provided in conjunction with age at weighing, these data were used to calculate a 200-day adjusted weaning or 365-day adjusted yearling weights. Adjusted weaning weights were calculated by adding the product of 200 days and average daily gain to actual day of weaning to birth weight (BIF, 2010). If this information was not recorded, the adjusted weights calculated by Hays Ranches were used,
and CLRC adjusted weights were only used when they were the only weights available. Weaning and yearling weights were set to missing if they were outside ranges considered reasonable (WW, 200 to 1,500 lbs [90.7 to 580.3 kg]; YW, 350 to 2,000 lbs [158.8 to 907.2 kg]). Calves had to be weaned within the age range of 160 to 250 days as defined by the Beef Improvement Federation (BIF) to have their weaning weights included. Yearling weights had to be recorded between 320 to 410 days of age to be considered valid. Weaning weights and yearling weights had to have been taken at least 70 days apart for yearling weights to be used. On any occasion where an animal’s weaning or yearling weight was known to be a standard entry, the weight was removed and considered missing. For a calf’s birth weight to be included, the calf must have survived to register a weaning weight. This was done to remove calves that were aborted, stillborn, or were born in a condition not compatible with survival and had a birth weight recorded. Data containing a standard input birth weight of 70 lbs (31.8 kg) for female calves and 75 lbs (34.0 kg) for male calves when birth weight was unavailable were removed. Weight records were originally recorded in imperial units and converted to metric units after editing was completed. Animals were assigned to contemporary groups of herd prefix, year of birth, and cow group. For yearling weight sex management group was added to the contemporary group definition based on the different handling of replacement heifers, replacement bulls, fed heifers, and steers. The cow group term is a classification based on the separate management of first-calf heifers and mature cows. Weight records of animals in a group with fewer than five contemporaries were discarded. The number of records, mean, and standard deviation for each weight trait for males and females after edits were performed are displayed in Table 4.1.
4.3.3. Ultrasound trait data

Live-animal ultrasound data was recorded on select animals born between 2002 and 2010 and included measurements for back fat (UBF; n=539), marbling (UMAR; n=539), ribeye area (UREA; n=539), and lean meat yield (ULMY; n=348). Ultrasound measurements were collected for all recorded animals born in 2002, and 2008 to 2010, while only replacement females had ultrasound measurements done in all other years. Lean meat yield (ULMY) was only determined in six of the nine years, and the method of calculating ULMY was not provided. Ultrasound measures were taken on animals at approximately one year of age. All ultrasound measurements performed in a given year were done on the same day by a single technician. In years where UREA records were less than 40 units it was assumed these values were recorded in square inches and were therefore converted to square centimetres to ensure consistent units. Animals were allocated into contemporary groups based on herd prefix, year of birth, cow group, and sex management group. Records for animals in a group with fewer than five contemporaries were discarded. Table 4.2 contains the number of records, mean, and standard deviation for each ultrasound trait for replacement heifers, fed heifers, replacements bulls, and fed steers recorded after edits were performed.

4.3.4. Carcass trait data

Carcass data for animals born in 2007 and 2010, slaughtered in 2008 and 2011, consisted of carcass hot weight (CHW; n=194), fat cover (CFAT; n=62), ribeye area (CREA; n=58), marbling score (CMAR; n=135), and percent saleable meat (CSAL; n=113). Depending on the year, not all traits were recorded for each evaluated carcass. Animals were allocated into contemporary groups based on herd, year of birth, cow group, sex management group, and slaughter date. Records for animals in a group with fewer than five contemporaries were
discarded. Table 4.3 contains the number of records, mean, and standard deviation for each carcass trait for replacement heifers, fed heifers, replacements bulls, and fed steers recorded after edits were performed.

4.3.5. Genetic parameter estimation

Each trait was initially considered separately with a univariate animal model. Unknown parents were left as unknown in the analysis. Birth weight and weaning weight were analyzed with direct and maternal genetic effects using the following linear animal model:

\[ y = Xb + Z_1a + Z_2m + Z_3p + e, \]

where \( y \) is the phenotypic observations, \( b \) is a vector of fixed effects, \( a \) is a vector of random additive genetic effects, \( m \) is a vector of random maternal genetic effects, \( p \) is a vector of maternal permanent environment effects, and \( X \) and \( Z_{1:3} \) are known incidence matrices relating the observations to their respective fixed and random effects.

The variance-covariance structure is:

\[
\begin{pmatrix}
\sigma_a^2 & \sigma_{am} & 0 & 0 \\
\sigma_{am} & \sigma_m^2 & 0 & 0 \\
0 & 0 & I\sigma_e^2 & 0 \\
0 & 0 & 0 & I\sigma_e^2 \\
\end{pmatrix},
\]

where \( \sigma_a^2 \) is the additive genetic variance, \( \sigma_m^2 \) is the maternal genetic variance, \( \sigma_{am} \) is the additive genetic by maternal genetic covariance, and \( \sigma_e^2 \) is the maternal permanent environmental variance.

The model assumes the following distributions for the random effects:

\[
\begin{pmatrix}
a \\
m \\
p \\
e
\end{pmatrix} | G_0 \sim N \left( \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}, G_0 \otimes \Lambda \right), \text{ and } p | I, \sigma_p^2 \sim N \left( 0, I\sigma_p^2 \right), \text{ and } e \sim N \left( 0, I\sigma_e^2 \right)
\]
where A is the numerator relationship matrix, \( G_0 \) is the (co)variance matrix of additive genetic effects:

\[
G_0 = \begin{bmatrix}
\sigma^2_j & \sigma_{dm} \\
\sigma_{dm} & \sigma^2_m
\end{bmatrix}.
\]

The remainder of the traits were analyzed using a general linear animal model:

\[
y = Xb + Za + e
\]

The expectations and assumed variances are \( \text{E}(y) = Xb; \text{E}(a) = \text{E}(e) = 0; \text{V}(a) = G; \text{V}(e) = R; \)
\( \text{V}(y) = ZGZ' + R \), where G is the direct product of A and \( G_0 \), R is the direct product of an identity matrix and the matrix of error variances and covariances.

The model used to evaluate BW was:

\[
\text{BW}_{ijklmo} = \text{cg}_i + \text{sex}_j + \text{s Breed}_k + \text{db Breed}_l + \text{d Age}_m + a_n + m_o + p_e + e_{ijklmo}
\]

where BW is the birth weight of the \( n \)th animal, cg is the fixed effect of the \( i \)th contemporary group (herd, year, cow group), sex is the fixed effect of the \( j \)th sex (male; female), sbreed is the fixed effect of the \( k \)th breed of the sire, dbreed is the fixed effect of the \( l \)th breed of dam o, dage is the fixed effect of the \( m \)th age of the dam (1; 2; 3; 4; 5 to 10; ≥11), a is the random additive genetic effect of animal n, m is the random maternal genetic effect of dam o, pe is the permanent environmental effect of dam o, and e is the residual effect.

The model used to evaluate WW was:

\[
\text{WW}_{ijklm} = \text{cg}_i + \text{source·sex·d age}_j + \text{s Breed}_k + \text{db Breed}_l + a_m + m_o + p_e + e_{ijklm}
\]

where WW is the 200d weaning weight of the \( m \)th animal, cg is the fixed effect of the \( i \)th contemporary group (herd, year, cow group), source·sex·dage is the fixed effect of the \( j \)th data
source by sex (male; female) and dam age (1; 2; 3; 4; 5 to 10; ≥11), sbreed is the fixed effect of the kth breed of the sire, dbreed is the fixed effect of the lth breed of dam o, a is the random additive genetic effect of animal m, m is the random maternal genetic effect of dam n, pe is the permanent environmental effect of dam n, and e is the residual effect.

The model used to evaluate YW was:

\[ YW_{ijklm} = cg_i + source_j + sbreed_k + dbreed_l + a_m + e_{ijklm} \]

where YW is the 365d yearling weight of the mth animal, cg is the fixed effect of the ith contemporary group (herd, year, cow group, sex management group), source is the fixed effect of the jth data source, sbreed is the fixed effect of the kth breed of the sire, dbreed is the fixed effect of the lth breed of the dam, a is the random additive genetic effect of animal m, and e is the residual effect.

All ultrasound and carcass traits were analyzed using the following model:

\[ y_{ijklm} = cg_i + age_j + sbreed_k + dbreed_l + a_m + e_{ijklm} \]

where y is the record of the mth animal, cg is the fixed effect of the ith contemporary group (herd, year, cow group, sex management group, slaughter date [for carcass slaughter records only]), age is a covariate for age at ultrasound or slaughter, sbreed is the fixed effect of the kth breed of the sire, dbreed is the fixed effect of the lth breed of the dam, a is the random additive genetic effect of animal m, and e is the residual effect.

Table 4.4 summarizes the effects included in the model for each trait analyzed. Weaning weight and yearling weight were additionally analyzed using a bivariate animal model as they are highly correlated traits and contained the most records for more reliable estimates. This was
also done to allow for more accurate EBVs to be calculated and eliminate any culling bias present.

Variance components were estimated and heritability and genetic correlations determined using the ASReml software package (Gilmour et al., 2009). Estimated breeding values (EBVs) for all traits analysed were calculated. For BW, UBF, CBF, CHW, CMAR, CREA, and CSAL, heritability values could not be accurately estimated and therefore EBVs were estimated using average heritability estimates from the literature. Variance components were restricted to heritability estimates of 0.50, 0.10, 0.30, 0.34, 0.40, 0.46, 0.47, and 0.40 for BW\textsubscript{d}, BW\textsubscript{m}, UBF, CBF, CHW, CMAR, CREA, and CSAL, respectively. The trends in EBVs by year of birth were examined. The accuracy for a given trait is dependent on the heritability and the amount of information available on the individual and its relatives for the trait of interest and any genetically correlated traits. The accuracy of an EBV is the correlation between the true breeding value and the EBV and was calculated following Henderson (1984):

$$ r = \sqrt{1 - \frac{P}{\sigma^2_a}} $$

where P is the prediction error variance, and $\sigma^2_a$ is the additive genetic variance.

4.4. Results

Heritability estimates and standard errors are shown in Table 4.5 for growth and ultrasound traits calculated from univariate animal models. Heritability estimates for carcass traits are not reported because they were not in the range of acceptable values and had large standard errors associated with them. Genetic parameters for both ultrasound and carcass back fat records could not be estimated.
4.4.1. Growth traits

The calculated heritability for both BW\textsubscript{d} and BW\textsubscript{m} using Hays Converter data were much lower than expected and therefore EBVs were calculated using a heritability estimate of 0.5 and 0.1 for BW\textsubscript{d} and BW\textsubscript{m}, respectively. The trends in EBVs for BW\textsubscript{m} and BW\textsubscript{d} are shown in Figure 4.1. A large decrease in the average EBV for BW\textsubscript{d} began after 2004. The opposite occurred in the trend for the average EBV of BW\textsubscript{m}. A negative genetic correlation with a large standard error between direct and maternal effects was found (-0.36±0.30).

The heritability estimates of birth weight for direct (BW\textsubscript{d}) and maternal effects (BW\textsubscript{m}) were very low at 0.06±0.03 and 0.03±0.02, respectively. The genetic correlation between direct and maternal variance was moderate and negative but had a large standard error associated (-0.37±0.3). Direct weaning weight (WW\textsubscript{d}) was found to be moderately heritable (0.35±0.04) while maternal weaning weight (WW\textsubscript{m}) effects had a low heritability (0.05±0.02). The genetic correlation between the two was large and negative (-0.77±0.10). Yearling weight (YW) had a moderate heritability of 0.4±0.03. Weaning and yearling weights had a strong phenotypic correlation of 0.75±0.02. A bivariate analysis of WW and YW resulted in heritability estimates of WW\textsubscript{d} and WW\textsubscript{m} decreasing slightly and YW increasing a small amount. Table 4.6 displays the genetic parameters estimated from the bivariate analysis. The genetic correlation between WW\textsubscript{d} and WW\textsubscript{m} was negative and moderate (-0.25±0.01), smaller than the estimation from the WW univatiate model. The genetic correlation was 0.81±0.04 between WW\textsubscript{d} and YW.

The Hays Converter breed was developed and selected with weaning weight and yearling weight having a large bearing. Estimated breeding values were calculated using the solutions of the bivariate animal model for WW\textsubscript{d}, WW\textsubscript{m}, and YW. The average EBV for WW\textsubscript{m}, by year of birth is displayed in Figure 4.2. The average EBV by year of birth was only presented for 1966
onward because very few animals born prior to this year were recorded in the pedigree, and therefore average EBVs were only representative of a small number of selected animals. A slight positive trend was observed for $\text{WW}_m$ in the last couple of decades. The average EBV is variable depending on the year. The average EBV for Hays Converter cattle in the pedigree file by year of birth for $\text{WW}_d$ is shown in Figure 4.3. The EBVs are close to zero until 1980 when a positive trend begins. The trend is moderately flat in the 1990s and a sharp increase occurs for animals born in 2001. The trend for the average EBV for YW by year of birth largely follows that observed for $\text{WW}_d$ (Figure 4.4). Estimated breeding values for YW had the greatest accuracy on average compared to all other traits. For all animals in the pedigree file with an estimable breeding value the average accuracy for $\text{WW}_d$, $\text{WW}_m$, and YW were 0.59, 0.41, and 0.63 respectively. Figure 4.5 displays the distribution of accuracies for $\text{WW}_d$ and YW.

4.4.2. Ultrasound traits

The heritability for ultrasound traits was estimated for ULMY, UMAR, and UREA. Genetic parameters for UBF could not be estimated. The heritabilities calculated for ULMY, UMAR, and UREA were moderate and equalled 0.21±0.14, 0.23±0.10, and 0.19±0.10, respectively. The standard errors for the heritability estimates were all high. Genetic progress was evaluated using EBVs calculated with the determined variance components. Estimates for UBF were calculated with variance components restricted to a given ratio producing a heritability of 0.3. For all animals in the pedigree the average accuracies of the EBVs for UMAR, UREA, ULMY, and UBF were 0.20, 0.15, 0.14, and 0.17, respectively. Figure 4.6 displays the distribution of accuracies for all ultrasound traits. Most animals had EBVs with very low accuracies for all four ultrasound traits. Animals born in the earlier years of the breed’s history generally had lower accuracies for calculated EBVs. The trend in UMAR, UREA, ULMY, and...
UBF EBVs are shown in Figure 4.7. The average EBVs for ULMY were negative for all observable years. The period between 1969 and 2003 for ULMY is moderately flat and values became closer to zero in the 2000s. For UREA, values are around zero for much of the past and became more variable in the 2000s. UMAR exhibits a positive genetic trend from 1966 to 2000. A sharp decrease is observed for animals born in 2001 followed by another upwards trend. A very similar trend was also observed for UBF.

4.4.3. Carcass traits

Estimated breeding values for carcass traits were calculated using heritabilities from the literature. Figure 4.8 shows the distribution of accuracies for EBVs of CHW, CMAR, CREA, CSAL, and CFAT. Carcass hot weight EBVs had the greatest accuracy on average (0.14), but all carcass traits had EBVs with very low accuracies. The genetic trend for CFAT, CHW, and CMAR did not see any genetic progress over time (Figure 4.9). Average EBVs for CFAT and CMAR were mostly negative. There was a negative trend observed for CREA and positive genetic trend for CSAL (Figure 4.9).

4.5. Discussion

The estimated heritability for BW_d was much lower than other estimates in the literature. Gregory et al. (1995) found heritability estimates were similar for birth weight in purebred (0.24±0.10) and composite (0.26±0.17) beef breeds. In four lines of Hereford cattle, Dodenhoff et al. (1998) estimated heritabilities for birth weight direct effects ranging from 0.38 to 0.47. Maternal heritability was less than that for direct heritability which suggests that birth weight is more influenced by the genetics of the calf than those of its dam. A lower maternal heritability compared to direct heritability is frequently reported for birth weight (Bertrand and Benyshek, 1987; Trus and Wilton, 1988; Dodenhoff et al., 1998; Eriksson et al., 2004). However, the
opposite has been found by Nelson et al. (1984) and Cantet et al. (1988). Estimates of maternal heritability for birth weight in the literature are greater than what was found in this study and range from 0.06 to 0.15 (Bennett and Gregory, 1996; Dodenhoff et al., 1998; Eriksson et al., 2004). The genetic correlation between direct and maternal effects was moderate and negative but had a large standard error. Trus and Wilton (1988) found negative correlations for birth weight direct and maternal effects of -0.22, -0.39, -0.34, and -0.39 for Simmental, Hereford, Angus, and Charolais breeds, respectively, and a positive correlation of 0.55 for Shorthorns. The extremely low estimate of the direct heritability for birth weight in Hays Converter cattle even with a large number of records available (n=5,564) suggests potential problems with the data. A large error variance was found and produced the small heritability estimates. Standard entries may still be present in the data and there was no information indicating how birth weights were obtained or how long after birth they were acquired. Invalid birth weights may have been unintentionally included in the analysis. The accuracy and completeness of the pedigree used may also have had an impact on the precision of the calculated parameters from the model. The negative genetic trend in BW$_d$ since 2004 may have been caused by an increase in the accuracy of the recording of birth weights and the increased use of low birth weight Angus bulls on Hays Converter first-calf heifers.

Weaning weight and yearling weight were the main traits of interest in the development of the Hays Converter breed, and therefore these traits had the greatest number of records available. Standard errors for estimates of heritability and genetic correlations for WW$_d$, WW$_m$, and YW were all low. Heritability estimates were relatively unchanged when weaning weight and yearling weight were analyzed together. Heritability estimated for WW$_d$ was moderate while the heritability of WW$_m$ was found to be low. The estimated heritability for WW$_d$ was consistent
with those reported in the literature. The heritability estimated for \( WW_m \) was lower than expected and slightly below estimates in the literature for beef cattle. Bennett and Gregory (1996) found average heritabilities for direct 200-day weight of 0.28 and 0.37, and average heritabilities for maternal 200-day weight of 0.13 and 0.06 for purebred and composite beef breeds, respectively. In a multibreed population of beef cattle Tosh et al. (1999) estimated direct and maternal weaning weight heritabilities as 0.33 and 0.13, respectively. Similar direct and maternal 200-day weight heritabilities of \( 0.30 \pm 0.04 \) and \( 0.19 \pm 0.04 \) were found by MacNeil (2003).

The genetic correlation of \( WW_d \) and \( WW_m \) was large and negative when weaning weight was analyzed alone. When estimated in a bivariate model with \( YW \), the correlation between \( WW_d \) and \( WW_m \) exhibited an increase but remained moderate and negative. The additional information from using two traits may have resulted in improved estimates because of the high genetic correlation between the traits. The negative genetic correlation between direct and maternal effects suggests an antagonistic genetic relationship. Negative direct-maternal genetic correlations have been widely reported in the literature (Meyer, 1992a; Koots et al., 1994b). It has been suggested the negative estimate may be influenced by a negative dam-offspring environmental correlation (Baker, 1980), or additional, unaccounted for variation between sires (Robinson, 1996). These errors may be especially prominent with the use of field data as was the case with this analysis. The estimation of the correlation between direct and maternal genetic effects also depends on the structure of the data and pedigree relationships (Meyer, 1992b). Estimates are dependent on the proportion of dams with their own performance records and the number of offspring per dam. The Hays Converter data contained a small number of dams in comparison to the number of total animals with records which may explain the large negative correlation between direct and maternal effects.
A moderate heritability was found for yearling weight for the Hays Converter (0.4). Yearling weight heritabilities of 0.50, 0.48, and 0.39 were reported by Bennett and Gregory (1996), Tosh et al. (1999), and MacNeil (2003), respectively. In the present study yearling weight was found to be highly genetically correlated with direct weaning weight (0.81). The genetic correlation between yearling weight and maternal weaning weight was moderate and had a sizeable standard error. Bennett and Gregory (1996) found genetic correlations of 0.87 and 0.93 for direct 200-day and 368-day weights, and 0.16 and 0.17 for maternal 200-day weight and direct 368-day weight for purebred and composite beef breeds, respectively. Tosh et al. (1999) reported genetic correlations of 0.89 and 0.07 for yearling weight with direct and maternal weaning weights, respectively.

Animals in the Hays Converter breed were largely selected for weaning weight and yearling weight from the beginning of the breeding program. Both traits showed a similar genetic trend and displayed increases in average EBVs over time. This trend corroborates the selection strategy used for the breed. The increase is not seen until the 1970s when more animals started being identified in the pedigree and the recording of WW and YW became standard. A noticeable increase was observed for animals born in 2001 for both traits. In 2000, the Hays Converter herd experienced a reduction in size and cows that remain in the new breeding herd were mainly selected based on their records and their progeny’s records for WW and YW. Progeny of these animals in subsequent years would therefore be expected to have greater EBVs on average than those born prior to the downsizing and selection of a superior breeding group. There was no apparent genetic trend for WWm likely due to the poor estimation of genetic parameters for the trait. Calculated EBVs were small in magnitude for WWm. It was not a trait of interest for the breed and was not selected for. The influence of the Holstein and Brown Swiss
may have provided more than sufficient amounts of milk and therefore an increase in milk production was not needed or observed.

Heritability was estimated for ULMY, UMAR, and UREA. The calculated heritabilities for all three traits were lower than expected and had large standard errors. Variance components could not be estimated for UBF despite the number of records available being equal to those for UMAR and UREA. This may be due to additional sources of variation that are not accounted for, or technician and recording errors. In addition, variance components could not be estimated for CFAT. A very small number of animals had records for CFAT, however. Heritabilities were not reported for any of the carcass traits due to unreasonable estimates with very large standard errors. Ultrasound data was only collected for a short time and only on select animals, and carcass data for even fewer animals. A larger dataset needs to be collected and analysed to attain more accurate estimates for the Hays Converter breed.

Heritability estimates in the literature for other beef cattle breeds were greater than those found for the Hays Converter. In a summary of literature estimates, Bertrand et al. (2001) found an average heritability for ultrasound ribeye area, fat thickness, and percentage of intramuscular fat of 0.32, 0.28, and 0.41, respectively. Kemp et al. (2002) examined data from Angus steers and reported age-adjusted heritability estimates for ultrasound ribeye area and fat thickness of 0.29 and 0.39, respectively. Heritability estimates calculated by Bergen et al. (2006) for ultrasound age-constant yearling bull lean percentage estimates ranged from 0.26 to 0.42 depending on the calculation method employed.

A limited number of animals had measurements recorded for ultrasound and carcass traits and these represented only select animals born after 2002 for ultrasound data and 2007 for carcass slaughter data. As a result the majority of EBVs calculated had low accuracies associated
with them, especially for the more historical animals in the pedigree. This made long-term genetic trends problematic to ascertain. The Hays Converter breed was selected predominately for growth records and traits pertaining to carcass merit were not considered. Strong selection on WW and YW may have had an effect on carcass measurements because of genetic correlations between traits. It is accepted in the literature that selection for WW and YW increases age-adjusted carcass ribeye area and hot carcass weight (Koots et al., 1994b; Marshall, 1994). In Angus steers, Kemp et al. (2002) found genetic correlations for yearling weight with age-adjusted carcass weight, carcass ribeye area, and ultrasound ribeye area of 0.96, 0.45, and 0.71, respectively. Bertrand et al. (2001) reported average genetic correlations from the literature for ultrasound ribeye area-weaning weight and ultrasound ribeye area-yearling weight of 0.49 and 0.46, respectively. This indicates the selection for growth traits in the Hays Converter may have also been inadvertently selecting for increased ribeye area and carcass weight. There is no observable genetic trend for UREA in the Hays Converter breed. The average EBV by birth year after 2002 when animals begin to have their own records for the trait is inconsistent. The genetic trend in CREA is generally downwards which is opposite to what is expected with the increase in WW and YW, although there is not enough information available for CREA to formulate a proper trend.

The potential impact of selection on WW and YW in the Hays Converter on back fat and marbling is not as clear. Bertrand et al. (2001) provided average genetic correlation literature estimates of 0.18 for weaning weight–ultrasound fat depth and 0.04 for yearling weight–ultrasound fat depth, though there was large variation in magnitude and direction in the reported estimates. Arnold et al. (1991) found a greater genetic correlation between age-adjusted ultrasound fat depth and measurement weight of 0.37. Kemp et al. (2002) found a genetic
correlation of 0.33 between yearling weight and ultrasound fat depth than for yearling weight and carcass fat depth (0.10). They also reported a genetic correlation between yearling weight and carcass marbling of 0.30. Koots et al. (1994b) and Marshall (1994) reported average literature genetic correlation estimates of -0.17 and 0.37, respectively, for weaning weight-marbling score displaying a large range in estimates. Lean meat yield is dependent on fat depth and ribeye area of the animal scanned and would thereby increase with an increase in ribeye area, decrease in fat depth, or both. A larger number of records are required to accurately estimate genetic parameters and EBVs for the Hays Converter population to support selection decisions and improve carcass quality and increase marketability. Measures of carcass merit collected through ultrasound or carcass evaluation after slaughter should continue to be recorded to construct a larger dataset for analysis.

The Hays Converter pedigree is lacking completeness which may have caused some of the deviation of the calculated parameters for the Hays Converter from those expected based on literature estimates of other beef populations. Proper assignment of relatives and connectedness between animals is required for estimation of genetic parameters. In the analysis, unknown parents were left as unknown and were treated as base individuals of a single population. The Hays Converter pedigree file, as discussed in Chapter 3, is incomplete throughout the examined time frame. Animals with missing parents occur throughout the pedigree file and are not from a homogenous base population. The unknown parents of animals born in a particular year are expected to be genetically similar. It may therefore be suitable in future analyses to assign a parent group to an animal with an unknown parent based on year of birth. Forming a more correct and complete pedigree should be a priority for increasing the usefulness of the data, and future work should examine methods for use when parentage is unknown.
4.6. Conclusion

Increased growth rate was the principal objective of the Hays Converter breed. This study found moderate heritabilities for $WW_d$ and $YW$ for the Hays Converter cattle studied. A positive genetic trend was observed for both traits which corroborates the selection process used for the breed. A low number of dams compared to animals with records were present in the dataset. This may have caused the low heritability for $WW_m$ and large negative genetic correlation between maternal and direct weaning weight effects estimated.

The small number of animals with records for ultrasound and carcass measurements made the estimation of genetic parameters for these traits difficult. In addition, the short time frame for ultrasound and carcass trait recording did not allow for long term genetic trends to be observed. Heritability estimates calculated in this study for ULMY, UMAR, and UREA were all lower than expected. No reasonable heritabilities were estimable for the remaining traits. Because of the large standard errors in the present study, a larger dataset needs to be analyzed to achieve more accurate estimates.

The continued collection of weight and ultrasound traits on all animals and carcass measurements on those slaughtered will aid in expanding the dataset and enabling improved estimation of genetic parameters and EBVs. The use of genotyping technology to complete and correct pedigree information may also aid in the discovery of proper genetic parameters for the Hays Converter breed.
Table 4.1. Number of animals with records (N), mean, standard deviation (SD), minimum, and maximum records for growth traits.

<table>
<thead>
<tr>
<th>Trait(^1)</th>
<th>N</th>
<th>Mean</th>
<th>SD</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>BW (kg)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M</td>
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<td>41.2</td>
<td>5.3</td>
<td>23.1</td>
<td>68.0</td>
</tr>
<tr>
<td>F</td>
<td>2,794</td>
<td>39.2</td>
<td>5.0</td>
<td>15.4</td>
<td>65.8</td>
</tr>
<tr>
<td>total</td>
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<td>40.2</td>
<td>5.3</td>
<td>15.4</td>
<td>68.0</td>
</tr>
<tr>
<td>WW (kg)</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M</td>
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<td>276.5</td>
<td>36.3</td>
<td>95.0</td>
<td>409.5</td>
</tr>
<tr>
<td>F</td>
<td>5,636</td>
<td>249.9</td>
<td>30.5</td>
<td>103.0</td>
<td>394.2</td>
</tr>
<tr>
<td>Total</td>
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<td>260.8</td>
<td>35.5</td>
<td>95.0</td>
<td>409.5</td>
</tr>
<tr>
<td>YW (kg)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>1,891</td>
<td>503.3</td>
<td>46.2</td>
<td>242.1</td>
<td>643.6</td>
</tr>
<tr>
<td>RH</td>
<td>4,781</td>
<td>386.9</td>
<td>44.5</td>
<td>213.8</td>
<td>681.7</td>
</tr>
<tr>
<td>H</td>
<td>402</td>
<td>384.5</td>
<td>51.7</td>
<td>222.5</td>
<td>533.1</td>
</tr>
<tr>
<td>S</td>
<td>188</td>
<td>475.5</td>
<td>53.6</td>
<td>325.3</td>
<td>590.9</td>
</tr>
<tr>
<td>Total</td>
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<td>419.4</td>
<td>69.0</td>
<td>213.8</td>
<td>681.7</td>
</tr>
</tbody>
</table>

\(^1\) BW is birth weight; WW is 200d adjusted weaning weight; YW is 365d adjusted yearling weight

* M is male; F is female; B is bull; RH is replacement heifer; FH is fed heifers; S is steer
Table 4.2. Number of records (N), mean, standard deviation (SD), minimum, and maximum value for ultrasound traits.

<table>
<thead>
<tr>
<th>Trait</th>
<th>N</th>
<th>Mean</th>
<th>SD</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>UBF (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>6</td>
<td>3.4</td>
<td>0.8</td>
<td>1.8</td>
<td>4.0</td>
</tr>
<tr>
<td>RH</td>
<td>294</td>
<td>5.8</td>
<td>2.0</td>
<td>1.8</td>
<td>15.0</td>
</tr>
<tr>
<td>FH</td>
<td>65</td>
<td>6.4</td>
<td>1.7</td>
<td>2.3</td>
<td>10.0</td>
</tr>
<tr>
<td>S</td>
<td>174</td>
<td>5.1</td>
<td>2.2</td>
<td>1.3</td>
<td>12.1</td>
</tr>
<tr>
<td>Total</td>
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<td>5.6</td>
<td>2.1</td>
<td>1.3</td>
<td>15.0</td>
</tr>
<tr>
<td>UMAR</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>6</td>
<td>3.9</td>
<td>0.4</td>
<td>3.4</td>
<td>4.6</td>
</tr>
<tr>
<td>RH</td>
<td>294</td>
<td>4.9</td>
<td>0.6</td>
<td>3.5</td>
<td>7.3</td>
</tr>
<tr>
<td>FH</td>
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<td>0.5</td>
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<tr>
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<td>0.5</td>
<td>3.3</td>
<td>6.1</td>
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<tr>
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<td>0.6</td>
<td>3.3</td>
<td>7.3</td>
</tr>
<tr>
<td>UREA (cm²)</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>6</td>
<td>59.4</td>
<td>4.5</td>
<td>52.3</td>
<td>64.1</td>
</tr>
<tr>
<td>RH</td>
<td>294</td>
<td>68.7</td>
<td>12.2</td>
<td>43.8</td>
<td>96.2</td>
</tr>
<tr>
<td>FH</td>
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<td>69.6</td>
<td>7.7</td>
<td>48.1</td>
<td>83.5</td>
</tr>
<tr>
<td>S</td>
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<td>43.8</td>
<td>96.5</td>
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<tr>
<td>ULMY (%)</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>RH</td>
<td>169</td>
<td>60.7</td>
<td>1.9</td>
<td>54.5</td>
<td>64.3</td>
</tr>
<tr>
<td>FH</td>
<td>64</td>
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<td>1.8</td>
<td>57.0</td>
<td>64.2</td>
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<td>61.6</td>
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</tr>
<tr>
<td>Total</td>
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<td>61.0</td>
<td>1.9</td>
<td>54.5</td>
<td>65.3</td>
</tr>
</tbody>
</table>

¹ UBF is ultrasound back fat; UMAR is marbling score; UREA is ribeye area; ULMY is lean meat yield
* B is bull; RH is replacement heifer; FH is fed heifer; S is steer.
Table 4.3. Number of records (N), mean, standard deviation (SD), minimum, and maximum value for carcass traits.

<table>
<thead>
<tr>
<th>Trait</th>
<th>N</th>
<th>Mean</th>
<th>SD</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>CREA (cm²)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FH</td>
<td>15</td>
<td>91.3</td>
<td>8.7</td>
<td>77.0</td>
<td>108.0</td>
</tr>
<tr>
<td>S</td>
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<td>86.8</td>
<td>7.8</td>
<td>73.0</td>
<td>101.0</td>
</tr>
<tr>
<td>Total</td>
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<td>88.0</td>
<td>8.2</td>
<td>73.0</td>
<td>108.0</td>
</tr>
<tr>
<td>CHW (kg)</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FH</td>
<td>32</td>
<td>332.2</td>
<td>29.1</td>
<td>255.4</td>
<td>384.6</td>
</tr>
<tr>
<td>S</td>
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<td>359.7</td>
<td>30.4</td>
<td>289.8</td>
<td>436.7</td>
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<tr>
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<td>355.2</td>
<td>31.8</td>
<td>255.4</td>
<td>436.7</td>
</tr>
<tr>
<td>CFAT (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FH</td>
<td>15</td>
<td>13.2</td>
<td>3.8</td>
<td>6.7</td>
<td>21.3</td>
</tr>
<tr>
<td>S</td>
<td>47</td>
<td>10.1</td>
<td>2.4</td>
<td>5.7</td>
<td>18.7</td>
</tr>
<tr>
<td>Total</td>
<td>62</td>
<td>10.8</td>
<td>3.1</td>
<td>5.7</td>
<td>21.3</td>
</tr>
<tr>
<td>CMAR</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FH</td>
<td>25</td>
<td>4.9</td>
<td>0.5</td>
<td>4.0</td>
<td>5.8</td>
</tr>
<tr>
<td>S</td>
<td>110</td>
<td>4.5</td>
<td>0.5</td>
<td>3.0</td>
<td>5.3</td>
</tr>
<tr>
<td>Total</td>
<td>135</td>
<td>4.6</td>
<td>0.5</td>
<td>3.0</td>
<td>5.8</td>
</tr>
<tr>
<td>CSAL (%)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FH</td>
<td>32</td>
<td>56.8</td>
<td>3.8</td>
<td>49.9</td>
<td>64.1</td>
</tr>
<tr>
<td>S</td>
<td>81</td>
<td>59.4</td>
<td>2.3</td>
<td>53.8</td>
<td>65.8</td>
</tr>
<tr>
<td>Total</td>
<td>113</td>
<td>58.6</td>
<td>3.0</td>
<td>49.9</td>
<td>65.8</td>
</tr>
</tbody>
</table>

1 CREA is carcass ribeye area; CHW is carcass hot weight; CFAT is backfat; CMAR is marbling score; CSAL is percent saleable meat.

FH is fed heifer; S is steer.
Table 4.4. Summary of contemporary group classification term definitions (cg), fixed effect (F), covariates (C), and random (R) model terms.

<table>
<thead>
<tr>
<th>Model Term</th>
<th>Trait</th>
<th>BW</th>
<th>WW</th>
<th>YW</th>
<th>ultrasound</th>
<th>carcass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herd prefix</td>
<td>cg</td>
<td>cg</td>
<td>cg</td>
<td>cg</td>
<td>cg</td>
<td>cg</td>
</tr>
<tr>
<td>Birth year</td>
<td>cg</td>
<td>cg</td>
<td>cg</td>
<td>cg</td>
<td>cg</td>
<td>cg</td>
</tr>
<tr>
<td>Cow group (1st calf vs. mature cow herd)</td>
<td>cg</td>
<td>cg</td>
<td>cg</td>
<td>cg</td>
<td>cg</td>
<td>cg</td>
</tr>
<tr>
<td>Sex management group (B, RH, FH, S)</td>
<td>-</td>
<td>-</td>
<td>cg</td>
<td>cg</td>
<td>cg</td>
<td>cg</td>
</tr>
<tr>
<td>Slaughter date</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>cg</td>
<td></td>
</tr>
<tr>
<td>Contemporary group</td>
<td>F</td>
<td>F</td>
<td>F</td>
<td>F</td>
<td>F</td>
<td>F</td>
</tr>
<tr>
<td>Sex (M, F)</td>
<td>F</td>
<td>F</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Dam age (1; 2; 3; 4; 5 to 10; ≥11)</td>
<td>F</td>
<td>F</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Sire breed</td>
<td>F</td>
<td>F</td>
<td>F</td>
<td>F</td>
<td>F</td>
<td></td>
</tr>
<tr>
<td>Dam breed</td>
<td>F</td>
<td>F</td>
<td>F</td>
<td>F</td>
<td>F</td>
<td></td>
</tr>
<tr>
<td>Age at ultrasound or slaughter</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>C</td>
<td>C</td>
</tr>
<tr>
<td>Additive genetic effect</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td></td>
</tr>
<tr>
<td>Maternal genetic effect of dam</td>
<td>R</td>
<td>R</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Permanent environmental effect for dam</td>
<td>R</td>
<td>R</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Residual error term</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
</tr>
</tbody>
</table>

1 BW is birth weight; WW is weaning weight; YW is yearling weight; ultrasound is all ultrasound traits; carcass is all carcass traits
Table 4.5. Heritability ($h^2$), genetic correlations ($r_g$), and standard errors (SE) for weight and ultrasound traits from a univariate analysis.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weight</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$h^2$WW$_d$</td>
<td>0.35</td>
<td>0.04</td>
</tr>
<tr>
<td>$h^2$WW$_m$</td>
<td>0.05</td>
<td>0.02</td>
</tr>
<tr>
<td>$r_g$WW$_d$, WW$_m$</td>
<td>-0.77</td>
<td>0.10</td>
</tr>
<tr>
<td>$h^2$YW</td>
<td>0.40</td>
<td>0.03</td>
</tr>
<tr>
<td>$h^2$BW$_d$</td>
<td>0.06</td>
<td>0.03</td>
</tr>
<tr>
<td>$h^2$BW$_m$</td>
<td>0.03</td>
<td>0.02</td>
</tr>
<tr>
<td>$r_g$BW$_d$, BW$_m$</td>
<td>-0.36</td>
<td>0.30</td>
</tr>
<tr>
<td>Ultrasound</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$h^2$UBF</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$h^2$ULMY</td>
<td>0.21</td>
<td>0.14</td>
</tr>
<tr>
<td>$h^2$UMAR</td>
<td>0.23</td>
<td>0.10</td>
</tr>
<tr>
<td>$h^2$UREA</td>
<td>0.19</td>
<td>0.10</td>
</tr>
</tbody>
</table>

$^1$ WW$_d$ is weaning weight direct; WW$_m$ is weaning weight maternal; YW is yearling weight; BW$_d$ is birth weight direct; BW$_m$ is birth weight maternal; UBF is ultrasound back fat; ULMY is ultrasound lean muscle yield; UMAR is ultrasound marbling score; UREA is ribeye area
Table 4.6. Heritabilities ($h^2$), genetic correlations ($r_g$), and phenotypic correlation ($r_p$) and their standard errors (SE) for the bivariate analysis of weaning weight (WW) and yearling weight (YW).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>$h^2$WW$_d$</td>
<td>0.30</td>
<td>0.03</td>
</tr>
<tr>
<td>$h^2$WW$_m$</td>
<td>0.04</td>
<td>0.01</td>
</tr>
<tr>
<td>$h^2$YW</td>
<td>0.42</td>
<td>0.03</td>
</tr>
<tr>
<td>$r_g$WW$_d$, WW$_m$</td>
<td>-0.25</td>
<td>0.01</td>
</tr>
<tr>
<td>$r_g$WW$_d$, YW</td>
<td>0.81</td>
<td>0.04</td>
</tr>
<tr>
<td>$r_g$WW$_m$, YW</td>
<td>0.26</td>
<td>0.10</td>
</tr>
<tr>
<td>$r_p$WW, YW</td>
<td>0.75</td>
<td>0.02</td>
</tr>
</tbody>
</table>
Figure 4.1. Average estimated breeding value for birth weight maternal ($\text{BW}_m$) and direct ($\text{BW}_d$) effects by year of birth.
Figure 4.2. Average estimated breeding value for maternal weaning weight by year of birth.
Figure 4.3. Average estimated breeding value for direct weaning weight by year of birth.
Figure 4.4. Average estimated breeding value for yearling weight by year of birth.
Figure 4.5. Distribution of animals by accuracies of estimated breeding values for direct weaning weight (WWd) effects and yearling weight (YW).
Figure 4.6. Distribution of animals by accuracies of estimated breeding values for ultrasound marbling (UMAR), ribeye area (UREA), lean meat yield (ULMY), and back fat (UBF).
Figure 4.7. Average estimated breeding value for ultrasound ribeye area (UREA), marbling (UMAR), lean meat yield (ULMY), and back fat (UBF) by year of birth.
Figure 4.8. Distribution of animals by accuracies of estimated breeding values for carcass hot weight (CHW), marbling score (CMAR), ribeye area (CREA), percent saleable meat (CSAL), and fat cover (CFAT).
Figure 4.9. Average estimated breeding value for carcass hot weight (CHW), marbling score (CMAR), ribeye area (CREA), percent saleable meat (CSAL), and fat cover (CFAT) by year of birth.
CHAPTER 5

GENOTYPE IMPUTATION AND MARKER FREQUENCY DERIVED BREED COMPOSITION OF HAYS CONVERTER CATTLE

5.1. Abstract

Accurate genomic selection in cattle requires a large reference population of animals with dense genotypes. Genotyping an adequate number of individuals can be costly. Imputation allows breeders to genotype animals on less expensive, low density marker panels, and infer genotypes on a denser panel. The accuracy of genotype imputation was examined for Hays Converter cattle in the present study. The Illumina BovineSNP50 BeadChip (50k) was used to genotype 125 Hays Converter animals. The animals were distributed into either the reference group (n=100) or the imputation test group (n=25). The average relationship between the two groups was estimated to be approximately 5.95% from the available pedigree data. Imputation from 6k to 50k was carried out using the programs Beagle and FIImpute by population-based methods. FIImpute was found to impute genotypes more accurately for all animals. Average accuracy of imputed genotypes for FIImpute and Beagle were 94.6% and 88.4%, respectively. The breed compositions of all genotyped animals were examined with the objective of identifying cause for poor imputation results in certain individuals. Breed composition was predicted with the 50k SNP data using the regression method and average SNP frequency estimates of 13 other beef and dairy cattle breeds. On average the largest components of the Hays Converter cattle were found to be the breed’s three foundation breeds, Hereford, Holstein, and Brown Swiss at approximately 43.6%, 17.8%, and 7.0%, respectively. The four animals in the imputation test population with imputation accuracies less than 90% were found to have breed compositions inconsistent with what was discovered for the Hays Converter breed. These
animals likely have inaccurate breeding records and relatives which were breeds other than Hays Converter. Overall, imputation was found to be carried out accurately for pure Hays Converter animals from 6k to 50k with a small sized reference population.

5.2. Introduction

The use of genomic information in the evaluation of many beef and dairy cattle breeds has revolutionized how animals are being selected. A large number of genotypes of individuals are needed for the accurate estimation of marker effects used within genomic selection practices. Obtaining a sufficient number of animal genotypes can be difficult and costly, especially for breeds existing in small numbers such as the Hays Converter. Weigel et al. (2009) found high accuracy in the predictive ability of low density genotypes in Holstein cattle, although these reduced panels may be specific to a trait and population. Denser single nucleotide polymorphism (SNP) genotypes are likely necessary for the estimation of marker effects and prediction of total genetic merit of individuals in the Hays Converter population.

The current cost of genotyping an individual on a low density panel is considerably lower than that for a high density panel. Habier et al. (2009) proposed genotyping individuals with a low density SNP panel and imputing genotypes for the remaining SNPs using the high density genotypes of their ancestors. Imputation allows cattle breeders to genotype cattle with more affordable low density marker panels and determine in silico untyped markers on the higher density panel.

Several software packages have been produced to perform genotype imputation in humans and livestock. Imputation methods can be primarily classified as either family-based or population-based. Family-based imputation methods exploit pedigree information to utilize linkage and Mendelian segregation rules to impute missing genotypes. Population-based
methods rely on Linkage Disequilibrium (LD) between SNPs. LD is the non-random association of alleles at two or more loci. The extent of LD in a population is influenced by both present and past effective population size, and in sheep has been shown to be greater in populations with lower genetic diversity (Meadows et al., 2008). This may suggest a benefit for the Hays Converter population which has small numbers and animals are likely highly related.

Many studies have found high accuracy of genome imputation in cattle populations (Weigel et al., 2010a; Zhang and Druet, 2010; Berry and Kearney, 2011). Variation in imputation accuracy exists between animals and populations. Accuracy was been found to be dependent on the density of the markers (Zhang and Druet, 2010; Khatkar et al., 2012), size of the reference population (Druet et al., 2010; Browning and Browning, 2011), the population structure (Dassonneville et al., 2012), the relationship between individuals and the reference population (Druet, 2010; Zhang and Druet, 2010), and the imputation method used (Johnston et al., 2011). The effect of reference population size on imputation accuracy is dependent on the target population. Fewer reference individuals are required for populations exhibiting low levels of variability (Druet, 2010).

Knowing the breed composition of cattle would be helpful in predicting heterosis, evaluating adaptability to production environments, and sorting animals into management groups (Kuehn et al., 2011). Information on breed composition is also important for the Hays Converter population to identify impure animals and discover pedigree errors. Individual breed composition in an admixed livestock population has been traditionally derived using pedigree information. Breed composition can also be assessed using genotype information and the differences in SNP frequencies across breeds. The estimation of breed composition using SNP data may provide a more accurate estimate of breed components because recombination events of parental
chromosomes during meiosis may cause breed composition to deviate away from pedigree expectations. In addition, SNP data allows for breed composition to be estimated in animals with unknown ancestors, as is the case with the Hays Converter population. During the development of the Hays Converter breed, as outlined in Chapter 2, there was no pedigree recording or documentation of the proportion of each of the foundation breeds remaining in the Hays Converter population beyond the initial crosses. It is unknown if animals with more or less of one of the foundation breeds was more often culled or selected to remain in the herd. As well, at various periods in the history of the breed, an unrecorded number of animals from other cattle breeds beyond the foundation breeds were bred to animals within the Hays Converter population, and their progeny may have remained in the herd.

The Hays Converter herd studied is managed in a manner in which some pedigree errors are expected to exist. Breed composition predicted using SNP data will allow for ancestor breed determination and potential pedigree error discovery in animals with non-genotyped parents. Genotype imputation in an individual requires their haplotypes to be present in the reference group. If an animal has ancestors of a breed other than Hays Converter their genotypes will not be adequately represented in a reference population of Hays Converter ancestors, and imputation will likely not be performed with any accuracy.

The purpose of this study was to quantify the accuracy of imputation from a low density marker panel to a higher density marker panel in Hays Converter cattle. In addition, the study looked to identify the composition of Hays Converter animals with the objective of discovering an explanation for low imputation accuracy for specific individuals.
5.3. Materials & Methods

5.3.1. Genotyping of animals

DNA samples were provided by Hays Ranches and were in the form of either semen or hair follicles. A total of 125 Hays Converter cattle were genotyped using the Illumina BovineSNP50 BeadChip (Illumina Inc., San Diego, CA). One hundred Hays Converter cattle with DNA samples available were selected as a reference population. All bulls with DNA available which had descendants born between 2006 and 2011 were included in the reference population. This represented 32 bulls born between 1973 and 2006. The remaining 68 animals were cows selected based on their total genetic contribution to Hays Converter cattle born between 2006 and 2011, and the number of their daughters selected to join the breeding herd, while limiting the relationship between animals within the reference population. The birth year of the selected cows ranged from 1993 to 2003. A group of 25 Hays Converter cattle born between 2004 and 2011 were selected to represent the current Hays Converter breed. Animals were selected to include a variety of different sires and dams, and animals with unknown parentage. There were 53,185 SNPs successfully genotyped. All samples had call rates greater than 99.8%.

5.3.2. Genotype imputation

Imputation was carried out from the Illumina BovineLD (6k) to the Illumina BovineSNP50 (50k) marker panel (Illumina Inc., San Diego, CA). Nearly all SNPs on the 6k panel are contained on the 50k panel. The 50k genotypes of the 25 animals in the test group were reduced to the SNPs on the 6k panel by masking all SNPs but those found on the 6k panel. This left 6,675 SNPs to be considered.
Population-based imputation methods used by FImpute v2 and Beagle v3.3 software were employed separately to compare their achieved accuracies. FImpute (Sargolzaei et al., 2011) is capable of performing imputation using both family and population-based methods. No pedigree information was utilized in this study and imputation was only performed with population-based procedures. Population-based procedures of FImpute are unique, however, in that it assumes all animals are related to some degree. The FImpute population imputation method is based on overlapping sliding windows used to capture haplotypes consistent between individuals from a common ancestor. The program starts with a long window that sweeps across each chromosome finding large segments consistent with reference animals. The window length is gradually decreased in each sweep until missing markers have been filled in successfully. The haplotype frequencies in the reference population are used to determine the most likely haplotype when multiple haplotypes are possible.

The methodology used by Beagle is described in detail by Browning and Browning (2007). Beagle was developed for and widely used in human studies. Beagle uses a localised haplotype-cluster model to cluster haplotypes at each marker. A Hidden Markov Monte-Carlo (HMM) is used to find the most likely haplotype for each animal based on that animal’s known genotype.

Imputed genotypes of the test group animals were compared to their actual 50k genotypes. Imputation accuracy was determined as the percentage of correctly predicted calls for the masked markers.

5.3.3. Breed composition

Breed composition was predicted for all 125 animals genotyped using the regression method (Chiang et al., 2010) with allele frequencies estimates from a sample of reference breeds.
SNP frequency estimates representing ten beef breeds and three dairy breeds were obtained from Kuehn et al. (2011). Frequencies for the beef breeds were from bulls genotyped for the USMARC 2,000 Bull Project. Beef breeds included in the analysis included Angus, Hereford, Shorthorn, Braunvieh, Charolais, Gelbvieh, Limousin, Maine-Anjou, Simmental, and Brahman. Average SNP frequency estimates for Holstein, Jersey, and Brown Swiss dairy breeds were reported for animals from the USDA ARS Animal Improvement Program Laboratory (Beltsville, MD). Angus allele frequency estimates used were from a combination of Angus and Red Angus animals. The estimation of breed allele frequencies and the animals utilized is described by Kuehn et al. (2011). There were 40,872 SNPs from the Illumina BovineSNP50 with estimated frequencies for all the included breeds. Genotypes of the 125 Hays Converter animals were converted to the number of copies of Illumina allele B and divided by two (0, 0.5, or 1). Breed composition was predicted by regression analysis with stepwise selection with SAS 9.3 software (SAS Institute, Cary, NC) using the following model:

\[ y = Xb + e \]

where \( X \) is a 40,872 by 13 matrix of SNP frequencies of Illumina allele B for each breed, \( b \) is a vector of regression coefficients representing the percent contribution of each animal in \( y \).

To compare the results when only a decreased number of SNPs are available, as would be for animals where imputation would be performed, breed composition of the 125 Hays Converters was subsequently estimated using SNPs included on the Illumina BovineLD BeadChip. Animal genotypes were reduced to the marker set contained on the BovineLD. The same model was employed with an \( X \) matrix of 5,740 by 13 SNP frequencies of Illumina allele B.
5.4. Results

5.4.1. Genotype imputation

Of the 53,185 SNPs successfully genotyped, 37,502 had minor allele frequencies greater than 3%. For the 125 animals genotyped, 35 had at least one of their listed parents also genotyped, with genotype data revealing that the sire had been incorrectly identified in the pedigree file for 14 of these animals. This represented a pedigree error rate of approximately 34% within this group of 35 animals genotyped with a genotyped parent. Correct sire identity was discovered for two of the animals with erroneous paternity records and for 11 animals with previously unknown paternity.

Using the corrected pedigree data, the relationship between and among the reference and test populations was examined. The average relationship among animals within the reference population was 5.95%, and the average relationship among animals within the test population was 14.4%. The average relatedness between animals in the reference group and animals in the test group was approximately 5.95%. All but one animal in the test group had at least one 2nd degree relative in the reference population. For the 25 animals in the test group, the genotypes of 19 sires, 3 dams, 7 paternal grandsires, 7 paternal grand-dams, 14 maternal grandsires, and 16 maternal grand-dams were found in the reference group.

The accuracy of population-based imputation methods using FImpute and Beagle were compared. Accuracy results of the imputation are displayed in Figure 5.1. FImpute was more accurate than Beagle for every animal in the test population. The average accuracy of the imputed genotypes determined by FImpute and Beagle were 94.6% and 88.4%, respectively. Accuracies ranged from 67.2% to 98.7% for FImpute and from 65.6% to 95.6% for Beagle. The
imputation accuracy for an individual animal was up to 16.5% higher using FImpute than that found using Beagle.

5.4.2. Breed composition

Predicted breed compositions using the BovineSNP50 data for each of the 125 genotyped animals are in Figure 5.2. R-squared values for the 125 models averaged 0.81 and ranged from 0.782 to 0.826. Regression coefficients were the greatest for the Hereford breed representing a large component of the Hays Converter animals at an average of 43.6%, ranging from 19.3% to 60.9%. Holstein and Brown Swiss breeds represented the next largest components on average at 17.8% and 7.0%, respectively. The next largest components on average were Charolais at 6.6% and Angus at 4.6%. Three Hays Converter animals had Angus components estimated at greater than 45%. The cow HAY298G97 had an Angus component of approximately 52%, and her genotyped calf, HAY015X10, had an Angus component of approximately 33%. The breeds constituting the remainder of the composition of the Hays Converter cattle appeared in low quantities.

Similar results were discovered when breed composition was estimated using the reduced number of SNPs contained on the BovineLD BeadChip. Breed components are shown in Figure 5.3 for the 125 individual Hays Converter animals genotyped. There was a strong correlation between the estimated breed components calculated using the BovineSNP50 and the BovineLD SNPs (r=0.94). The R-squared values decreased when fewer SNPs were used and averaged 0.70. The number of breeds with regression coefficients estimated decreased with the reduced number of SNPs, as more breeds had no estimated contribution to the Hays Converter animals. Very small regression coefficients seen from using the BovineSNP50 data were largely not significant
with the reduced SNP number and therefore were not estimated and assumed to be zero for most Hays Converter animals.

5.4.3. Imputation accuracy considering breed composition

Figure 5.4 displays the breed composition and accuracy of imputation for the 25 animals in the test population. HAY435W09, the animal with the lowest imputation accuracy (67.2%), was found to be not a pure Hays Converter and was approximately half Angus. The four animals with imputation accuracies less than 90% had the lowest proportion of the three founding breeds. The cumulative sum of the Hereford, Holstein, and Brown Swiss components were 53% or less for the four animals. In addition, they were the only four animals with components greater than 19% for breeds other than the three formation breeds.

Imputation accuracy was compared to the breed composition calculated using the reduced number of SNPs to determine if animals can be identified as impure Hays Converters where imputation is not likely to be performed accurately. The four animals with imputation accuracies less than 90% were the only animals with a sum of the three foundation breeds less than 60% (Figure 5.5). Again, large components of non-foundation breeds were found.

5.5. Discussion

Greater imputation accuracies were achieved by FImpute on average and for each individual compared to Beagle. Population-based methods of each program were used and no pedigree information was considered. Larmer (2012) compared imputation accuracy in Canadian dairy breeds performed by population-based methods and found FImpute outperformed Beagle in breeds with small reference populations. The Hays Converter reference population was very small and animals were highly related which suited the FImpute program. FImpute can also
apply both family and population-based methods if family information is provided to maximize imputation accuracy (Sargolzaei et al., 2011).

Imputation was performed using population-based methods alone. This was done largely because of the incompleteness and uncertainty of the available pedigree information. High imputation accuracy was achieved using population-based methods for the Hays Converter population, although accuracy may increase with the use of family-based imputation methods. Low-density SNP genotypes of animals can be used to confirm or assign parentage in the Hays Converter population, and a reliable pedigree can be assembled prior to imputation. If pedigree information is available, haplotypes in the reference population can be assigned to descendants, and imputation accuracy may improve. The inclusion of family-based methods has been shown to increase accuracy when family information is available (Zhang and Druet, 2010). Sun et al., (2012) however, found sequential use of population and family information did not necessarily improve accuracy compared to population methods alone in a population with a high amount of LD. Future studies should evaluate the potential gains in imputation accuracy when pedigree information is used where available.

The relationship between the test and reference groups was high in this study. Most animals in the test population had close ancestors in the reference group. The estimated average relationship between groups was estimated to be 5.59%, but this value is likely underestimated. Chapter 2 of this thesis examined the pedigree of the Hays Converter population and concluded the incomplete pedigree data underestimates the relationships between animals. The high pedigree error rate found using the genotype data of a small subset of individuals with parents also genotyped suggests the estimated average relationship value may be a misrepresentation of the true value. More pedigree errors are likely present but are undiscovered. In addition, animals
in the test group with currently unknown parentage are likely highly related to the reference population although the relationship is presently calculated as zero. Hays Converter animals have a high degree of relatedness that likely aided imputation as imputation accuracy is dependent on the relationship between the animals being imputed and the reference population. Berry and Kearney (2011) found a positive correlation between animal mean genotype concordance rate and average relatedness to the reference population. Khatkar et al. (2012) reported test animals with a sire in the reference population had an average allelic error rate across all imputation scenarios of 2.61%, while those without a sire in the reference population had greater error rates of 3.34% on average. They also found the decrease mean allelic error rate due to increased relationships was more pronounced with less dense SNP panels and small references sizes.

A small reference group of only 100 individuals was used in this study. This number is considerably smaller than reference populations used in other imputation studies. Imputation accuracy has been shown to increase as the size of the reference population increases (Weigel et al, 2010b; Khatkar et al., 2012). The effect of the number of individuals in the reference population on imputation accuracy is dependent on the structure of the population examined. A population like the Hays Converter herd, where there is little variability, suggests a smaller reference population will be adequate. Animals derived from a small number of ancestors have greater levels of LD and imputation can be performed more accurately. Zhang and Druet (2010) observed a decrease in mean imputation error rate with each increase in the number of reference individuals for one method and little effect using a second method. Druet et al. (2010) found the benefit of increasing the number of individuals in the reference group on imputation accuracy was more prominent when reference groups had less than 500 individuals with little benefit gained with reference groups greater than 1,000 individuals. A reference population needs to be
of a great enough size to cover all haplotypes in a population and capture rare alleles. Large reference populations are generally required to effectively represent the population and increase the relationship of animals with the reference population. For the Hays Converter population this is accomplished with a small number of animals.

The incomplete pedigree of all the Hays Converter animals did not allow for validation of the breed composition estimates. Kuehn et al. (2011), with the reference beef breed SNP frequencies used in this study, found the accuracy of the breed composition prediction depended on the breed and averaged 89% for eight beef breeds. Kuehn et al. (2011) also found the Hereford breed to be unexpectedly distant from the other *B. taurus* breeds used in the analysis. They concluded this result may be due to a true evolutionary distance or a bias in SNP discovery in the development of the BovineSNP50 BeadChip. This may result in increased accuracy in estimating the percentage of Hereford in crossbred cattle due to the number of unique alleles. The large Hereford component of the genotyped Hays Converter population is likely an accurate measure. Breeds used to discover the SNPs included in the BovineSNP50 BeadChip have more unique, breed specific SNPs included in the analysis and their contribution may therefore be more accurately determined. The genetic distance between the dairy breeds (Holstein, Brown Swiss, and Jersey) and the beef breeds was not calculated using the SNP frequencies used in this study. The close genetic relationship between Brown Swiss and Braunvieh breeds, which were both included in the analysis, may have made it difficult to distinguish between the breeds using SNP frequencies. This may have caused a lower than expected Brown Swiss breed component in the Hays Converter population as a proportion of the Brown Swiss contribution may have been allocated to the Braunvieh breed. The same may also be true for other cattle breeds that display similar SNP frequencies as a result of their evolutionary past. Purebred animals used as the
foundation animals may also have small components of other breeds due to their breed’s history, which may have caused some of the small breed component estimates in the Hays Converters. Some breeds were estimated to comprise a small portion of a number of the Hays Converter animals. This includes breeds such as Brahman which has not been included in the Hays Converter breed. Non-zero regression coefficients for these other breeds may be due to the breeds being genetically similar to breeds represented in the Hays Converter. Similarities in SNP frequencies between breeds will result in a breed to be falsely presumed as being a genetic contributor to an animal. The accuracy of the breed composition estimates calculated using the regression method could not be verified using pedigree information. Other methods of determining breed composition can be used in the future to compare the results of the regression analysis for genotyped Hays Converter animals.

The three breeds used to create the Hays Converter breed were Hereford, Holstein, and Brown Swiss. All 13 of the reference breeds had at least one non-zero regression coefficient estimate for the 125 Hays Converter animals. The foundation cow herd used to create the Hays Converter breed was primarily comprised of Hereford females although it has been mentioned that it was a commercial beef herd and an unknown number of females from other breeds were included. Also, other cattle breeds were used by Hays Ranches and their genetics may have been combined with Hays Converter cattle. Breeding records confirm animals with Angus, Charolais, Hereford, Holstein, Simmental, Brown Swiss, Gelbvieh, and Jersey breeding have been bred to Hays Converter animals, although it is unclear how many of the progeny if any contributed to the present Hays Converter population. The greater than zero regression coefficients for these breeds may partially be a reflection of these other cattle breeds being used in the Hays Converter herd.
Hereford, Holstein, and Brown Swiss were the breeds with the largest contribution to the majority of the Hays Converter cattle, as expected. In the pedigree simulation performed in Chapter 2 that considered only these three breeds, breed levels became fixed at approximately 54% Hereford, 27% Holstein, and 19% Brown Swiss. This is similar to the ratio of the three foundation breeds found in the regression analysis. The average percentage of Hereford, Holstein, and Brown Swiss out of the total component composed of the three foundation breeds were 63%, 26%, and 10%, respectively. Several animals were found to have larger than expected Angus components with three animals estimated to be around 50% Angus and two around 25% Angus. This is expected to be due to incorrect parent identification and parent breed recording. Angus sires used on Hays Converter females and Angus crossbred dams remaining in the cow herd probably resulted in these progeny with high Angus contributions.

A relationship between the accuracy of the genotype imputation and the breed composition of the animal was found. Animals in the test group that were found to have a large portion of non-foundation breeds, such as Angus, generally had lower imputation accuracies. This implies that these animals are not pure Hays Converters and are therefore less related to the animals in the reference group than previously believed. Three of the animals with imputation accuracies less than 90% had large Angus components and the fourth had a large Simmental component. These breeds are not represented in the reference population and as a result imputation could not be accurately performed.

The accuracy of the breed composition predictions is expected to be lower when calculated using the reduced number of SNPs included in the BovineLD BeadChip. Accuracy may be particularly lower for cattle from advanced generations of outcrossed populations. The original combination of Hereford, Holstein, and Brown Swiss animals to create the Hays
Converter occurred approximately 50 years ago, with many generations of cattle produced during that period. Distinctive breed alleles may not have been passed on to advanced generations. In addition, DNA segments originating from each breed decrease in size over generations and may be difficult to capture with a smaller number of markers. In this study there was a strong correlation between the breed composition estimates calculated using the full and reduced number of SNPs. Regression coefficients representing the major breed contributions were able to be estimated using the SNPs found in the BovineLD BeadChip. This signifies breed composition can be predicted for animals genotyped using the BovineLD. This information can be valuable in identifying impure animals in the breed and discovering animals in which genotype imputation can likely not be performed accurately.

5.6. Conclusion

Results of this study indicate imputation can be successfully performed from the BovineLD (6k) to the BovineSNP50 (50k) panel in the Hays Converter population with a small reference population of 100 animals. FImpute was found to have greater imputation accuracy than Beagle. The high imputation accuracy with a small reference population was likely realized due to the high relationship between animals in the test population and the reference population. In addition, the population structure of the Hays Converter breed with the very small effective population size maintained throughout its history likely helped attain high imputation accuracy.

Low-density SNP panels genotyping followed by imputation is an appealing, low cost genotyping approach. Further genotyping of individuals on the 6k panel and imputing genotypes to 50k will serve to increase the number of animals with higher-density genotypes. Genotyping animals will also help to assemble a more accurate pedigree which will be beneficial for several aspects of selection and management of the Hays Converter population. An improved pedigree
may also serve to increase the accuracy of the imputation by use of family-based methods in addition to population-based imputation methods already employed.

Imputation was found to be performed with lower accuracy for animals which were not pure Hays Converters, and therefore had ancestors not represented in the reference population. For animals where parentage could not be established using genotype information, breed composition analysis provided a means for identifying impure animals in which imputation cannot be performed accurately. Hays Converter animals should be examined for large proportions of non-foundation breeds using 6k genotypes prior to performing imputation.
Figure 5.1. Accuracy of imputation from Illumina BovineLD to Illumina BovineSNP50 panel for 25 test animals using FImpute and Beagle programs.
Figure 5.2. Breed composition of 125 Hays Converter animals calculated with regression analyses on Illumina 50K SNP frequency within breed.
Figure 5.3. Breed composition of 125 Hays Converter animals calculated with regression analyses on Illumina 6K LD SNP frequency within breed.
Figure 5.4. Accuracy of imputation from Illumina BovineLD to Illumina BovineSNP50 panel using FImpute with breed composition of test animals (n=25) calculated with regression analyses on Illumina 50K SNP frequency within breed.
Figure 5.5. Accuracy of imputation from Illumina BovineLD to Illumina BovineSNP50 panel using FImpute with breed composition of test animals (n=25) calculated with regression analyses on Illumina 6K LD SNP frequency within breed.
CHAPTER 6

GENERAL CONCLUSIONS

In the present work, the main goals were to utilize pedigree data, phenotypic records, and genotypic data from the Hays Converter breed to investigate the level of genetic diversity, genetic parameters and trends, accuracy of genotype imputation, and breed composition. The Hays Converter was found to have experienced a decrease in genetic diversity throughout its history, especially with the herd downsizing in 2000. Inbreeding was found to be increasing, and with the low effective population size, will continue to increase at a high rate. A positive genetic trend for weaning weight and yearling weight attested to the selection practices of the breed. More data is necessary to obtain more accurate estimates of genetic merit for carcass quality traits. Imputation from 6k to 50k SNP panel was highly accurate for individuals with a large proportion of Hays Converter breeding and similarity to the reference population. The breed composition analysis was able to identify the three foundation breeds, Hereford, Holstein, and Brown Swiss, in the greatest proportion, and detect breeds inadvertently added.

The declining level of genetic diversity indicates that a breeding program which incorporates measures to decrease relatedness between animals may be necessary. The use of genetic parameters and estimated breeding values to advance the breed in traits of interest should be considered in combination with the conservation of the genetic health. Genotype imputation can be performed on Hays Converter individuals, provided they are confirmed to not have large portions of other breeds. This will allow for the possibility of future genomic analysis of the breed.

The largest limitation of this work is the pedigree data used in the analysis, which can have an impact on the measures examined in this thesis. The discovered level of genetic diversity
in the population studied in Chapter 3 is affected by the completeness of the pedigree. The relationship between Hays Converter individuals is misrepresented in many instances due to common ancestors not being known. This resulted in an underestimation of the current level of inbreeding. In addition, the genotyping of animals in Chapter 5 revealed a large number of parentage recording errors. This included incorrect breed identification of the ancestors of some individuals. The improper assignment of ancestors and descendants wrongly assigns relationships between animals, conceivably affecting the estimated genetic parameters and breeding values calculated in Chapter 4. Knowledge of an individual’s breed composition will also allow for improved estimation of genetic parameters by recognizing and eliminating non-Hays Converter animals. The pedigree and breed corrections found with the now and future genotyped animals can be used to repeat the analyses with more accuracy. The small number of animals with records for carcass quality traits also limited the estimation of genetic parameters and trends. Increasing the number of animals with records will provide more information to be used in these calculations.

The success of the imputation of genotypes of Hays Converter animals provides the opportunity to increase the number of individuals with imputed 50k genotypes. Future studies on the Hays Converter breed can use genotypic information to re-examine the level of genetic diversity and genetic merit of animals through the identification of SNPs associated with traits of interest for the breed. In addition, further work can investigate areas of the genome under selection and detect potentially maintained blocks of the original foundation breeds. A better understanding of the genetic distance between the Hays Converter breed and other beef breeds will enable comparisons between the breeds, and help determine the best breeds to cross Hays Converter cattle with to maximize potential heterosis.
The future of the Hays Converter breed will depend on maintaining the genetic health of the population while improving performance in traits of interest and defining its role in Canada’s beef production industry. The influence of the breed in today’s beef industry is minor. The Hays Converter possesses a strong historical significance, is unique within the industry, and may excel in certain environments and production systems. This thesis is the first in depth genetic examination of the Hays Converter and can be used as a framework for future management and development of the breed.
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