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Quantifying the change in estimated breeding values of elite sires throughout their lifespan

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A Dissertation

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by

Mitchell Joseph Koot

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Abstract of a Dissertation submitted in partial fulfilment of the requirements for the Degree of Bachelor of Agricultural Science with Honours

Quantifying the change in estimated breeding values of elite sires throughout their lifespan

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Quantification of the change in Friesian and Jersey sires' estimated breeding values (eBVs) was carried out between their initial proof, reproof, and latest proof. Alongside the eBV change quantification, these three estimates of genetic merit were analysed to predict which provides the best estimate of the genetic merit that is passed onto the sires' offspring. The study was based on data sourced from NZAEL New Zealand Dairy sire summaries. Each bulls' initial proof, reproof, and latest proof eBVs were entered into an excel spread sheet and were sorted to only include CRV Ambreed and Livestock Improvement Company (LIC) Friesian and Jersey bulls born in New Zealand between 2000 and 2006, with eBV reliabilities greater than 96% in 2016; totalling 316 sires. The key traits analysed were milk protein, milk fat, milk volume, live-weight, fertility, and somatic cell count.

To evaluate which measurement provides the best estimate of a sire's genetic merit that is transmitted to their offspring, the original 316 sires' milk protein eBVs for the initial proof, reproof, and latest proof were compared to their son's (total 1876) initial proof eBV for milk protein.

Sire eBVs for milk protein, milk fat, and milk volume declined between their initial and latest proof with an average decline of 6.36kg (43.1%), 8.22kg (53%) and 340.6 litres (70.1%) respectively. Jersey sires showed a greater decline in eBVs than Friesian sires for milk protein (7.97kg vs 5.2kg), milk fat (9.65kg vs 7.2kg), and milk volume (426 litres vs 280 litres). CRV Ambreed sires declined significantly less than LIC sires' eBVs for milk protein (5kg vs 7.1kg), milk fat (6.4kg vs 9.3kg), and milk volume (300 litres vs 364 litres). Sires' initial proof, reproof, and latest proof all had a strong correlation to that of their son's initial proof, 84%, 84% and 85% respectively.

The findings of this study highlight the decline in New Zealand's elite Friesian and Jersey sires estimated genetic merit over their life time, and poses factors potentially causing this decline.

Keywords: Estimated breeding value, initial proof, reproof, latest proof, sire, Friesian, Jersey, traits.

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Chapter 1

Introduction

Genetic merit in the New Zealand dairy industry is a key driver of the efficiency and production levels attained in today's dairy production systems. Animal evaluation is key to identifying animals which are the most efficient at converting feed into profit, typically identified through breeding indexes. Breeding indexes are estimated for all animals and comprise estimates of the animal's genetic merit (estimated breeding value, eBV) for multiple traits. For each animal, each eBV is multiplied by an economic weighting unique to each trait, and the products added, allowing individual animals to be ranked on a monetary value pertaining to their overall genetic value relative to other animals in the population. This provides a clear indication to farmers and breeders about which animals have the highest estimated genetic merit and are the most desirable to breed replacements from.

In the New Zealand dairy industry, the Breeding Worth (BW) index is the main tool used to rank individual animals based on their ability to convert five tonnes of feed to profit. Introduced in 1996, the BW index allows for across breed genetic evaluation of milk fat and milk protein yield for a 270-day lactation using a statistical animal model (Harris *et al.*, 1996). This has since been developed using the herd test data to calculate estimated breeding values (eBVs) of traits used in the BW index (Harris *et al*., 2006). The BV's are estimated, as the actual gene transfer from one generation to the next cannot be specifically measured. The BW index is currently made up of eight economically important traits (Milk Protein, Milk Fat, Milk Volume, Live-weight, Fertility, Somatic Cell Count, Residual Survival, Body Condition Score), but many other traits are also evaluated on the genetic merit of an animal.

Sire eBVs for specific traits are expected to change as the reliability of the estimation increases as more information about a bull's genetic merit is established, through the increased number of evaluated progeny. In addition, the relative economic weighting of each individual trait varies annually due to changes in consumer demand for traits. This ultimately causes fluctuations in individual animals' BW, while also determining the overall direction in which the dairy industry is breeding towards.

Typically, the reliability and accuracy of a bull's eBV and thus BW increases with the number of progeny being evaluated, alongside other pedigree information from siblings and relatives (DairyNZ, 2016). It is therefore expected that half of the bulls evaluated will increase in their eBVs for traits, and half will decline as more information about the bull is known. However, most bulls' eBVs are seen to decline throughout their lifetime, but due to the complexities involved, a reason for why this decline occurs has not been established.

1.1 Aim and objective of the study

This study aims to quantify the change in elite sires' eBVs throughout their lifespan and provide potential reasons for the change in eBVs. Furthermore, it investigates whether a bull's initial proof, reproof, or latest proof is the best estimate of its genetic merit that is passed onto their offspring.

Chapter 2

Review of Literature

2.1 Breeding worth index

Breeding worth (BW) is a selection index which ranks dairy cattle based on their ability to breed replacements which convert five tonnes of feed to profit. Hence, an animal's BW relative to other cattle in the population allows farmers to select bulls and cows with superior genetics to produce profitable and efficient replacements (Clarke, 2013).

The genetic values of the eight key traits in the index are represented by individual eBVs. These are an estimation of the cow or bull's genetic merit for specific traits, which are calculated using a statistical modelling approach on the performance of a cow or bull's ancestors, siblings, progeny, and in the case of a cow, on her own milking performance. The statistical model used is a single trait animal model, where production in different lactations is treated as repeated measures of the same trait (Harris *et al*., 2006). The ability to compare across breeds is particularly important in New Zealand dairy farm systems where 85% of herds have mixed breeds (Harris *et al*., 2007). Hence the statistical model used in New Zealand is designed for multi-breed comparisons.

2.1.1 Equation for BW

An Animal's eBVs for the eight key traits are multiplied by a relative economic value (REV) specific to each trait to give a product that sums with the other seven terms, to give an overall BW value. This allows comparisons of bulls and cows regardless of their age, herd, breed, when they calved, or how long they have been in milk (Dairy NZ, 2016).

BW of animal y = (Protein eBV(y) x Protein REV) + (Fat eBV(y) x Fat REV) + (Milk Volume eBV(y) x Milk Volume REV) + (Live-weight eBV(y) x Live-weight REV) + (Fertility eBV(y) x Fertility REV) + (Somatic cell count eBV(y) x Somatic cell count REV) + (Residual survival eBV(y) x Residual survival REV) + (Body condition score eBV(y) x Body condition score REV)

2.2 Traits involved

The BW index currently includes eight traits of economic importance to New Zealand dairy farming; milk fat, milk protein, milk volume, Live-weight, somatic cell count, residual survival, fertility, and body condition score (Dairy NZ, 2016).

2.2.1 Milk fat

Milk fat is one of the main traits which makes up the BW index, having a 10.9% emphasis on an individual cow or bull's overall BW in 2017 (Figure 1). Dairy farmers in New Zealand are typically paid on a per kilogram of milk solids basis which is the protein and fat component of milk. Thus, milk fat has a positive economic weighting. Jersey cows on average will have a higher eBV for milk fat than Friesian cows (DairyNZ, 2016a). The annual genetic gain for milk fat regardless of breed is currently on average +1.0kg per year (DairyNZ, 2016a).

2.2.2 Milk protein

Milk protein is the other component of milk solids and has the greatest emphasis on an individual's breeding worth in 2017, 26.9% (Figure 1). Greater milk protein results in more kilograms of milk-solids and therefore has a positive economic weighting. Friesian cows on average will have a higher eBV for milk protein than Jersey cows (DairyNZ, 2016a). The annual genetic gain for milk protein regardless of breed is on average +1.1kg per year, similar to that of milk fat (DairyNZ, 2016a).

2.2.3 Milk volume

Milk volume eBV has a negative economic weighting in the BW index due to the value of milk coming from the milk solid components, rather than the volume of milk which consists largely of water. The genetic gain in milk volume is continuing to increase at around 19 litres per year (DairyNZ, 2016a).

2.2.4 Live-weight

Cow live-weight is important in the BW index as it effects the maintenance requirement of the cow. Therefore, live-weight has a negative economic weighting as greater live-weight results in increased feed requirements for maintenance, resulting in reduced feed conversion efficiency for milk production (Beever & Doyle, 2007). Cow live-weight eBVs should aim to be maintained, while the positively weighted traits continue to increase, improving the efficiency of production (DairyNZ, 2016a).

2.2.5 Somatic cell score

Somatic cell count is a measure of the amount of white blood cells in the milk to analyse udder health and milk quality (Schukken *et al.*, 2003). White blood cells enter the milk to fight udder infections, commonly mastitis (Sharif & Muhammad, 2008). High somatic cell count is related to infections in the udder, and milk is penalised if the somatic cell count exceeds a value where milk quality is deemed to be affected. Thus, making a low somatic cell count beneficial to the cow's overall BW. To obtain the

somatic cell score used as an eBV, the somatic cell count is log transformed in the statistical animal model (DairyNZ, 2016a).

2.2.6 Residual survival

Residual survival is the additional days in which a cow remains in the milking herd for reasons other than high merit in the other BW traits compared to a baseline average (DairyNZ, 2016a). This has positive economic implications in terms of reducing heifer replacements, which in turn reduces farm expenditure, hence making the farm more profitable.

2.2.7 Fertility

The fertility eBV is based on the percentage of cows calving in the first 42 days of calving (DairyNZ, 2016a). This is an important trait to maximise the cow's lactation length which ultimately results in greater milk production.

2.2.8 Body condition score

Body condition score is a visual assessment of the cow's body fat reserves, and was added to the BW index in February 2016 (DairyNZ, 2016a). The advantage of cows with a high body condition score means that cows do not have to be dried off as early, extending the lactation length and reducing the feed requirement to return to a BCS of 5 by the following mating (DairyNZ, n.d.).

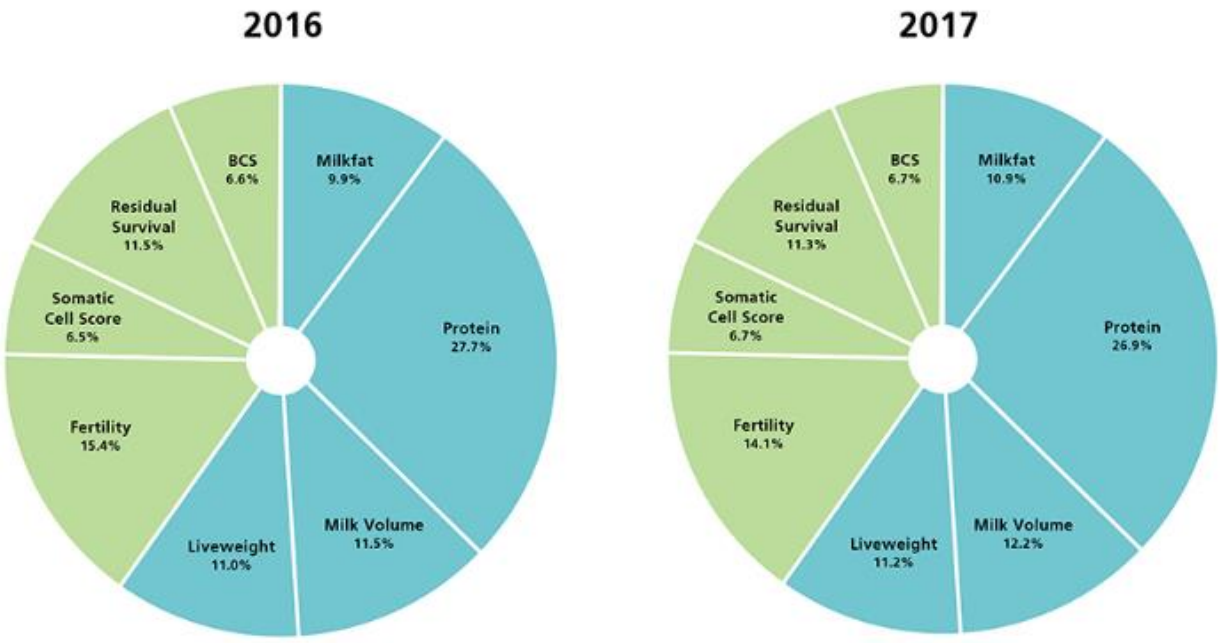

Figure 1: Effective emphasis on individual traits within the Breeding Worth index (DairyNZ, 2017)

2.3 Measurement of traits

EBVs for milk fat, milk protein, milk volume, and somatic cell score are calculated based on herd testing. The data collected from herd testing is run through a test day model. This model accounts for variables such as the animals contemporary group (age 2, 3, 4, 5, mature), temporary environmental and permanent environmental random effects on the traits (Harris *et a*l., 2006). By considering these variables, the test day model gives an improved accuracy of the cow's evaluation for a given trait (Harris *et al*., 2006).

EBVs for fertility, residual survival, body condition score, and live weight are calculated using data collected by the farmer. Fertility is calculated as the percentage calving in the first 42 days of the planned start of calving and recorded on MINDA or MISTRO software (DairyNZ, 2016a). The fertility eBV also uses information on whether the cow presented itself for mating within twenty-one days of the planned start of mating, milk volume in the cow's first lactation, and BCS at 60 days in milk (DairyNZ, 2016a). These additional measures are either positively or negatively associated with fertility. For example, high milk volume and a low body condition score is associated with lower cow fertility (Dobson et. al., 2007, Pryce et. al., 2001). These traits are then put into a multiple trait fertility model to come up with an accurate fertility eBV. This is particularly important when a sire's daughters have completed their first lactation, which becomes the sire's initial proof (Harris, 2005).

Residual survival is calculated through an equation which separates out the other eBVs effect on the cow's additional productive life in the herd (DairyNZ, 2016a). The relationship between the other eBVs and residual survival change over time, which requires the equation to be updated periodically (DairyNZ, 2016a). The current equation for residual survival sourced from DairyNZ (2016a), updated in February 2016 is as follows:

Residual survival = Total Longevity – [(4.848 x Fat) + (7.612 x Protein) - (0.0429 x Milk) - (1.5 x Live weight) + (18.078 x Fertility) - (70.666 x SCC) + (364.931 x BCS)]

Live weight eBV is calculated through weighing animals and the two-year-old weight scores (DairyNZ, 2016a). These values are then entered into a single trait model and the animals are compared based on their contemporary group (includes age, year, season of calving) to give an estimation of the animal's live weight BV.

Body condition score is a visual assessment of an animal's body energy reserves (Pryce, 2006), which is measured on a scale of 1-10. BCS eBV is estimated based on two-year-old heifer records collected in early lactation. BCS of cows is converted into 60 lactation equivalents and entered into the animal evaluation model to establish their BCS eBV (DairyNZ, 2016a).

2.4 Reliability

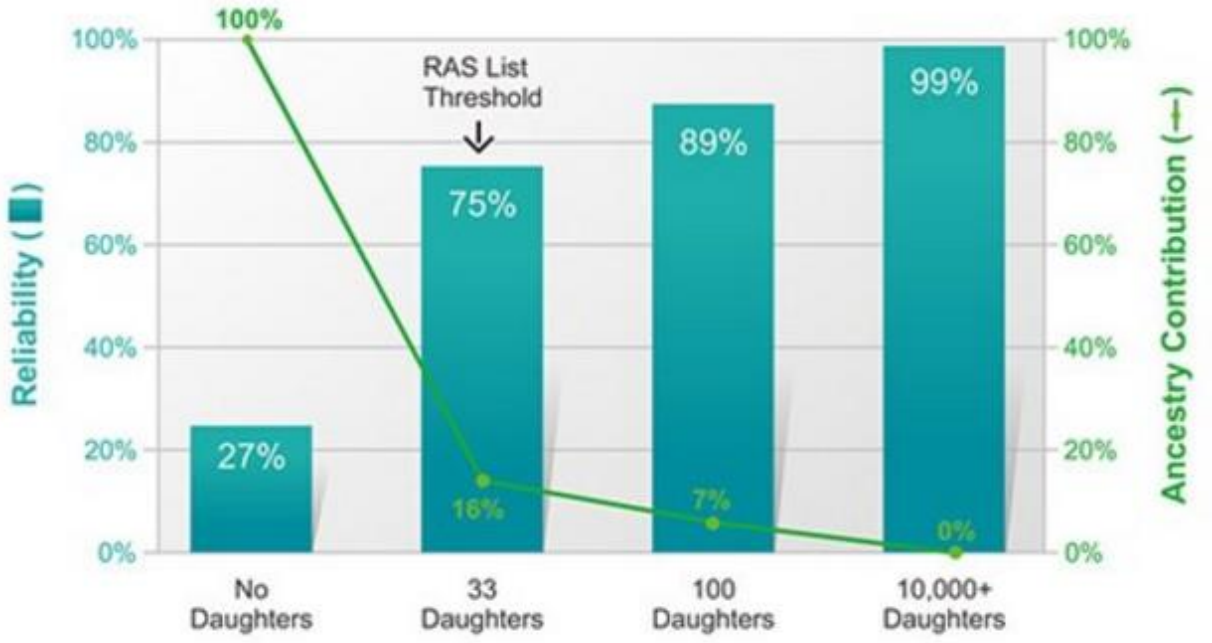

Figure 2: Sire breeding worth reliability and ancestry contribution based on the number of daughters (DairyNZ, n.d.)

For New Zealand genetic evaluation, the Animal Model BLUP (Best Linear Unbiased Prediction) is used (Harris & Johnson, 1998). The reliability of individual eBVs and the overall BW depends upon the amount of information that has contributed to the genetic evaluation (Harris & Johnson, 1998). Through the Animal Model, reliability is calculated based on the prediction error variance (PEV). The PEV is calculated from the mixed model equation, which consists of 100,000 to 20,000,000 equations for most genetic evaluations (Harris & Johnson, 1998), making the model highly complex. Reliability is used to derive confidence intervals around the eBVs (Harris & Johnson, 1998). Therefore, as the number of daughters from a sire increases, the accuracy of the sire's eBVs compared to its true genetic merit increases (Figure 2). The contribution of ancestry information also reduces as the number of daughters increases. As shown in Figure 2, bulls which attain their initial proof with 33 daughters have a reliability value of 75%. Once these bulls have been widely used their reliability increases to 99% after 10,000 daughters. EBVs then become more stable, and are expected to not fluctuate greatly.

2.5 Economic weighting

Each of the eight eBVs are multiplied by an economic value to create the BW index. The economic values are calculated based on a five-year rolling average, taking into account the past four years pricing and one future season (DairyNZ, 2017). Because of this rolling average, and to reflect consumer demands, the economic value of each eBV is recalculated each year. To calculate the value of eBVs an economic model consisting of over 40 equations is used, making it highly complex (DairyNZ, 2017). In brief terms, to assign an eBV an economic value, the monetary value of that milk component needs to be determined, feed costs to produce that component, and the reduced stocking rate to supply the additional feed need to be established. These economic values are calculated on a per unit basis, for example, one kilogram of protein creates $6.63 additional income to the farmer in 2017 (DairyNZ, 2017).

The economic weightings account for a portion of the variation in the animal's BW. As market preference changes, such as reduced demand for milk protein, so does the animals BW. Between the 2016 and 2017 change in economic values for the eight eBVs, most bulls born after 2000 with a reliability greater than 75% lost or gained no more than $10 in their BW (Figure 3).

Note: This graph was produced using data from the Nov 2016 AE run, and inculdes AE enrolled dairy sires that were born after 2000 and have a BW reliability of 75% or greater.

Figure 3: Expected change in breeding worth between 2016 and 2017 Animal Evaluation enrolled dairy sires (DairyNZ, 2017)

2.6 Base cow for genetic evaluation

EBVs of animals are based on a base cow set by NZAEL. A base cow is required because evaluation of an animal's genetic merit is not absolute, and the exact genetic merit of an animal cannot be predicted, rather comparisons can be made between animals (Van Vleck, 1992). The base cow is created by averaging the production traits of a large population of well recorded cows born in the particular base year. For example, the 2005 base cow consists of 21,585 cows (28% Holstein-Friesian, 21% Jersey, 3% Ayrshire, 48% HF x J and 0.4% other breeds). To make these comparisons more realistic and relative to the current cows and bulls being used, the base cow is updated typically every five years as per international conventions. Changes in the New Zealand base cow occurred in June 2008 when the genetic base changed from 1985 base to a 1995 base, followed by June 2010 when the genetic base changed from 1995 base to a 2000 base and most recently June 2016 when the genetic base changed from 2000 base to a 2005 base. The next base change will occur in June 2020 where the genetic base will change from the 2005 base to a 2010 born base.

2.7 Lifecycle of elite sires

Elite sires used commercially in the New Zealand dairy industry are initially chosen as bull calves based on their parents estimated genetic merit and genomic information, providing bulls with their first eBVs. The top calves from this selection process will have their semen collected at 12 months of age. This semen will then be used across 80-100 daughters in the progeny test programmes of genetics company's such as CRV Ambreed, and Livestock Improvement Company (LIC). The daughters of these young bulls will be in their first lactation when the sire is four years of age. Data collected about the daughters' first lactation from herd testing will provide the bull's initial proof. The initial proof is the second eBVs that the bull receives, ranging in reliability from 75% with 33 herd tested daughters to 89% with 100 herd tested daughters (DairyNZ, n.d.). Bulls which have high genetic merit based on their initial proof eBVs will graduate the progeny test programmes and their semen will be sold commercially to farmers. Four years later when the bull is eight years of age, its progeny will be spread throughout New Zealand dairy herds, with the potential to have thousands of daughters contributing to the bulls eBVs. This is known as the bull's reproof. Each year onwards the bull continues to increase the number of progeny, and therefore the number of herd tested daughters contributing to its trait eBVs. Continuing to increase the reliability of its trait eBVs until it has over 10,000 herd tested daughters, resulting in an eBV reliability of 99%.

2.8 Decline in genetic merit

As the reliability of bulls' eBVs increase from their initial proof with 80-100 daughters to 1000's of daughters in commercial herds at their reproof and latest proof, it is expected that changes in bull eBVs for traits will occur, with half the bulls likely to increase in eBVs and half to decline. Therefore, on average, bulls' eBVs should not change with the increasing number of herd tested daughters.

However, the detailed recording of animal evaluation in New Zealand has revealed that estimation of bulls' genetic merit is seen to decline throughout their lifespan. The reason for this decline is currently unknown, and has not been quantified in other species. The following section outlines several factors that have the potential to affect the estimation of bulls' genetic merit throughout their lifespan.

2.9 Potential factors influencing changes in genetic merit

2.9.1 Influence of genetic variation on estimated breeding values

The Animal Model BLUP (Best Linear Unbiased Prediction) used in the estimation of animal breeding values assumes a certain degree of genetic variation amongst animals. However, the amount of genetic variation in progeny test evaluations is greater than that seen with cows and bulls used in commercial herds. This is because a substantial proportion of young bulls which enter the progeny test programme do not reach the eBVs expected based on parent and genomic information. However, the elite bulls which progress through the progeny test programmes all have similar genetic merit, and therefore have lower genetic variation. Potentially, the animal model BLUP predicting eBVs is not suitable to account for the genetic variation seen in progeny test evaluations, causing an overestimation of eBVs in the initial proof.

2.9.2 Inbreeding

The increasing use of artificial breeding in the New Zealand dairy industry has allowed individual bulls to be mated to thousands of cows. Combined with selecting sires with high eBVs increases the likelihood of inbreeding because there is a greater chance they are related (Daetwyler *et al*., 2007). Inbreeding has a significant effect on key traits of cows, as shown by Cassell (1999) where each percentage increase in inbreeding reduced the total milk fat production by 13kg, milk protein by 11kg, and milk volume by 358kg over the cow's productive life. Thus, a potential cause for the decline in sires estimated genetic merit throughout their lifespan. Furthermore, it would be expected that the inbreeding effect on sires' estimated genetic merit would be more prominent in the Jersey population due to the smaller population size.

2.9.3 Parent identification

Identifying the parents of calves in commercial dairy herds in New Zealand is an area where errors in assigning the correct progeny to dam and sire can occur. A recent study of 97 herds and 20,000 cows found that 23% of the cows tested had incorrect sire information (Winkelman, 2013, DairyNZ, 2014). Similar inaccuracies in sire daughter identification have been seen in other countries, such as the Netherlands with 12% inaccuracy (Bovenhuis & Van Arendonk, 1991), Germany 4-23% (Gelderman *et al*., 1986) and Ireland 8-20% (Beechinor & Kelly, 1987). A reason for this high percentage of mismatched dams and daughters is the miss-mothering which can occur in large herds when multiple cows are calving in a short period of time. This can result in elite sires not getting recognition for their progeny or being attributed to calves sired by inferior bulls. Thus, leading to a decrease in the bulls eBVs and overall BW due to incorrect data collection as seen in the study by Banos *et al*. (2001). Incorrect sire identification of 11% was seen to reduce sire eBVs for milk volume, milk protein and milk fat by 15.9%, 13.2% and 14.3% respectively (Banos *et al*., 2001).

The inaccuracies in matching dam and sire to their offspring is a potential reason for sire eBVs, come reproof, being lower than that attained in the sire's initial proof. The differences lie with sires' initial proof coming from 80-100 herd tested daughters, compared to the hundreds or thousands of herd tested daughters which make up the sire's reproof. Because of this, typical errors in assigning the correct sire and dam to their offspring at the sire's initial proof is 5% compared to 23% come sire reproof (Winkelman, 2013, DairyNZ, 2014). Therefore, potential errors in the recording process could be influencing the decline in sire eBVs through their lifespan.

2.9.4 Epigenetics

Epigenetics is a potential pathway which could suppress the genetic merit of an animal. During the mid-1980's epigenetics was discovered as a different type of inheritance that was not based on changes in the DNA sequence (Holliday, 2006). Epigenetics refers to a change in the gene expression that occurs due to chemical changes in the DNA and the surrounding chromatin, rather than changes to the DNA sequence itself (Singh *et al*., 2012). The high cost of screening an individual's epi-genotype is a major limiting factor to understanding the impact of epigenetics in large populations (González-Recio *et al*., 2015). Because of this, no studies have been carried out on whether epigenetics is the cause of bulls eBV decline over their lifespan. However, traditional genetics is said to account for 30% of the variation in dairy cattle genetic merit, meaning that a portion of the remaining 70% variation is potentially epigenetic related (Pryce & Harris, 2006).

2.9.5 DNA methylation

DNA methylation is an epigenetic mechanism which effects the chromatin structure surrounding DNA (Singh *et al*., 2012). This can either enhance or suppress the gene expression of an animal. DNA methylation typically occurs on the fifth position of cytosine on Cytosine-Phosphate-Guanine (CpG) dinucleotides (Singh *et al*., 2012). These are related to protein coding genes, with a substantial portion of them found on the promoter region (Bird, 2002).

There are two mechanisms in which DNA methylation can suppress gene expression, as follows. Methylated CpG's may prevent the binding of the transcriptional activators (Bird & Wolffe, 1999). Secondly, transcription could be blocked by transcriptional repressors which have methyl binding domains combining with the methylated CpG's. Thus, modifying the chromatin or preventing interactions by the activator, which can suppress gene expression (Singh *et al.*, 2012).

The effect of DNA methylation in supressing gene expression has been seen in dairy cow's mammary glands. DNA methylation plays a role in the silencing of the αS1-casein expression when the cow's udder is infected and in its non-lactating state. When mammary glands are infected, methylation occurs at three CpG dinucleotides and causes chromatin condensation. In a study by Vanselow *et al*. (2006) this resulted in αS1-casein synthesis shutting down, mRNA dropping to 50% and protein levels reduced to 2.5% of that in non-mastitis control glands. This demonstrates that epigenetic pathways reducing milk traits can occur, further suggesting the potential of an epigenetic mechanism causing estimated genetic merit to decline in either the cow or bull.

2.9.6 Transgenerational epigenetics

Transgenerational epigenetics is where epigenetic marks (e.g. DNA methylation) can be transferred to the following generation via gametes (Jablonka & Raz, 2009). These genetic marks have a role in determining the functional output of the information that is stored in the genome, and therefore the variation in expressed phenotype (Jertle & Skinner, 2007). Therefore, transgenerational epigenetic marks suppressing milk production traits have the potential to be passed on from the sire to its progeny.

2.9.7 Transgenerational epigenetics in animals

There is currently no evidence that transgenerational epigenetic effects occur in dairy cows. One of the reasons for this is the large generation interval making it challenging to design a transgenerational epigenetic trial (Singh *et al*., 2012). However, a recent study on dairy cows conducted in Ireland by Berry *et al*. (2008) suggested that greater metabolic stress during pregnancy may have negative effects on the daughter's lactation. The effect was small, but could be argued that transgenerational epigenetics occur in dairy cows, but the complexities behind setting up a trial makes measuring the effect challenging.

Scottish blackface ewes showed the effect of nutrition during pregnancy on the health of their offspring. In this study by Sinclair *et al*. (2007), Scottish black face ewes had restricted intakes of methyl donor dietary proteins (Vitamin B6, B12, folate and methionine) during pregnancy. The resulting offspring exhibited higher blood pressure, greater obesity rates and insulin resistance than that of the control ewe's offspring (Sinclair *et al*., 2007).

Epigenetic studies of mice have shown that epigenetic inheritance can occur. DNA methylation in mice caused the silencing of the gene controlling coat colour, resulting in mice with an agouti (Yellow) coat (Morgan *et al*., 1999). In addition, nutrition during pregnancy also affected mice offspring coat colour. This was shown when mice diets, both maternal and paternal, were supplemented with methyl donors, which shifted their offspring's coat colour from yellow to brown (Waterland & Jirtle, 2003, Wolff *et al*., 1998).

2.9.8 Transgenerational epigenetics in humans

Studies of human epidemiology have highlighted that prenatal and early postnatal environments influence the risk of developing disease later in life (e.g. cancer, diabetes, and cardiovascular disease) (Jertle & Skinner, 2007). This was shown by a study on the Dutch famine which found that women pregnant during the famine gave birth to smaller than average infants, who were more susceptible to health problems (diabetes and cardiovascular disease). The offspring of these children were also smaller than average (Lumey, 1992). It has been suggested that these environmental factors play a part in transgenerational epigenetics, although it has not been proven on a molecular level that these are caused by epigenetic mechanisms over social factors in humans (Morgan & Whitelaw, 2008; Singh *et al.*, 2012).

From the literature, variation in nutrition during pregnancy can influence subsequent offspring performance. If animals are not fed an adequate diet during pregnancy, the resulting offspring's performance and health could be negatively affected. Poor dam nutrition during pregnancy or another

unknown epigenetic effect resulting in reduced offspring performance, has the potential to reduce the estimated genetic merit of bulls.

2.9.9 Paternal transgenerational epigenetic effects

Transgenerational epigenetic effects derived from paternal (male) ancestry has also been studied. Potential epigenetic effects such as DNA Methylation caused by increased exposure and age have the potential to result in variation in offspring's phenotype (Curley *et al*., 2011). Recent studies have shown that male exposure to carcinogens (e.g. pesticides and herbicides) such as pentachlorophenol (PCP) used in timber related industries increase the risk of lymphoma and leukaemia in their offspring (Zheng *et al*., 2015, Castro-Jiménez *et al*. 2011). In addition, a study of mice by Lane *et al*. (2003) showed that retro-transposable elements and imprinted genes are seen to be affected by environmental exposures (e.g. toxins) and can retain epigenetic marks, thus being passed onto following generations. A further example of transgenerational epigenetics from the paternal side is the methylation of the $Auxin^{FU}$ allele which causes mice offspring to have kinked tail phenotypes (Rakyan *et al*., 2003).

Feeding level on the paternal side, predominantly obesity, can influence offspring's health and performance (Loomba *et al*., 2008). In the study by Loomba *et al*. (2008), there was an association between obesity and greater levels of circulating alanine transaminase (ALT) in the progeny. ALT is seen to be associated with dysfunction of the liver and obesity. However, the mechanism by which this is passed on trans-generationally is currently unknown (Loomba *et al*., 2008).

Decline in the genetic merit of sires could potentially be a result of paternal transgenerational epigenetic effects as opposed to maternal influences. However, further study on transgenerational epigenetic effects in dairy cattle would be required to establish their influence on animal's genetic merit.

2.9.10 Environmental effects

Varying environmental conditions to which cows are exposed will also influence their performance. In the dairy industry this has the potential to occur as bulls get used more widely in the industry, moving from their initial proof based off 80-100 daughters on sire proving farms, to having thousands of daughters spread throughout New Zealand. As sires become more widely used in the industry, environmental factors could influence how traits interact in certain environments such as climate, pests, diseases, feed quality and daily walking distance for example. The environmental effect could potentially affect sires' genetic merit if daughter proven farms are not spread throughout the country to account for this variability.

2.10 Summary

The New Zealand BW index is used to evaluate the estimated genetic merit of bulls and cows in the New Zealand dairy industry, which has been a key driver to the improvement of dairy herds' productivity and profitability, particularly over the last 20 years. Because the importance of the eight traits are weighted based on an individual trait monetary value, the BW index can follow market trends based on what the end consumer demands; whether that's high milk fat or protein for example. This determines which direction the New Zealand dairy industry breeds towards.

The in-depth use of animal evaluation has highlighted the decline in bulls estimated genetic merit for key traits that occur over their lifespan. This decline has the potential to be caused by errors in the animal model BLUP that is not accounting for differences in genetic variation between sire proving farms and commercial herds, incorrect parent identification, inbreeding, environmental or epigenetic effects. The following study aims to quantify the change in eBVs of sires between their initial proof, reproof, and latest proof to establish the significance and potential underlying cause of declining eBVs throughout their lifespan.

Chapter 3

Materials and Methods

To quantify the changes in bulls' estimated breeding values (eBVs) and to determine which evaluation (initial proof, reproof, or latest proof) is the best estimate of the sire's son's genetic merit, NZAEL New Zealand Dairy Sire summaries were used. Produced in May each year, the NZAEL New Zealand Dairy Sire summaries were used to enter bulls' initial proof and reproof eBVs into an excel spread sheet. The 2016 NZAEL New Zealand Dairy Sire summary was sourced online from the DairyNZ website in the Animal Evaluation section to enter the 2016 eBVs (latest proof) of Jersey and Friesian bulls which had a BW reliability value of 96% and above. Alongside having a BW reliability of 96% and above, the bulls had to be born prior to 2007 so that both initial and reproof values occurred prior to 2016. The bulls were further sorted to only include bulls born in New Zealand and enrolled by either CRV Ambreed or Livestock Improvement Company (LIC), so they have had an official progeny test. All eight traits; milk fat, milk protein, milk volume, somatic cell count, fertility, residual survival, live weight and body condition score, as well as total longevity and the number of herd tested daughters were entered into an excel spreadsheet. BW reliability of less than 85% was used as the Initial proof, typically four years after the bull was born when its first daughters are in their first production season. Reproof eBVs were entered when the BW reliability was 95% and the 2016 eBVs were used as the bulls' latest proof.

Initial proof and reproof eBVs were corrected to the 2005 base so that breeding worth and eBVs could be compared between bulls' initial, reproof, and 2016 eBVs. The following table outlines the changes in eBVs to bring them to the 2005 base cow.

Table 1: Estimated breeding value changes required to be based on the 2005 base cow

	Evaluation prior to 2009	2009-2010	2011-2016
Fat	-26.68	-11.18	-6.08
Protein	-25.42	-9.72	-5.12
Milk Volume	-605.21	-115.21	-68.21
Fertility	1.69	0.59	0.49
Liveweight	-20.78	4.72	3.22
Residual survival	25.12	22.12	15.12
Somatic Cell Count	-0.19	-0.03	0.04

From the bulls that were entered from this selection criteria, a new spreadsheet was created to enter in each bull's son's (1876 in total) initial proof milk protein eBV. Milk protein eBVs were then corrected to the 2005 base, so they could be compared against the sires initial, reproof, and 2016 eBV for milk protein.

3.1 Statistical analysis

The statistical software package Genstat (Version 16, VSN International Ltd, Hemel Hempstead, UK) was used to analyse the raw data. The six traits of focus were milk protein, milk fat, milk volume, live-weight, fertility, and somatic cell count. Analysis of variance (ANOVA) was carried out on each trait for initial proof, reproof, latest proof, change in initial to reproof, initial to latest proof, and reproof to latest proof (dependant variables). This analysis showed the effect that breed, company, year sold, year of reproof and herd tested daughters (Independent variables) had on each of the eBVs. The variables were deemed significant if the P value was less than 5% ($P<0.05$).

Table 2: Number of bulls included in each category for statistical analysis

Category	Number
Friesian	185
Jersey	131
CRV Ambreed Friesian	67
CRV Ambreed Jersey	50
LIC Friesian	118
LIC Jersey	81
CRV Ambreed total	117
LIC total	199
Total Bulls	316

Table 2 shows the total number of bulls used in this study, also separating them out into breed, company and breed within company.

3.1.1 Initial proof ANOVA

A general ANOVA was carried out for milk protein, milk fat, milk volume, live-weight, fertility, and somatic cell count eBVs to compare the initial proof between enrolee's (LIC and CRV Ambreed), breed, and the interaction between enrolee and breed. The year sold was included in the model as a covariate. Mean values were calculated for grand mean, enrolee mean, breed mean, and breed within enrolee mean.

3.1.2 Reproof ANOVA

A general ANOVA was carried out for milk protein, milk fat, milk volume, live-weight, fertility, and somatic cell count eBVs to compare the Reproof between enrolee's (LIC and CRV Ambreed), breed, and the interaction between enrolee and breed. The year of reproof was included in the model as a covariate. Mean values were calculated for grand mean, enrolee mean, breed mean, and breed within enrolee mean.

3.1.3 Latest proof ANOVA

A general ANOVA was carried out for milk protein, milk fat, milk volume, live-weight, fertility, and somatic cell count eBVs to compare the latest proof between enrolee's (LIC and CRV Ambreed), breed, and the interaction between enrolee and breed. The number of herd tested daughters were included in the model as a covariate. Mean values were calculated for grand mean, enrolee mean, breed mean, and breed within enrolee mean.

3.1.4 Change between initial and reproof ANOVA

A general ANOVA was carried out for milk protein, milk fat, milk volume, live weight, fertility, and somatic cell count eBVs to compare the change between initial and reproof between enrolee's (LIC and CRV Ambreed), breed and the interaction between enrolee and breed. The year of initial and reproof were included in the model as a covariate. Mean values were calculated for grand mean, enrolee mean, breed mean, and breed within enrolee mean.

3.1.5 Change between initial and reproof ANOVA

A general ANOVA was carried out for milk protein, milk fat, milk volume, live-weight, fertility, and somatic cell count eBVs to compare the change between initial and latest proof between enrolee's (LIC and CRV Ambreed), breed, and the interaction between enrolee and breed. The year of initial proof and herd tested daughters were included in the model as a covariate. Mean values were calculated for grand mean, enrolee mean, breed mean, and breed within enrolee mean.

3.1.6 Change between reproof and latest proof ANOVA

A general ANOVA was carried out for milk protein, milk fat, milk volume, live weight, fertility, and somatic cell count eBVs to compare the change between reproof and latest proof between enrolee's (LIC and CRV Ambreed), breed, and the interaction between enrolee and breed. The year of reproof and herd tested daughters were included in the model as a covariate. Mean values were calculated for grand mean, enrolee mean, breed mean, and breed within enrolee mean.

3.1.7 Correlation

To determine the best estimate of a sires breeding worth, in terms of the genetic merit it passes onto its sons, a correlation was carried out. This correlation was carried out on the protein eBV to compare the sire's initial, reproof, and latest proof against their son's initial eBV.

Chapter 4

Results

4.1 Milk protein

4.1.1 Initial proof milk protein eBV

Friesian bulls had significantly greater milk protein eBVs than Jersey bulls in their initial proof. The year of initial proof also had a significant effect on bulls' initial proof milk protein eBV. The year of initial proof had a covariate of 0.53kg. Initial proofs occurred between 2001 and 2011 inclusive, therefore 11 years. This means that having an initial proof in 2011 vs 2001 increased bulls' milk protein eBVs by 5.83kg. There was no significant effect of enrolee (CRV Ambreed, LIC) or interaction between enrolee and breed on bulls' initial proof milk protein eBV.

4.1.2 Reproof milk protein eBV

Friesian bulls had significantly greater milk protein eBVs than Jersey bulls in their reproof. The year of reproof also had a significant effect on bulls' reproof milk protein eBV. The year of reproof had a covariate of 0.40kg. Reproof measurements occurred between 2005 and 2015 inclusive, therefore 11 years. This means that having a reproof in 2015 vs 2005 increased the bulls milk protein eBV by 4.40kg. There was no significant effect of enrolee (CRV Ambreed, LIC) or interaction between enrolee and breed on bulls' reproof milk protein eBV.

4.1.3 Latest proof milk protein eBV

Friesian bulls had significantly greater milk protein eBVs than Jersey bulls in their latest proof. CRV Ambreed had a significantly greater milk protein eBV than LIC in the latest proof. The number of herd tested daughters also had a significant effect on bulls' milk protein eBV in the latest proof. The number of herd tested daughters had a covariate of 0.000067. This means that each additional daughter increases the bulls latest proof milk protein eBV by 0.000067. There was no significant interaction between enrolee and breed on bulls' latest proof milk protein eBV.

4.1.4 Change in milk protein eBV between initial and reproof

On average, bulls eBVs for milk protein declined between their initial and reproof (I-R). Jersey bulls milk protein eBVs declined significantly more than Friesian bulls between the initial and reproof. There was no significant effect of enrolee (CRV Ambreed, LIC), year of initial proof, year of reproof or the interaction between enrolee and breed on bulls change in milk protein eBV between the initial proof and reproof.

4.1.5 Change in milk protein eBV between reproof and latest proof

On average, bulls eBVs for milk protein declined between their reproof and latest proof (R-L). LIC bulls milk protein eBVs declined significantly more than CRV Ambreed between their reproof and latest proof. Jersey bulls milk protein eBVs declined significantly more than Friesian bulls between the reproof and latest proof. The year of reproof had a significant effect on the change in milk protein eBV between reproof and latest proof. The coefficient -0.318 means that each additional year reduces the difference in initial to latest by 0.32kg. Reproof measurements occurred between 2005 and 2015 inclusive, therefore 11 years. This means that having a reproof in 2015 vs 2005 reduces the decline in milk protein eBVs between reproof and latest by 3.52kg. Herd tested daughters had a significant effect on the change in milk protein eBV between reproof and latest proof. However, the coefficient 0.0000432 means that each additional daughter increases the difference in reproof to latest by 0.0000432, a minimal change. There was no significant effect of the interaction between enrolee and breed on bulls change in milk protein eBV between the reproof and latest proof.

4.1.6 Change in milk protein eBV between initial and latest proof

On average, bulls eBVs for milk protein declined between their initial and latest proof (I-L). LIC bulls milk protein eBVs declined significantly more than CRV Ambreed between their initial and latest proof. Jersey bulls milk protein eBVs declined significantly more than Friesian bulls between the initial and latest proof. The year of initial proof had a significant effect on the change in milk protein eBV between initial and latest proof. The coefficient 0.295 for the change in milk protein eBV between initial and latest proof means that each additional year reduces the difference in initial to latest by 0.295kg. Initial proofs occurred between 2001 and 2011 inclusive, therefore 11 years. This means that having an initial proof in 2011 vs 2001 reduces the decline by 3.25kg. There was no significant effect of the interaction between enrolee and breed or the number of herd tested daughters on bulls change in milk protein eBV between the initial proof and latest proof.

Table 3: P-values and mean values for sire milk protein eBV

	Initial	Reproof	Latest	I-R	R-L	I-L
Source of variation	F pr.					
Enrollee	n/s	n/s	0.002	n/s	0.003	0.001
Breed	<.001	<.001	<.001	0.01	<.001	<.001
Enrollee.Breed	n/s	n/s	n/s	n/s	n/s	n/s
Yr of Initial Proof	<.001			n/s		0.001
Yr of Reproof		0.002		n/s	<.001	
Herd Tested Daughters			0.001		<.001	n/s
Grand Mean	14.75	9.49	8.39	-5.26	-1.1	-6.36
Friesian Mean	25.94	21.23	20.47	-4.71	-0.45	-5.21
Jersey Mean	-1.06	-7.08	-8.67	-6	-2.01	-7.97
CRV Ambreed Mean	13.98	9.19	9.44	-4.78	-0.47	-5.06
LIC Mean	15.2	9.67	7.77	-5.54	-1.47	-7.12
CRV Friesian Mean	25.49	21.76	22.48	-3.73	0.13	-3.45
LIC Friesian Mean	26.21	20.93	19.31	-5.28	-0.79	-6.23
CRV Jersey Mean	-1.45	-7.65	-8.03	-6.2	-1.27	-7.21
LIC Jersey Mean	-0.84	-6.75	-9.03	-5.91	-2.45	-8.41

(I-R: Change between Initial and Reproof, R-L: Change between Reproof and Latest, I-L: Change between Initial and Latest)

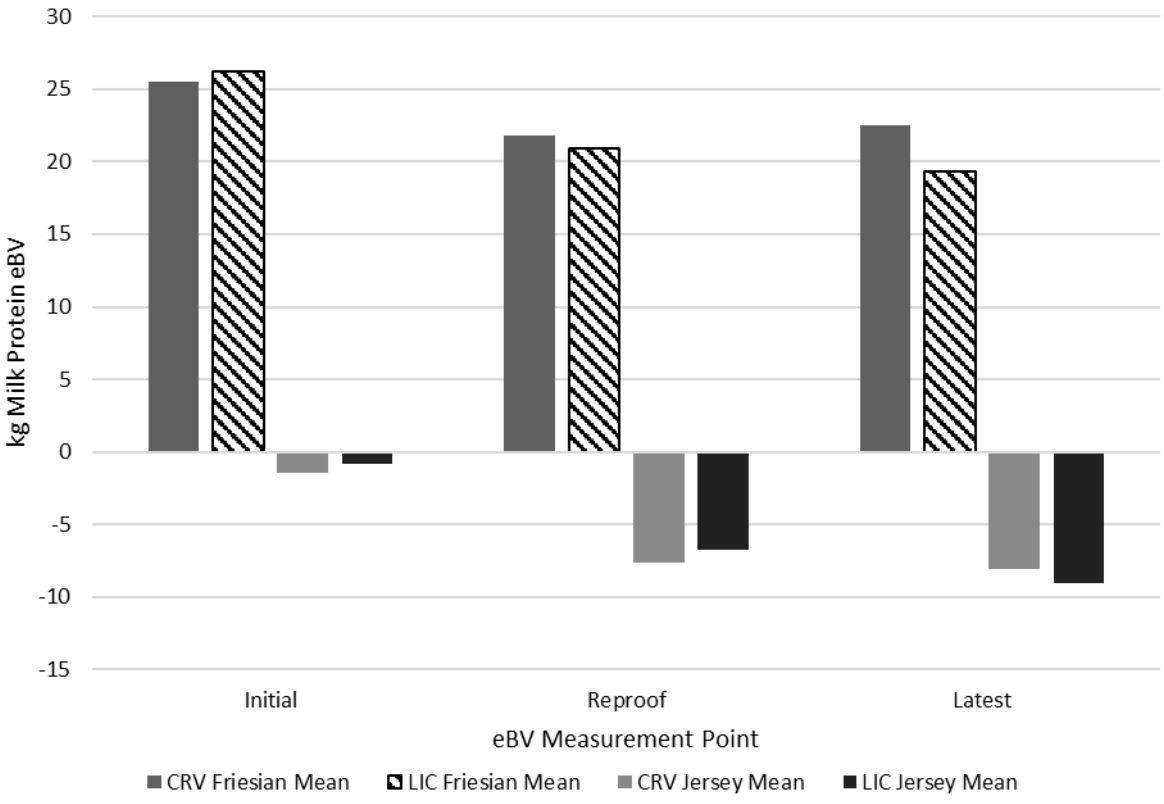

Figure 4: Breed within company mean milk protein eBV for initial proof, reproof and latest proof

4.2 Milk fat

4.2.1 Initial proof milk fat eBV

Friesian bulls had significantly greater milk fat eBVs than Jersey bulls in their initial proof. LIC had significantly greater milk fat eBVs than CRV Ambreed in the initial proof. There was no significant effect of the year of initial proof or interaction between enrolee and breed on bulls' initial proof milk fat eBV.

4.2.2 Reproof milk fat eBV

Friesian bulls had significantly greater milk fat eBVs than Jersey bulls in their reproof. There was no significant effect of enrolee (CRV Ambreed, LIC), year of reproof or interaction between enrolee and breed on bulls' reproof milk fat eBV.

4.2.3 Latest proof milk fat eBV

Friesian bulls had significantly greater milk fat eBVs than Jersey bulls in their latest proof. CRV Ambreed had a significantly greater milk fat eBV than LIC in the latest proof. The number of herd tested daughters also had a significant effect on bulls' milk fat eBV in the latest proof. The number of herd tested daughters had a covariate of 0.000079. This means that each additional daughter increases the bulls latest proof milk fat eBV by 0.000079. There was no significant interaction between enrolee and breed on bulls' latest proof milk fat eBV.

4.2.4 Change in milk fat eBV between initial and reproof

On average, bulls eBVs for milk fat declined between their initial and reproof (I-R). LIC bulls milk fat eBVs declined significantly more than CRV Ambreed between their initial and reproof. Jersey bulls milk fat eBVs declined significantly more than Friesian bulls between the initial and reproof. There was no significant effect of the year of initial proof, year of reproof or the interaction between enrolee and breed on bulls' change in milk fat eBV between the initial proof and reproof.

4.2.5 Change in milk fat eBV between reproof and latest proof

On average, bulls eBVs for milk fat declined between their reproof and latest proof (R-L). LIC bulls milk fat eBVs declined significantly more than CRV Ambreed between their reproof and latest proof. Jersey bulls milk fat eBVs declined significantly more than Friesian bulls between the reproof and latest proof. The year of reproof had a significant effect on the change in milk fat eBV between reproof and latest proof. The coefficient 0.33 means that each additional year reduces the difference between initial to latest proof by 0.32kg. Reproofs occurred between 2005 and 2015 inclusive, therefore 11 years. This means that having a reproof in 2015 vs 2005 reduces the decline in milk fat eBV between reproof and latest by 3.33kg. Herd tested daughters had a significant effect on bulls' milk fat eBV between reproof

and latest proof (R-L). However, the coefficient 0.00005 means that each additional daughter increases the difference in reproof to latest by 0.00005 a minimal change. There was no significant effect of the interaction between enrolee and breed on bulls' change in milk fat eBV between the reproof and latest proof.

4.2.6 Change in milk fat eBV between initial and latest proof

On average, bulls eBVs for milk fat declined between their initial and latest proof (I-L). LIC bulls milk fat eBVs declined significantly more than CRV Ambreed between their initial and latest proof. Jersey bulls milk fat eBVs declined significantly more than Friesian bulls between the initial and latest proof. The year of initial proof had a significant effect on the change in milk fat eBV between initial and latest proof. However, the coefficient 0.25 means that each additional year reduces the difference in initial to latest by 0.25kg. Initial proofs occurred between 2001 and 2011 inclusive, therefore 11 years. This means that having an initial proof in 2011 vs 2001 reduces the decline between initial and latest by 2.75kg. There was no significant effect of the interaction between enrolee and breed or the number of herd tested daughters on bulls change in milk fat eBV between the initial proof and latest proof.

Table 4: P-values and mean values for sire milk fat eBV

	Initial	Reproof	Latest	I-R	R-L	I-L
Source of variation	F pr.					
Enrollee	0.005	n/s	0.002	0.029	0.011	<.001
Breed	<.001	<.001	<.001	0.025	0.009	<.001
Enrollee.Breed	n/s	n/s	n/s	n/s	n/s	n/s
Yr of Initial Proof	n/s			n/s		0.033
Yr of Reproof		n/s		n/s	<.001	
Herd Tested Daughters			0.001		<.001	n/s
Grand Mean	15.85	9.3	7.63	-6.55	-1.67	-8.22
Friesian Mean	20.18	14.22	12.71	-5.96	-1.19	-7.21
Jersey Mean	9.75	2.36	-0.46	-7.38	-2.35	-9.65
CRV Ambreed Mean	13.9	8.24	8.15	-5.66	-0.95	-6.4
LIC Mean	17	9.93	7.33	-7.07	-2.09	-9.29
CRV Friesian Mean	19	14.41	14.63	-4.6	-0.51	-4.94
LIC Friesian Mean	20.88	14.14	11.62	-6.75	-1.6	-8.53
CRV Jersey Mean	7	-0.02	-0.52	-7.07	-1.56	-8.36
LIC Jersey Mean	11.35	3.8	-1.08	-7.55	-2.81	-10.4

(I-R: Change between Initial and Reproof, R-L: Change between Reproof and Latest, I-L: Change between Initial and Latest)

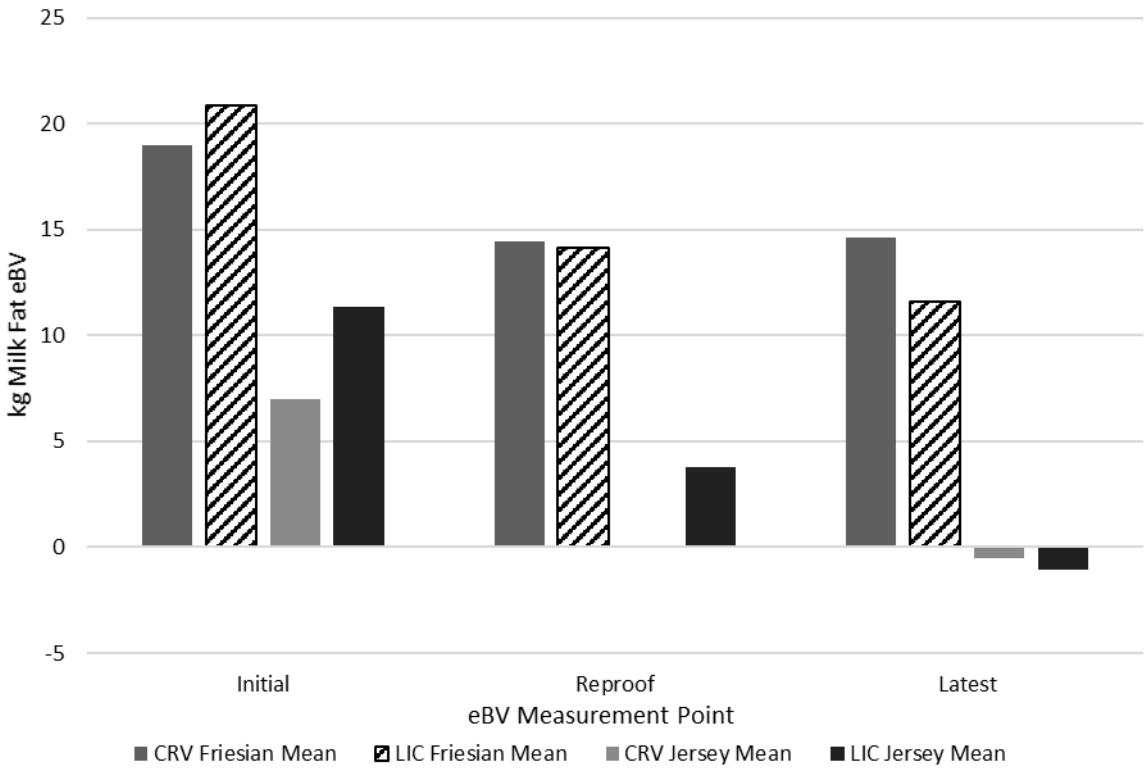

Figure 5: Breed within company mean milk fat eBV for initial proof, reproof and latest proof

4.3 Milk volume

4.3.1 Initial proof milk volume eBV

Friesian bulls had significantly greater milk volume eBVs than Jersey bulls in their initial proof. The year of initial proof had a significant effect on bulls' initial proof milk volume eBV. The year of initial proof had a covariate of 9.1 litres. Initial proofs occurred between 2001 and 2011 inclusive, therefore 11 years. This means that having an initial proof in 2011 vs 2001 increased the bulls milk volume eBV by 100 litres. There was no significant effect of enrolee or the interaction between enrolee and breed on bulls' initial proof milk volume eBV.

4.3.2 Reproof milk volume eBV

Friesian bulls had significantly greater milk volume eBVs than Jersey bulls in their reproof. There was no significant effect of enrolee (CRV Ambreed, LIC), year of reproof or interaction between enrolee and breed on bulls' reproof milk volume eBV.

4.3.3 Latest proof milk volume eBV

Friesian bulls had significantly greater milk volume eBVs than Jersey bulls in their latest proof. CRV Ambreed had a significantly greater milk volume eBV than LIC in the latest proof. The number of herd tested daughters also had a significant effect on bulls' milk volume eBV in the latest proof. The coefficient 0.0015 means that each additional daughter increases the decline between reproof and latest by 0.0015, a minimal change. There was no significant interaction between enrolee and breed on bulls' latest proof milk volume eBV.

4.3.4 Change in milk volume eBV between initial and reproof

On average, bulls eBVs for milk volume declined between their initial and reproof (I-R). Jersey bulls milk volume eBVs declined significantly more than Friesian bulls between the initial and reproof. The year of the bulls' initial proof had a significant effect on the change in milk volume eBV between initial and reproof. The coefficient -5 litres mean that each additional year reduces the difference between initial to reproof by 5 litres. Initial proofs occurred between 2001 and 2011 inclusive, therefore 11 years. This means that having an initial proof in 2011 vs 2001 reduces the decline between initial and latest by 55 litres. There was no significant effect of enrolee, year of reproof or the interaction between enrolee and breed on bulls' change in milk volume eBV between the initial proof and reproof.

4.3.5 Change in milk volume eBV between reproof and latest proof

On average, bulls eBVs for milk volume declined between their reproof and latest proof (R-L). LIC bulls milk volume eBVs declined significantly more than CRV Ambreed between their reproof and latest proof. Jersey bulls milk volume eBVs declined significantly more than Friesian bulls between reproof and latest proof. The year of reproof had a significant effect on the milk volume eBV for the change between reproof and latest proof. The coefficient 13.6 means that each additional year reduces the difference in initial to latest by 13.6 litres. Reproofs occurred between 2005 and 2015 inclusive, therefore 11 years. This means that having a reproof in 2015 vs 2005 reduces the decline in milk volume eBV between reproof and latest by 149.6 litres. Herd tested daughters had a significant effect on bulls' milk volume eBV for the change between reproof and latest proof (R-L). However, the coefficient 0.0014 means that each additional daughter increases the difference in reproof to latest by 0.0014 a minimal change. There was no significant effect of the interaction between enrolee and breed on bulls' change in milk volume eBV between the reproof and latest proof.

4.3.6 Change in milk volume eBV between initial proof and latest proof

On average, bulls eBVs for milk volume declined between their initial and latest proof (I-L). LIC bulls milk volume eBVs declined significantly more than CRV Ambreed between their initial and latest proof. Jersey bulls milk volume eBVs declined significantly more than Friesian bulls between the initial and latest proof. The year of the bulls' initial proof had a significant effect on the change in milk volume eBV between initial and latest proof. The coefficient 7.4 means that each additional year reduces the difference in initial to latest by 7.4 litres. Initial proofs occurred between 2001 and 2011 inclusive, therefore 11 years. This means that having an initial proof in 2011 vs 2001 reduces the decline between initial and latest by 81.4 litres. There was no significant effect of the interaction between enrolee and breed or the number of herd tested daughters on bulls' change in milk volume eBV between the initial and latest proof.

Table 5: P-values and mean values for sire milk volume eBV

	Initial	Reproof	Latest	I-R	R-L	I-L
Source of variation	F pr.					
Enrollee	n/s	n/s	<.001	n/s	<.001	<.001
Breed	<.001	<.001	<.001	<.001	<.001	<.001
Enrollee.Breed	n/s	n/s	n/s	n/s	n/s	n/s
Yr of Initial Proof	0.042	n/s		0.006		0.009
Yr of Reproof				n/s	<.001	
Herd Tested Daughters			0.051		<.001	n/s
Grand Mean	486	316	145	-169.7	-170.9	-340.6
Friesian Mean	973	836	687	-136.8	141.9	-280.2
Jersey Mean	-203	-419	-620	-216.2	-211.8	-425.9
CRV Ambreed Mean	487	329	201	-158.3	-147.2	-300.1
LIC Mean	485	308	112	-176.4	-184.8	-364.4
CRV Friesian Mean	984	879	776	-105.5	-118.5	-219.3
LIC Friesian Mean	967	812	635	-154.8	-155.7	-315.5
CRV Jersey Mean	-178	-408	-570	-229.1	-185.7	-408.3
LIC Jersey Mean	-218	-426	-650	-207.9	-227	-435.6

(I-R: Change between Initial and Reproof, R-L: Change between Reproof and Latest, I-L: Change between Initial and Latest)

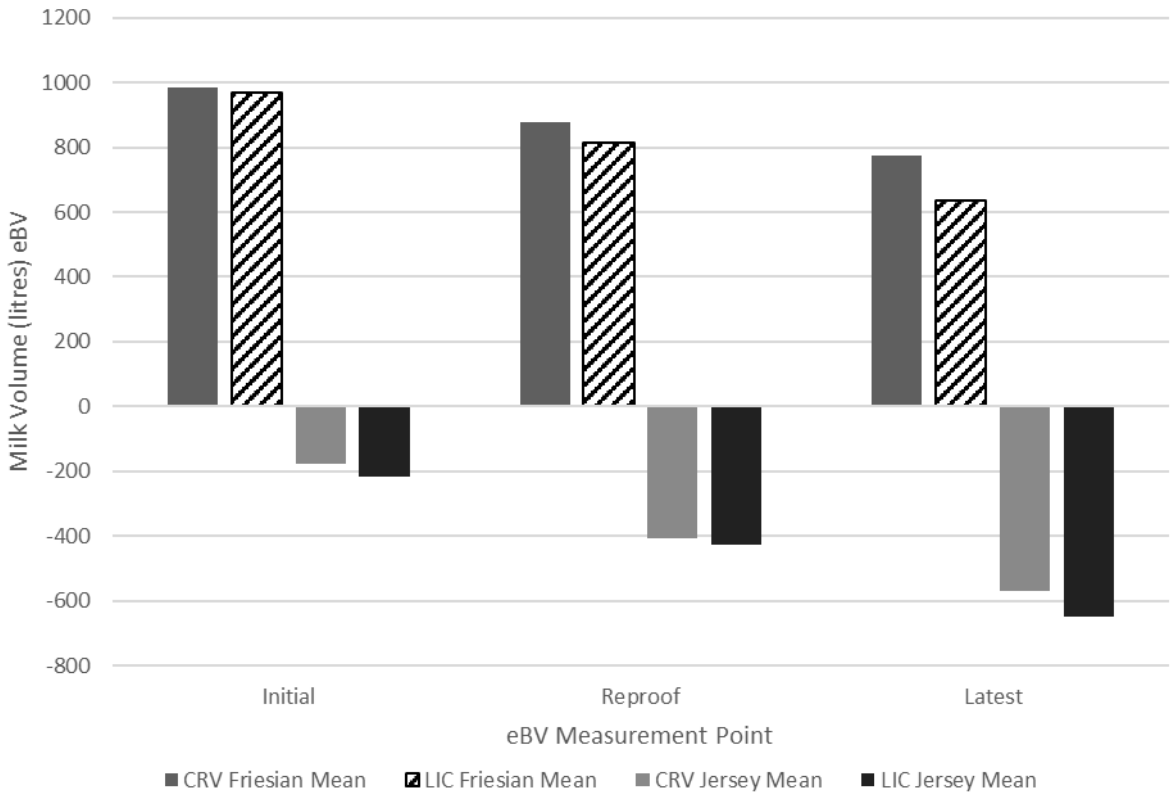

Figure 6: Breed within company mean milk volume eBV for initial proof, reproof and latest proof

4.4 Live-weight

4.4.1 Initial proof live-weight eBV

Friesian bulls had significantly greater live-weight eBVs than Jersey bulls in their initial proof. Enrolee and breed had a significant interaction, with CRV Ambreed Friesian sires having a greater live-weight than LIC sires. Also, CRV Ambreed Jersey sires had significantly lower live-weights than LIC Jersey sires. There was no significant effect of enrolee or the year of initial proof on bulls' initial proof live-weight eBV.

4.4.2 Reproof live-weight eBV

Friesian bulls had significantly greater live-weight eBVs than Jersey bulls in their reproof. Enrolee and breed had a significant interaction, with CRV Ambreed Friesian sires having a greater live-weight than LIC sires. Also, CRV Ambreed Jersey sires had significantly lower live-weights than LIC. There was no significant effect of enrolee or the year of reproof on bulls' reproof live-weight eBV.

4.4.3 Latest proof live-weight eBV

Friesian bulls had significantly greater live-weight eBVs than Jersey bulls in their latest proof. Enrolee and breed had a significant interaction, with CRV Ambreed Friesian sires having a greater live-weight than LIC sires. Also, CRV Ambreed Jersey sires had significantly lower live-weights than LIC. There was no significant effect of enrolee or the year of reproof on bulls' reproof live-weight eBV.

4.4.4 Change in live-weight eBV between initial and reproof

On average, bulls eBVs for live-weight declined between their initial and reproof (I-R). Friesian bulls live-weight eBVs declined significantly more than Jersey bulls between the initial and reproof. The year of the bulls' initial proof had a significant effect on the change in live-weight eBV between initial and reproof. The coefficient -2.4kg means that each additional year reduces the difference between initial and reproof by 2.4kg. Initial proofs occurred between 2001 and 2011 inclusive, therefore 11 years. This means that having an initial proof in 2011 vs 2001 reduces the decline between initial and latest by 26.4kg. There was no significant effect of enrolee, year of reproof or the interaction between enrolee and breed on bulls' change in milk volume eBV between the initial proof and reproof.

4.4.5 Change in live-weight eBV between reproof and latest proof

On average, bulls live-weight declined between reproof and latest proof. However, there was no significant effect of enrolee, breed, year of reproof, herd tested daughters or an interaction between enrolee and breed on the change in bulls live-weight eBV between reproof and latest proof.

4.4.6 Change in live-weight eBV between initial and latest proof

On average, bulls eBVs for live-weight declined between their initial and latest proof (I-L). Friesian bulls live-weight eBVs declined significantly more than Jersey bulls between the initial and latest proof. There was no significant effect of enrolee, year of initial proof, the number of herd tested daughters or the interaction between enrolee and breed or on bulls change in live-weight eBV between the initial and latest proof.

Table 6: P-values and mean values for sire live-weight eBV

	Initial	Reproof	Latest	I-R	R-L	I-L
Source of variation	F pr.					
Enrollee	n/s	n/s	n/s	n/s	n/s	n/s
Breed	<.001	<.001	<.001	<.001	n/s	0.004
Enrollee.Breed	<.001	<.001	0.019	n/s	n/s	n/s
Yr of Initial Proof	n/s			0.037		n/s
Yr of Reproof		n/s		n/s	n/s	
Herd Tested Daughters			n/s		n/s	n/s
Grand Mean	10.6	5.09	3.2	-2.29	-5.1	-7.4
Friesian Mean	55.49	46.66	45.2	-5.61	-4.8	-10.4
Jersey Mean	-52.79	-53.61	-56	2.4	-5.5	-3.1
CRV Ambreed Mean	12.06	7.11	4.8	-1.69	-5.8	-7.4
LIC Mean	9.74	3.91	2.3	-2.64	-4.7	-7.3
CRV Friesian Mean	62.75	53.74	52.1	-5.83	-5.2	-10.9
LIC Friesian Mean	51.33	42.6	41.2	-5.49	-4.5	-10.1
CRV Jersey Mean	-55.87	-55.37	-58.5	3.86	-6.6	-2.8
LIC Jersey Mean	-50.85	-52.47	-54.4	1.52	-4.9	-3.3

(I-R: Change between Initial and Reproof, R-L: Change between Reproof and Latest, I-L: Change between Initial and Latest)

4.5 Fertility

4.5.1 Initial proof fertility eBV

Jersey bulls had significantly higher fertility eBVs than Friesian bulls in their initial proof. The year of initial proof had a significant effect on the initial proof eBV. There was no significant effect of enrolee or interaction between enrolee and breed on bulls' initial proof fertility eBV.

4.5.2 Reproof fertility eBV

Jersey bulls had significantly higher fertility eBVs than Friesian bulls in their reproof. Enrolee and breed had a significant interaction, with CRV Ambreed Friesian sires had a lower fertility eBV than LIC sires. Also, CRV Ambreed Jersey sires had significantly higher fertility eBVs than LIC Jersey sires. There was no significant effect of enrolee or the year of reproof on bulls' reproof fertility eBV.

4.5.3 Latest proof fertility eBV

Friesian bulls had significantly lower fertility eBVs than Jersey bulls in their latest proof. LIC bulls had significantly higher fertility eBVs than CRV Ambreed. Enrolee and breed had a significant interaction, with CRV Ambreed Friesian sires having a lower fertility eBV than LIC sires. Also, CRV Ambreed Jersey sires had significantly higher fertility eBVs than LIC. There was no significant effect of the number of herd tested daughters on bulls' latest proof fertility eBV.

4.5.4 Change in fertility eBV between initial and reproof

On average, bulls eBVs for fertility increased between their initial and reproof (I-R). The year of initial proof had a significant effect on bulls' fertility eBVs. However, there was no significant effect of enrolee, breed, year of reproof or the interaction between enrolee and breed on bulls' change in fertility eBV between the initial proof and reproof.

4.5.5 Change in fertility eBV between reproof and latest proof

On average, bulls' fertility declined between reproof and latest proof. However, there was no significant effect of enrolee, breed, year of reproof, herd tested daughters or an interaction between enrolee and breed on the change in fertility eBV between reproof and latest proof.

4.5.6 Change in fertility eBV between initial and latest proof

On average, bulls eBVs for fertility increased between their initial and latest proof (I-L). CRV Ambreed bulls increased significantly more than LIC bulls' fertility eBV between the initial and latest proof. There was a significant interaction between enrolee and breed, with CRV Ambreed Friesian and Jersey sires' increasing significantly more than LIC Friesian and Jersey sires'. There was no significant effect of breed or the number of herd tested daughters on bulls' change in fertility eBV between the initial and latest proof.

Table 7: P-values and mean values for sire fertility eBV

	Initial	Reproof	Latest	I-R	R-L	I-L
Source of variation	F pr.					
Enrollee	n/s	n/s	0.015	n/s	n/s	0.031
Breed	<0.001	<0.001	0.041	n/s	n/s	n/s
Enrollee.Breed	n/s	<0.001	0.012	n/s	n/s	0.003
Yr of Initial Proof	<0.001			0.004		<0.001
Yr of Reproof		n/s		n/s	n/s	
Herd Tested Daughters			n/s		n/s	n/s
Grand Mean	-0.29	0.94	0.45	1.23	-0.49	0.74
Friesian Mean	-0.84	0.33	-0.06	1.3	-0.85	0.44
Jersey Mean	-0.47	1.8	1.17	1.14	0.02	1.17
CRV Ambreed Mean	-0.38	0.51	-0.52	0.92	0.22	1.19
LIC Mean	-0.24	1.19	1.02	1.41	-0.91	0.48
CRV Friesian Mean	-0.65	-0.86	-1.85	1.31	-0.34	0.94
LIC Friesian Mean	-0.94	1.01	0.98	1.3	-1.15	0.15
CRV Jersey Mean	-0.02	2.35	1.26	0.41	0.98	1.52
LIC Jersey Mean	0.78	1.45	1.09	1.59	-0.56	0.97

(I-R: Change between Initial and Reproof, R-L: Change between Reproof and Latest, I-L: Change between Initial and Latest)

4.6 Somatic cell count

There was no effect observed with somatic cell count between enrolee, breed, year sold, year of reproof, and herd tested daughters (see appendix 1, Table 9).

4.7 Sire-son correlation

There is a strong correlation of sires' initial, reproof, and latest proof compared to their son's initial proof for milk protein. There was no significant difference between sire's initial proof, reproof and latest proof when compared to their son's initial proof milk protein eBV (Table 8).

Table 8: Correlation of sires' milk protein eBVs for initial, reproof and latest proof to sires' sons initial proof milk protein eBV

	Correlation
Initial	0.84
Reproof	0.84
Latest	0.85

Chapter 5

Discussion

Elite Friesian and Jersey sires estimated breeding values (eBVs) declined between their initial, reproof and latest proof, in milk protein, milk fat and milk volume (Tables 3, 4 and 5). Because sire proving farms are distributed throughout New Zealand, following sires' initial proofs it would be expected that half the sires increase in their eBVs and half decline. However, 87.7% of sires dropped in milk protein, 92% in milk fat and 98.7% in milk volume eBVs between their initial and latest proof. This has commercial implications, as sires are sold commercially based on their initial proof eBVs. However, sires estimated genetic merit in commercial herds is much lower, shown by the decline in milk protein, milk fat and milk volume eBVs between their initial and reproof (Tables 3, 4 and 5).

Decline in sires' eBVs between their initial and reproof also has commercial implications on bulls that are widely used in the industry based solely on ancestry and genomic information. As any bias in the genetic evaluation, flows onto greater inaccuracies when predicting a cow's genetic merit. Thus, establishing the cause of sires' eBV decline is important to the NZ dairy industry.

5.1 Genotype by environment interactions

A potential cause of the decline in sires' eBVs is the interaction between the genotype and the environment. This interaction would influence a sire's eBVs if the initial proof occurred in one area of New Zealand. Once their genetics were used throughout the country, sire's genotype potentially would not provide the same genetic merit as estimated from their initial proof in sire proving herds, causing a decline in sires' eBVs. However, sire proving farms are distributed throughout New Zealand, allowing each sire's daughters to be tested in a range of environments. This eliminates a sire's initial proof being overestimated because of the sire proving farms favourable environmental conditions.

If the interaction between genotype and environment was the sole contributing factor to the decline in sire eBVs, it would be expected that sires' eBVs would decline as the number of herd tested daughters spread throughout New Zealand increases. However, the number of herd tested daughters did not influence the decline in sires' eBVs between the initial and latest proof. For example, FAIRMONT MINT-EDITION (AB code: 105038) gained 0.55kg in milk protein eBV between the initial and latest proof after 97,546 herd tested daughters across 7,426 herds. New Zealand has 11,927 herds (DairyNZ, 2016b), meaning this bull has been used over an estimated 62% of New Zealand dairy herds, in a wide range of environmental conditions. Hence, it is unlikely that environmental effects are causing sires' eBV decline.

Potentially, progeny test herds have favourable farm systems regarding the quality of feed allocated to cows, compared commercial herds. In turn, this would overestimate the genetic merit of bulls' initial proof. Without knowing the exact distribution of daughters throughout the country, and the type of farm systems they are in, means environmental effects cannot be ruled out in contributing to sires' eBV decline.

5.2 Potential genotype by genotype interaction

The decline in sire eBVs was particularly prominent in the moderately heritable traits of milk protein, milk fat, and milk volume, with an average decline of 6.36kg (43.1%), 8.22kg (53%) and 340.6 litres (70.1%) respectively. Milk volume has been reported to consist of 4.65% milk fat and 4.64% milk protein (Looper, 2012), thus a reduction in milk volume would be correlated with reduced milk protein and milk fat eBVs. Assuming the environmental effect is accounted for through progeny testing in a range of environments, this decline in sire eBVs for milk fat and milk protein is potentially the result of a genotype by genotype interaction that reduces a sire's genetic merit for milk volume traits. This interaction would be more prominent in smaller populations, such as the NZ Jersey herd, probably reflecting the smaller gene pool for that breed in NZ, when compared to the much larger Friesian population. This aligns with Jersey sires having a greater decline in eBVs than Friesian sires for milk protein (7.97kg vs 5.2kg), milk fat (9.65kg vs 7.2kg) and milk volume (426 litres vs 280 litres).

Interestingly, Friesian and Jersey sires' fertility eBVs increased between their initial and latest proof. If inbreeding was causing the decline in sires estimated genetic merit, it would have been expected that sires' fertility eBVs would have declined (Cassell, 1999, González-Recio *et. al.*, 2007). Therefore, it is unlikely that inbreeding in the NZ dairy industry is causing the decline in sires estimated genetic merit.

5.2.1 Epigenetic effect

The decline in sires' milk protein, milk fat and milk volume eBVs throughout their lifespan is potentially caused by an epigenetic effect. Epigenetics refers to a change in the gene expression that occurs due to chemical changes in the DNA and the surrounding chromatin, rather than changes to the DNA sequence itself (Singh *et al*., 2012). A major mechanism driving epigenetic change is methylation which effects the chromatin structure surrounding DNA (Singh *et al*., 2012). Study's in both humans and mice have shown that transgenerational epigenetics can occur through paternal (male) ancestory. Exposure to methyl donors (e.g. Vitamin B) or carcinogens (e.g. toxins, pesticides and herbicides) have the potential to suppress the gene expression for traits that are passed onto the offspring (Castro-Jiménez *et al*. 2011, Morgan *et al*. 1999, Zheng *et al*., 2015,). Thus, sires' exposer to toxins, supplements (e.g. vitamins, minerals), drenches (e.g. selenium), feeding level or environmental stress could cause an epigenetic mechanism (e.g. methylation) to suppress the gene expression for milk traits. A targeted

epigenetic effect suppressing milk volume traits would in turn reduce sires' milk protein and milk fat eBVs, potentially explaining why milk volume, milk protein, and milk fat eBVs declined.

The level of exposure to factors influencing epigenetic effects could vary amongst bull farms, explaining why Livestock Improvement Company (LIC) bulls eBVs decreased significantly more than CRV Ambreed bulls in milk fat (54.6% vs 46% decline), milk protein (46.8%% vs 36.2% decline) and milk volume (75.1% vs 61.6%).

An interesting aspect of the decline in sire eBVs over their lifespan, is the similar trend in milk protein eBVs decline to that of their sons, between their initial and latest proof (Table 10-16, Appendix). This trend cannot be evaluated as to whether it is statistically significant due to the small sample size of sires' sons. However, this indicates that the decline in eBVs is potentially heritable, with sires' genetic makeup possibly affecting the suseptibility of epigenetic interactions, which are potentially causing the decline in sires' eBVs.

Further research on epigenetic effects triggered by drenches, feed, supplements, animal stress and the social aspects on the bull farms is necessary to establish their effect on eBV decline. The complexity of epigenetic and gene by gene interactions in dairy cattle, makes identifying the main driver of sire eBV decline extremely challenging. However, the question can be challenged; is genetic gain being lost due to epigenetic effects triggered by practices on genetics company's bull farms?

5.3 Paternity errors influencing sire ebv decline

One of the main reasons that I suggest is causing the decline in sires' eBVs between their initial and latest proof, is paternity errors. Winkleman (2013) found that 23% of cows over 97 herds in the New Zealand dairy industry had been incorrectly assigned to particular sires, compared to only 5% on progeny test farms (DairyNZ, 2014). Paternal misidentification has been reported to negatively affect sires' eBVs; 11% misidentification reduced sire eBVs for milk volume, milk protein and milk fat by 15.9%, 13.2% and 14.3% respectively (Banos *et. al.,* 2001). Thus, a misidentification rate similar to Winkleman (2013) is likely to cause the decline of 6.36kg (43.1%) in milk protein, 8.22kg (53%) milk fat, and 340.6 litres (70.1%) in milk volume. In addition, paternity errors in progeny test herds have the potential to overestimate a bulls' initial proof. This could occur by incorrectly assigning daughters of an elite sire to that of an inferior bull, thus overestimating the bull's genetic merit in the initial proof.

Sires which had initial and reproof measurements taken more recently showed reduced decline in milk protein, milk fat, and milk volume between their initial and latest proof (Tables 3, 4 and 5). Assuming the accuracy of sire daughter identification and recording systems in both progeny test herds and

commercial herds has improved overtime, aligns with paternal misidentification causing sire eBV decline.

5.4 Potential errors within the animal model BLUP calculation

Many young bulls which enter the progeny test programmes based on ancestry and genomic information do not reach their expected eBVs. This results in a greater amount of genetic variation in the sire proving herds compared to that across all herds in New Zealand, as commercial herds are typically offspring of sires which graduated the progeny test programmes. Therefore, the animal model BLUP could potentially be overestimating sires' eBVs in their initial proof, by not correctly accounting for the greater genetic variation in sire proving herds. Thus, causing the decline between sires' initial and latest proof eBVs (Tables 3, 4 and 5).

5.5 Best estimate of the bulls genetic merit

The best estimate of a bull's genetic merit, in terms of what is passed onto its progeny could not be established due to the similarity in correlations between sires initial, reproof, and latest proof to that of their son's initial proof for milk protein (Table 8). It was expected that the bulls latest proof would be the best estimate of the genetic merit that is passed onto their offspring, as more herd tested daughters provides greater information about the performance of their offspring, increasing the reliability and accuracy of eBVs for traits.

Using the latest proof as the best estimate of the sire's genetic merit would be valid if the decline in eBVs is caused by an epigenetic, inbreeding, or genotype by environment effect. However, using the initial proof would be the best method if the decline in eBVs is due to sire daughter misidentification in commercial herds.

5.6 Conclusion

New Zealand Friesian and Jersey sires' eBVs declined in the moderately heritable traits of milk protein, milk fat, and milk volume between their initial and latest proof. The decline in sires eBVs for key traits is potentially underestimated, as this study was based on bulls which had their latest proof in 2016 and were still in active use in the New Zealand dairy industry. Bulls which showed a greater decline in eBVs were not present in this study, as their use in the industry would have discontinued due to the lack of genetic merit after their reproof eBVs.

The effect of the environment is assumed to be correctly accounted for in sires' initial proof, as progeny test herds are distributed throughout New Zealand. Therefore, the decline in sire eBVs is potentially caused by sire daughter misidentification in commercial herds, transgenerational epigenetic effects, or errors in the animal model BLUP overestimating sires initial proof.

The influence of sire daughter misidentification on sires' eBVs in the New Zealand dairy industry needs to be established. If misidentification is causing the decline in sires' eBVs, potentially sires estimated genetic merit should be based off their initial proof on progeny test farms, as opposed to their latest proof in commercial herds, where a greater misidentification occurs. To prevent misidentification influencing sires estimated genetic merit, I suggest that only DNA tested daughters should contribute to sires' eBVs.

If misidentification is not causing sires' eBVs decline, further analysis of the animal model BLUP used in the estimation of eBVs is recommended. Particularly, how accurately the animal model BLUP accounts for genetic variation on sire proving farms, to understand the models influence on the estimation of sires' genetic merit. Potentially, the animal model BLUP is not accounting for the greater genetic variation on sire proving farms, causing an overestimation of sires' eBVs in the initial proof. An additional statistical model could be incorporated to account for the genetic variation on sire proving farms alongside the current model, to prevent overestimation of sires' eBVs in the initial proof.

Appendix

Table 9: P-values and mean values for sire somatic cell count eBV

	Initial	Reproof	Latest	I-R	R-L	I-L
Source of variation	F pr.					
Enrollee	0.136	0.041	0.092	0.304	0.186	0.977
Breed	0.254	0.856	0.12	0.21	0.105	0.918
Enrollee.Breed	0.499	0.468	0.619	0.152	0.128	0.77
Yr of Initial Proof	0.312			0.267		0.819
Yr of Reproof		0.827		0.413	0.122	
Herd Tested Daughters			0.453		0.338	0.179
Grand Mean	-0.01	0.034	0.006	0.044	-0.028	0.016
Friesian Mean	0.008	0.03	0.029	0.022	-0.004	0.018
Jersey Mean	-0.037	0.04	-0.002	0.077	-0.063	0.015
CRV Ambreed Mean	0.027	0.1	-0.044	0.072	-0.059	0.016
LIC Mean	-0.033	-0.006	-0.017	0.027	-0.008	0.017
CRV Friesian Mean	0.059	0.077	0.076	0.018	-0.006	0.013
LIC Friesian Mean	-0.023	0.002	<0.001	0.025	-0.002	0.02
CRV Jersey Mean	-0.02	0.134	-0.002	0.15	-0.135	0.02
LIC Jersey Mean	-0.047	-0.018	-0.042	0.031	-0.018	0.012

Table 10: Friesian sire and son's protein eBV at initial, reproof, latest and changes between initial to reproof, reproof to latest and initial to latest

Bull	ab code	Sire/son	Initial	Reproof	Latest	I-R	R-L	I-L
Whinlea Magley Extasy	663962	sire	34	28	29	-6	1	-5
Maire ex presso	104524	son	33.58	35	39.1	1.42	4.1	5.52
Bagworth Kalumburu	104658	son	32.3	32	32.5	-0.3	0.5	0.2
Beaufort Triumph	104055	son	25.6	26	28.5	0.4	2.5	2.9
Buchanans Earlytime S2F	104021	son	36.6	37	39.7	0.4	2.7	3.1
Carsons Radical S2F	104184	son	35.6	38	38	2.4	0	2.4
Guitrys Aura ET S2F	104108	son	23.6	21	23.2	-2.6	2.2	-0.4
Karioi Ex Kodiak S2F	104535	son	36.6	33	35	-3.6	2	-1.6
Higgins Format	104191	son	31.6	29	27.3	-2.6	-1.7	-4.3
HSS Extasy Prefect ET	103691	son	28	25	23.3	-3	-1.7	-4.7
					avg	-1.3	1.2	-0.2

Table 11: Friesian sire and son's protein eBV at initial, reproof, latest and changes between initial to reproof, reproof to latest and initial to latest

Bull	ab code	Sire/son	Initial	Reproof	Latest	I-R	R-L	I-L
Aurora Donor Favour	101650	Sire	33	32	35	-1	3	2
HSS Favour Peer ET S3F	107588	son	27	33	35	6	2	8
Maire FVR Phillospher ET	107515	son	29	25	28	-4	3	-1
					avg	0.3	2.7	3.0

Table 12: Friesian sire and son's protein eBV at initial, reproof, latest and changes between initial to reproof, reproof to latest and initial to latest

Bull	ab code	Sire/son	Initial	Reproof	Latest	I-R	R-L	I-L
Macfarlanes Dauntless	101140	sire	32	28	22	-4	-6	-10
Maori MD Summit S1F	107001	son	26	11	13	-15	2	-13
Blakelock MD Knight S3F	106179	son	32	28	21	-4	-7	-11
Culglen Daunt Blackout	107550	son	31	25	26	-6	1	-5
Jellymans MD Fellowship	107076	son	21	7	9	-14	2	-12
					avg	-8.6	-1.6	-10.2

Table 13: Friesian sire and son's protein eBV at initial, reproof, latest and changes between initial to reproof, reproof to latest and initial to latest

Bull	ab code	Sire/son	Initial	Reproof	Latest	I-R	R-L	I-L
SRB Corboys Lightning	99258	Sire	23.6	21.6	19	-2	-2.6	-4.6
Westland CL Jasper ET	106149	son	29.3	24	17	-5.3	-7	-12.3
Waiwira CL Dazzler ET S1F	105240	son	22.3	11	11.5	-11.3	0.5	-10.8
					avg	-6.2	-3.0	-9.2

Table 14: Jersey sire and son's protein eBV at initial, reproof, latest and changes between initial to reproof, reproof to latest and initial to latest

Bull	ab code	Sire/son	Initial	Reproof	Latest	I-R	R-L	I-L
Okura Manhatten ET SJ94	300534	sire	11.6	11.6	6	0	-5.6	-5.6
Tironui OM Joskin	306025	son	2.3	5	5.5	2.7	0.5	3.2
Crescent Man Dominic ET	307514	son	7	4	9	-3	5	2
Raynham Ozark S3J	305807	son	5.3	2	5	-3.3	3	-0.3
Okura OM Ideal	306001	son	5.3	2	1	-3.3	-1	-4.3
Lynbrook Tradesman S3J	305054	son	11	8	8	-3	0	-3
Lynbrook Om Titan ET S3J	306095	son	5	0	1	-5	1	-4
					avg	-2.1	0.4	-1.7

Table 15: Jersey sire and son's protein eBV at initial, reproof, latest and changes between initial to reproof, reproof to latest and initial to latest

Bull	ab code	Sire/son	Initial	Reproof	Latest	I-R	R-L	I-L
Bourkes Nimrod	301014	Sire	1.6	-4.5	-14	-6.1	-9.5	-15.6
Crescent Nim Delta	307091	son	3	-6	-7	-9	-1	-10
Green Park BN Tango	307097	son	1	-16	-14	-17	2	-15
Okura BN Insight	307011	son	-3	-18	-16	-15	2	-13
					avg	-11.8	-1.6	-13.4

Table 16: Jersey sire and son's protein eBV at initial, reproof, latest and changes between initial to reproof, reproof to latest and initial to latest

Bull	ab code	Sire/son	Initial	Reproof	Latest	I-R	R-L	I-L
TAWA GROVE MAUNGA ET SJ79	300528	sire	1.6	2.6	-6.14	1	-8.74	-7.74
MULLINS MAUNGA ORION S2J	306511	son	3.3	-12	-11.76	-15.3	0.24	-15.06
HILLSTAR MAUNGAS JONO	307537	son	-6	-16	-14.2	-10	1.8	-8.2
HILLSTAR MAUNGA JUNIOR	306550	son	-1.5	-9	-6.2	-7.5	2.8	-4.7
OKURA MAUNGA KAWAKAWA ET	306500	son	-5.5	-19	-16.7	-13.5	2.3	-11.2
ARRIETA TGM KAR	306070	son	-3.5	-15	-13.2	-11.5	1.8	-9.7
MULLINS MAUNGA ORION S2J	306511	son	3.3	-12	-11.8	-15.3	0.2	-15.1
WAIKARE MAUNGA BIGGLES	306525	son	5.3	-4	-3	-9.3	1	-8.3
WILLIAMS TGM HENRY	306047	son	-2.5	-14	-13	-11.5	1	-10.5
KERSTENS TGM REGAL ET S2J	306117	son	6.3	-1	-3	-7.3	-2	-9.3
					avg	-10.0	0.0	-10.0

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