

**GENETIC VARIATION IN THE PRODUCTION TRAITS OF WESTERN
FINNCATTLE**

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Masters Thesis
University of Helsinki
MBIOT
Biotechnology
February 2019

Tiedekunta/Osasto — Fakultet/Sektion — Faculty Faculty of Agriculture and Forestry		Laitos — Institution — Department Department of Agricultural Sciences	
Tekijä — Författare — Author Ajayi Busayo Rejoice			
Työn nimi — Arbetets titel — Title Genetic variation in the production traits of Western Finncattle			
Oppiaine — Läroämne — Subject Biotechnology			
Työn laji — Arbetets art — Level Master Thesis		Aika — Datum — Month and year February 2019	Sivumäärä — Sidoantal — Number of pages 59
Tiivistelmä — Referat — Abstract <p>The Finnish dairy cattle population has been subjected to systematic quantitative studies over decades. The Western Finncattle (WFC) has evolved over the last century with a production level comparable to other remaining local breeds in Europe. The heritability is used in designing the data collection and in predicting the changes expected from the selection and the variation parameters are used in constructing the economic selection indices genetic improvement scheme and in computing the bulls' and cows' breeding values. WFC has no recent studies on the genetic variation in milk production traits. The thesis research was set to estimate the heritability of milk, fat and protein yield, fat%, protein%, protein-fat ratio and somatic cell count (SCC) and the genetic correlation amongst them. Records from Western Finncattle primiparous cows calving in the period 2002–2016 were used for the genetic analyses. The raw data consisted of 5455 cows distributed across 2512 herds. The variance components were estimated with single and multi-trait animal model using a Bayesian approach and R studio package MCMCglmm. With requiring at least 5 cows in each herd-year subclass in the estimation, the data size was reduced to 1763 cows in 233 herds. The heritability of milk, protein and fat yield, protein%, fat% and SCC was in single (and in brackets for multi) trait analysis 0.36 (0.37), 0.27(0.30), 0.32 (0.30), 0.61(0.43), 0.52 (0.49) and 0.06 (0.15), respectively. Amongst yield traits and also between the content traits the genetic correlation was high, 0.73–0.94 and 0.43–0.59, respectively. The content traits (with milk yield in the denominator) had a negative genetic correlation with milk yield while no correlation with the protein and fat yield. There was an environmental correlation between content and yield traits for protein and fat. No correlations exist between SCC and other traits except an environmental correlation with milk yield and protein content. Despite the small population size of the WFC population, the effective population size is satisfactory and therefore no reduction in genetic variation is expected. Overall, the analysis on production traits and pedigree data shows that the Western Finncattle have much potential for genetic improvement.</p>			
Avainsanat — Nyckelord — Keywords yield traits, content traits, somatic cell count, Western Finncattle, heritability, genetic correlations			
Säilytyspaikka — Förvaringsställe — Where deposited Department of Agricultural Sciences and Viikki Campus Library			
Muita tietoja — Övriga uppgifter — Further information Supervisor(s): Professor Asko Mäki-Tanila			

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ABBREVIATIONS AND CONCEPT

BLUP	Best linear unbiased prediction
CVa	Coefficient of additive variation
DIM	Days in milk
DGV	Direct genomic values
EBV	Expected breeding value
ESS	Effective Sample Size
GBLUP	Genomic best linear unbiased prediction
HPD	Highest posterior density
P/F	Protein to fat ratio
REML	Restricted maximum likelihood
SCC	Somatic cell count
SCS	Somatic cell score
SD	Standard deviation
SNP	Single Nucleotide Polymorphism
QTL	Quantitative trait loci
WFC	Western Finncattle

1 INTRODUCTION

Dairy cattle farming is the most important sector of agriculture in Finland because of its production, competitiveness and feasibility even in the northern parts of the country. In Finland there are two international dairy breeds (Ayrshire and Holstein) and three local Finncattle breeds (Eastern, Western and Northern). Within EU, the European Agricultural Fund for Rural Development programme has been launched by the Ministry of Agriculture and Forestry with one of the aims to support diversity in local animal breeds. Funds are granted to farmers for raising Eastern, Northern and Western Finncattle animals. A farmer is given 530/livestock unit/year with commitment to rear a specified number of local breed animals for five years.

In 2017, there were 218,498 cows in Finland recorded in 5,028 herds (ProAgria webpage, oct. 2017). The milk recorded cows were 81% of the total number of cows in that year. Dairy cows were recorded in 72% of all cow herds with an average herd size of 43. Western Finncattle (WFC) have the largest population among the three Finncattle breeds. Back in 1930, 60% of cow milk records in Finland were accounted for this breed. 16). There has been a severe decline in the WFC population while the number of Finnish Ayrshire and Holstein cows have increased since 1950's and 1960's, respectively (Marleen Felius, 1995). The current animal register of Finland shows that there are 3000 WFC individuals linked to 1700 herds with two thirds of the cows belonging to the milk recording scheme. Presently, WFC semen storage has more than 260,000 doses from 160bulls. About 25% of the bulls were born before 1980.

The primary focus in selection is on protein yield, dry matter content, fertility, health, satisfactory accuracy for breeding value and durability. In the relatively small WFC population, the progeny groups are small to achieve an efficient selection scheme.

The WFC cows have the highest milk yield among the Finncattle breeds. The milk from WFC is known to have high dry matter content and good cheese making properties (MTT Agrifood research, regionalcattlebreeds.eu). WFC milk protein also contains kappa-casein B alleles which has been associated with improved milk manufacturing properties (Lien et al. 1999). Dairy cow milk yield and its components are essential traits affecting the profitability of the dairy enterprise. Milk yield is a very crucial part of the profitability equation (Dallas et al. 2013). High producing herds have been profitable in dairy enterprises regardless of herd size. The Finncattle breeding goal is to enhance the milk production traits to meet the expectations of the dairy industry and to reinforce the production profitability. The economic weight of WFC

according to FABA are udder conformation (20%), reproduction traits (15%), yield traits (45%), udder health (20%) (source: FABA page).

Concurrently, the genetic diversity within the breed and the unique properties of Finncattle sub-breeds are still maintained. Native cattle breeds have small populations and are endangered by increased level of inbreeding (Fernandez et al. 2011). The proper management of small populations will increase their likelihood of survival and ensure that the genetic information and variation is not lost (Fernandez et al. 2011). The estimation of genetic variation for production traits in dairy cows is essential for early prediction of selection response. Genetic variation creates a basis for adaptation of animal to varying environment and evolvability. Therefore, it is necessary to assess to which direction the variation is moving using current population size and pedigree information (Toro et al. 2011).

Often economically important traits are correlated, and the magnitude of this association can be determined by the genetic correlation. Genetic correlation may enhance the accuracy of the estimated breeding values. When there is an antagonistic relationship between traits, e.g. between production and fertility, this should be accounted for in setting the selection goal and collecting information on cows. When a correlation exists, it can be an essential tool for animal breeders and can as well result in improving several traits by selecting only for one of them.

In the global economy, milk production is the primary selection objective in dairy cattle breeding. Milk is a consumer product and its composition influence its economic value as well as its nutritional qualities. Genetic selection for essential traits has assisted the growth of dairy cattle industry. Specific traits considered for selection in dairy cattle populations have evolved with time as a response to the needs of producers, consumers, and society with the aid of advances in technology and trait recording. Shook (1989) outlined several criteria a trait must meet before it can be considered as a selection criterion in dairy cattle populations. First, either it needs to have financial value as a marketable commodity or its development ought to reduce manufacturing costs. Secondly, the trait must have a sufficient genetic variation and it can be accurately measured and recorded. A trait is a useful selection criterion if it is heritable, correlated with an economically important trait and can be measured with low cost.

By weighting each trait according to its effect on net profit and using genetic and phenotypic parameters to construct a practical selection index for the measurements obtained from individuals (and relatives), net profit can be maximised (Hazel 1943). Genetic parameters should be estimated regularly from the data collected through a well-organised milk recording

scheme. The traits considered in selection vary between countries because of differences in milk and component prices, costs of inputs and services, production environments, and availability of phenotypes. These traits can frequently change, and modifications need to be considered and researched continually. The identification of traits that are presently important for genetic selection and those that will be essential in the future is a vital aspect of animal breeding research.

To facilitate a better knowledge of improving the economically important traits in dairy cows, many studies have been carried out on Finnish dairy cows. However, too little attention has been paid to estimating the genetic variation in milk traits of Western Finncattle in recent times. Currently, there are no data available on the heritability and genetic correlation estimates which are important tools for breeders in the dairy industry.

2 LITERATURE REVIEW

2.1 Background

The economic value of traits has historically been the driver for genetic selection. From the 1930s to the 1970s, the focus of selection was solely on increasing milk yield. The economic value of a trait shows to what extent the efficiency of production is improved at the moment for a given genetic superiority for the trait (Groen, 1989). The cumulative discounted expression of the trait includes the elapsed time and the number of expressions of a superior genotype originating from using a selected individual in a breeding programme (Brascamp, 1978). The need to identify and select for several traits simultaneously emerged mainly from the recognition of the correlated genetic decline in important non-production traits. Existing studies recognise the critical role played by functional traits such as fertility and health traits in dairy cattle. These traits play a significant role in the biological, economic, and ethical aspects of animal production and animal productivity. The approach, however, has sometimes failed also to address genetic variation in economically important product quality traits (fat and protein percent). These traits are also a vital aspect of the milk composition. Many countries have shifted toward more balanced selection objectives by including more weight on previously undervalued yield traits (Miglior et al., 2005).

For a better understanding on which traits are essential for a breeding goal, some of the scientific literature which focuses on milk, fat, and protein yield, milk somatic cell count, their genetic variation and evaluations and other issues concerning the traits are been reviewed here. Essential criteria for selection concerns genetic variation and heritability of a trait, which has been studied by many researchers to establish the rate of genetic progress possible within a selection program. The genetic variation varies across breeds. The modern genetic improvement in dairy cattle is relying on the use of genomic information. Non-genetic factors are also affecting the variation in milk traits, such factors as herd, year, stage of lactation and parity.

2.2 Causes of variation in milk production traits

The milk production of a cow depends on her genetic capacity to utilize high quality nutrition in a stress-free environment. Variation in milk traits is a resultant effect of genetic or non-genetic factors. For the evaluation of milk yield and its components, lots of research has been done to estimate the heritability, genetic and phenotypic correlations amongst the traits like protein and fat yield and somatic cell count. Factors like herd, calving age and season also have an effect on these traits. These factors are used as a fixed effect in statistical analysis.

2.3 Non-genetic factors affecting variation in milk production traits

2.3.1 Calving age

One of the most important factors influencing the reproduction performance of a dairy cow is the age at first calving and season of calving (Pirlo et al. 2000). Age at first calving is extremely important economic trait determining the profit of life-time milk production.

Dommerholt (1975) found that age at calving accounted for about 46% of the variation in daily milk yield at the beginning of lactation, which decreased down to about 5% at the end.

Thompson et al. (1983) found out that calving problems increased significantly when age at first calving is less than 27 months. However, for Simerl et al. 1991 stated that dystocia was frequent in (27 months old) heifers, partially explaining the detrimental effect of early calving on milk yield. Maijala and Hanna (1974) stated that heritability of milk yield is low when the first calving is late and the loss in life-time milk production is proportional to the calving age. In conclusion, the adjustment for calving age should be considered as a fixed statistical effect in predicting breeding values or in estimating the genetic variation in milk production traits (Wilmink, 1987a).

2.3.2 Days open

Days open in a dairy cow is the number of days between calving and. A higher number of days open is typically associated with reduced profitability in dairy cows. Hammond and Sanders (1923) speculated that milk yields may vary ± 30 percent depending on whether the number of days open are high or low. Their conclusion was based on the close relationship that exists between the number of days open and the length of lactation period of the cow. Louca and Legates (1968) reported a decline in milk yield due to days open. Days open explained 4.5% and

3.8% of the variation in milk yield and fat yield, respectively, in the first lactation of Holstein Friesian cattle (Wilson et al. 1966).

2.3.3 Stages of lactation

The stage of lactation is described by the days in milk (DIM) since from calving. The stage of lactation impacts both milk yield and milk composition (Dodenhoff and Emmerling 2009). Leukkunen (1989) studied genetic parameters for the persistence of milk yield in the first lactation of the Finnish Ayrshire cattle and found a lower heritability than for milk yield. However, for the second lactation considerably higher estimates were obtained. The results agreed with the estimates obtained by Bar-Anan et al. (1981), Danell (1981) and Schneeberger (1978).

Pösö and Mäntysaari (1996) studied the relationship amongst milk yield, SCC and mastitis in different stages of lactation. They discovered that mastitis and SCC can be considered as the same. The incidence of mastitis is higher immediately after parturition (first 2 months of lactation) and first 2-3 weeks of dry period (Sundhan and Sharma, 2010) and Corbett (2009) suggests that clinical mastitis occurs most often during the first week of lactation and it is more likely during the first three months of lactation than the rest of the lactating period.

Schepers et al. (1997) reported that SCC (using the natural log of somatic cell count or somatic cell score, SCS) from uninfected quarters of first parity cows was highest during the early stage of lactation. A study conducted by Sethar et al. (1979) observed a high somatic cell count just after calving which later reduced at days 30 to 60 of lactation and thereafter increased slowly towards the end of lactation.

There is also research on how the heritability of SCC varies across lactation. Negussie et al. (2005) found that at the beginning of first lactation the heritability for SCS is higher, around 0.12, and fell to 0.06 and 0.08 at mid-lactation and increased in later lactation. The trend found for daily heritability was slightly different from what was reported by Mrode & Swanson (2003) who found the average daily yield heritability estimates of 0.09 for first lactation. The lower heritability estimates determined at the start of lactation can be due to sizeable environmental variation or especially decrease genetic variance in the course of the early stages. Using the first lactation Norwegian cattle test day SCS, Ødegard et al. (2003) suggested that heritability increased from 0.05–0.07 for DIM6 to 0.08–0.12 for DIM305.

2.3.4 Parity

Increase in milk yield is caused by maturation in body and mammary gland of dairy cows. Mammary gland growth and development is directly proportional to weight increase, maturation and recurring pregnancies and lactations (Anderson, 1985). Bagnato et al. (1994) reported that cows of the same age but of different parity have different production yield, and that differences are particularly evident for the first and second parity. The study of genetic correlations between lactations has been of interest considering the usefulness of the first lactation records as the basis of selection (Baker and Robertson 1966). Heringstad et al. (2004) found how selection on the first lactation data enhanced the selection for improved resistance to mastitis. Cows are culled due to low milk yield or poor fertility or disease resistance. Hence the estimates of genetic variation using late lactation records are biased downwards and the representative estimates can be obtained using the first lactation records.

2.3.5 Feeding and management

Feeding and management can directly impact milk yield. Darfour et al. (2010) emphasised the need to develop new systems that incorporate high feed intake as an essential component in productivity. Feed protein concentration is an essential factor for microbial protein synthesis which helps in productivity of the dairy cow. Kafi and Mirzaei (2010) discovered that energy and protein are the most limiting factors for milk yield in Holstein dairy cows, especially during early lactation. Much research has been carried out to study the effects of feeding and management on milk composition (Maurice-Van et al., 2011, Norrapoke et al. 2012, Terramoccia et al. 2012). Norrapoke et al. 2012 concluded that four lactating crossbreds of Holstein Friesian and Native Zebu dairy cattle (with 75% Holstein Friesian) fed with a concentrate containing 16% crude protein had a significant increase in milk yield and its components.

2.3.6 Year and season of calving

Weather differences across years can affect milk yield. Hot summer weather can cause heat stress in dairy cows. Heat stress does tend to reduce feed intake in dairy animals and to decrease milk fat content.

Season greatly affects the availability of feed and thereby milk production. Several studies have shown that calving season causes differences in milk production and in the shape of lactation curve. Cows which calved during autumn or winter had higher milk yield in comparison to cows calved in spring or summer (Wilmink 1987 and Stanton et al. 1992). Vlieghe et al. (2004) observed that heifers calving in the period April-June had highest SCC. Lievaart et al. (2007) reported that various management practices, herd characteristics, and seasonal variables contributed to the herd somatic cell count. De (2009) observed that the milk SCC was significantly higher ($p < 0.01$) in the autumn season while Dang and Singh (2001) reported that the hot humid season (July-August) increases SCC in milk of dairy animals in India, mainly due to favourable environment for the growth of bacteria during hot-dry season (May-June).

2.4 Genetic variation in milk production traits

The opportunity to change the average level in a quantitative trait a trait through breeding depends upon the amount of genetic variation. Estimation of genetic variation in dairy livestock is needed to provide the essential understanding and tools for genetic enhancements. Genetic parameters, such as heritability and genetic correlations are needed to assess the possibilities of altering milk protein composition by selective breeding. It is useful to acquire as many available data records regarding the traits of interest. An excellent understanding of how traits are related to each other in their variation is a crucial base in carrying out successful balance selection and development applications. Some results from previous investigations of heritability (yield and contents traits and SCC), genetic and phenotypic correlations are reviewed below.

2.4.1 Breed

Milk from different cattle breeds holds distinct composition profiles because of the genetic background (Poulsen et al. 2012). The breed of a dairy cattle is probably the first selection decision taken by breeders. WFC cow is a local breed which has been practically closed without any contribution from other breeds. It is interesting to compare it with local breeds in other European countries.

Table 1. Information on some local breeds from other European countries in 2017 (ICAR) and their population size

Country	No. recorded cows	Breed	Annual milk yield (kg)
Denmark	65000	Jersey	7339
France	24000	Abondance	5346
France	430000	Montpeliarde	6933
Sweden	735	Swedish Polled	5509
Netherlands	7500	MRY	7527
Estonia	8000	Estonian Red	3784

The common international dairy breeds in Finland at the moment are Ayrshire and Holstein while the local breeds are Western, Eastern and Northern Finncattle.

Table 2: Information on the dairy cattle breeds of Finland in 2017 (ProAgria).

Breed	Weight (kg)	Milk (kg)	Fat %	Protein %	Number of recorded cows
Ayrshire	604	9,228	4.45	3.56	67,735
Holstein	659	10,243	4.14	3.45	63,594
Western Finncattle	540	6,972	4.53	3.47	1,336
Northern Finncattle	529	5,429	4.35	3.43	423
Eastern Finncattle	488	4,057	4.36	3.46	267

2.4.2 Heritability

The heritability (h^2) of a trait expresses the genetic variation within breed as a proportion of the phenotypic variation. A low heritability means that only a small fraction of the differences observed between animals is due to genetic factor. A considerable amount of literature has been published about the heritability estimates of SCC, milk yield, its constituent traits for different breeds, different parities and stages of lactation.

Table 3. Heritability (h^2) estimates for annual averages of milk traits of Finnish Ayrshire and Finncattle breed.

Traits	Breed	h^2	Standard Error	Publication
Milk	Finncattle	0.29 - 0.24	0.06 - 0.07	Lindström 1969
	Ayrshire	0.25	0.02	Torniainen 1991
		0.40	0.02	Juga 1992
Protein	Ayrshire	0.17	0.01	Torniainen 1991
		0.31	0.02	Juga 1992
		0.37	0.05	Luttinen & Juga 1997
Fat	Ayrshire	0.21	0.01	Torniainen 1991
		0.43	0.05	Luttinen & Juga 1997
Protein%	Ayrshire	0.52	0.03	Torniainen 1991
		0.63	0.02	Juga 1992
Fat%	Finncattle	0.55	0.07	Lindström 1969
	Ayrshire	0.43	0.02	Torniainen 1991
		0.68	0.02	Juga 1992
Logsc	Ayrshire	0.14	0.03	Luttinen & Juga 1997
Protein/fat	Ayrshire	0.27	0.02	Torniainen 1991

The standard errors of the estimates in Table 2 are small, this signifies that a good amount of data was used for the analyses and the values are reliable.

Yield traits

In their review for heritability of milk traits in dairy cattle breeds Maijala and Hanna (1974) found estimates of 0.25 – 0.34 for milk yield, 0.11 – 0.25 for fat yield covering the 95% confidence intervals. The average heritability estimate was 0.27 for first lactation milk yield and 0.24 for fat yield in Holstein Friesian breeds.

For this study, the heritability estimates on Finncattle and Ayrshire were reviewed (see Table 3). The first study in this respect was on Finncattle by Lindström (1969). The heritability of annual

milk records for Finnish Ayrshire have been estimated by Torniainen (1991), Juga (1992) and Luttinen and Juga (1997). The differences in the estimates reflect the changes in methodology from dam-daughter regression (Lindström 1971) via pure random sire model with ANOVA (Torniainen 1991) to the use of mixed animal model with REML (Juga 1992). The heritability estimate in the review is around 0.4 for yield traits.

Content traits

Gacula et al. (1968) recorded heritability estimates for fat and protein percentage of 5 dairy breeds to be 0.38 and 0.32 respectively. Maijala and Hanna (1974) reported a range of 0.31 – 0.61 in their review. In the Finnish populations, the average estimate for the heritability for annual content traits was high, 0.5-0.7 (Table 3).

Somatic cell count

Health status affecting milk yield in general are mastitis and ketosis. SCC is found to be a useful indicator trait of mastitis (Pösö & Mäntysaari 1995). Mastitis has continuously been the most economically important disease of dairy cattle, accounting for 38% of the total direct costs of the common milk production diseases (Kossaibati and Esslemont, 1997). Some cross-sectional studies suggest an association between milk traits and health status of dairy cows. Querengasser et al. (2002) studied teat disease on milk flow and milk yield before and after symptoms. They observed significant growth in milk flow and milk yield after the affected teats had been treated, highlighting the impact of unhealthy udders in dairy production. As a result, many nations depend upon somatic cell count as the approach of figuring out and controlling mastitis. SCC (Somatic Cell Count) as an indicator trait for choice against mastitis has the gain of being noticeably heritable. Somatic cell count has been recorded in Finland since 1982 (Syväjärvi 1984). There are no heritability estimates for Finncattle. There are several heritability estimates for logSCC in the Finnish Ayrshire with values 0.14 (Luttinen and Juga, 1997), 0.07 (Koivula et al., 2005; Negussie et al. 2008) while Pösö et al. (1997) mentioned lactation yield SCS heritability of 0.13 for Finnish Ayrshire.

2.4.3 Genetic and phenotypic correlations

Milk traits

The earlier studies (Torniainen 1991; Juga 1992) on the genetic correlations in the Finnish Ayrshires (Table 4) indicate high (0.6-0.7) correlation between yield and contents traits. The

correlation of content traits with milk yield are negative for mere mathematical reason. The correlation of dry matter yields with content traits are very variable. The phenotypic correlations are similar to genetic correlations.

Table 4. Genetic and phenotypic correlation amongst milk trait in the Finnish Ayrshire breed. Phenotypic correlations are below the diagonal while the genetic correlations are above the diagonal. Standard errors are in parenthesis. Dim gray colours are for non-significant results. Superscript 'a' signifies results from Torniainen (1991) while 'b' represents results from Juga (1992). The standard errors were very low (0.02-0.05) in the estimates found by Torniainen (1991).

Traits	Milk	Protein	Fat	Protein%	Fat%	P/F
Milk		0.78 ^a	0.56 ^a	-0.61 ^a	-0.53 ^a	0.15 ^a
Protein	0.90 ^a		0.72 ^a	0.02 ^a	0.13 ^a	0.19 ^a
Fat	0.75 ^a	0.79 ^a		0.02 ^a	0.41 ^a	-0.54 ^a
Protein%	-0.29 ^a	0.13 ^a	0.01 ^a		0.68 ^a	
Fat%	-0.34 ^a	-0.16 ^a	0.36 ^a	0.44 ^a		-0.73 ^a
P/f	0.17 ^a	0.26 ^a	-0.38 ^a	0.20 ^a	-0.79 ^a	

Somatic Cell Count

SCC is known to be unfavourably correlated with milk yield (Emmanuelson 1988, Banos and Shook 1990) especially for first lactation. Pösö and Mäntysaari (1996) estimated the genetic and phenotypic correlations between milk yield and SCC in the first lactation of the Finnish Ayrshires to be 0.10 and -0.05 respectively.

The EBV's for the Finnish dairy cattle traits have been computed with the test-day animal model since 2000 therefore most of the research has been focused on the test-day records since late 1990s (e.g. Lidauer et al. 1999) with less attention to estimating heritability or genetic correlation on lactation averages.

2.5 Genomic information

The use of genomic tools in dairy production is on the rise especially in the studies of traits like milk yield. The availability of large numbers of records lead to milk traits being among the first targets for finding genomic regions affecting variation (Georges et al. 1995). The results on such mapping and the use of single map markers have been rather frustrating while the simultaneous use of wide marker sets with phenotypic data and family structure has revolutionized the computation of breeding values (Meuwissen et al. 2001; Legarra et al. 2009). Hence, there are two approaches by which genomic information is utilized in animal breeding. These are

- Mapping and characterizing genes or genomic regions (QTL) affecting the variation and;
- Using genomic markers in enhancing the breeding value estimation (GEBV)

2.5.1 QTL mapping

One technique to discover chromosomal regions affecting the trait of interest or quantitative trait loci (QTL) is linkage mapping. Bovenhuis & Schrooten (2002) and Khatkar et al. (2004) gave an overview of QTL found for milk production traits in dairy cattle (milk, fats and protein yield, and fats and protein percentage). One of these QTL was on the chromosome (BTA20) and contributed to variation in multiple traits in Holstein cattle. To understand the genetic architecture of the QTL, a genome-wide association study for milk, protein, and fat yields and clinical mastitis using a haplotype-based method was used. Sahana et al. (2014) recently reported about a QTL on BTA20 gene affecting mastitis and somatic cell score in Danish Holstein cattle. In a meta-analysis of three breeds (Holstein, Nordic Red dairy cattle, and Danish Jersey cattle), the most highly associated Single Nucleotide Polymorphism (SNP) with mastitis was located at 33,398,781 base pair on the chromosome (Sahana et al. 2014). Those authors also reported strong evidence for a QTL located at the same position milk, fat, and protein yield. A fat yield (F279Y) mutation in the growth hormone receptor gene at 31,909,478 base pair has been reported to affect milk, fat, protein, and somatic cell score in Holstein (Blott et al. 2003 and Rahmatalla et al. 2011). Viitala et al. (2003) detected QTL for milk, fat and protein yield on BTA12 in the Finnish

Ayrshire. Recent studies have confirmed the occurrence of the same QTL in the Nordic red population (Kadri et al. 2014). Viitala et al. (2006) suggested that the variant S18N in growth hormone receptor on chromosome 20 in Finnish Ayrshire may influence protein and fat yield.

2.5.2 Using genomic markers for predictions

Genomic predictions of breeding values using DNA markers can be obtained by either simultaneously fitting polygenic and QTL effects (Guillaume et al. 2008) or by computing the genomic prediction and combining it with estimated breeding values from the animal model (VanRaden et al, 2009). Gray et al. (2012a), in their study on the effectiveness of genomic prediction on milk yield traits in dairy cattle (Brown Swiss), produced reliability estimates for sire breeding values to compare those from genomic markers (GBLUP) and those from pedigree-based evaluations (BLUP) using different methods.

Legarra et al. (2009) and Christensen and Lund (2010) developed a single-step methodology to integrate the pedigree and genomic information in finding unbiased predictions for breeding values. The HBLUP method was the most successful of all the methods. It utilises the single-step which combines both phenotypic and genotypic information to obtain breeding values. This results in a joint distribution of genotyped and ungenotyped genetic values, with a pedigree-genomic relationship matrix H (Legarra et al. 2009).

The direct genomic values (DGV) were obtained by capturing all QTL that contributes to the variation in the trait and summing the effects of dense markers across the genome. They concluded that breeding values from markers performed better in predicting those of pedigree relationships and that given BLUP and genomic methods, genomic models showed a higher accuracy of prediction.

2.6 Effective population size

Wright (1931 and 1938) defined the effective size of a population as the size of an idealized population with no mutation, no selection, no overlapping generations and random, which would give rise to the same rate of inbreeding (ΔF).

Small population are expected to have less variation. The reduction in the variance can be predicted from effective population size (e.g. Toro et al. 2011). Animal with small population should consider maximizing the effective population size because this strategy allows for the maintenance of high levels of genetic diversity, while minimizing the increase in inbreeding and

its effects (Fernandez et al. 2010). According to Toro et al. (2011) the most interesting measure of genetic variation are the rate of inbreeding and co-ancestry (or effective population sizes) based on pedigree information. Toro et al. (2011) stated that different approaches taken in livestock populations to assess the acceptable rate of inbreeding agrees on an effective size of 50 to 100 animals ($\Delta F = 0.01$ to 0.001). The recent estimates about N_e for the WFC varied from 50 to 1300 per generation considering the level of equivalent complete generations being greater than 3 with a harmonic mean of 171 and the regression method gave values 89 and 109 (Toro et al. 2011).

3 OBJECTIVES

Improvement of production and development of WFC would benefit from continued selection programme. The Western Finncattle breed represents a productive dairy breed and has excellent possibilities to keep its well-deserved place in the Finnish animal production system. Therefore, the objective of this research was

- 1) to estimate the genetic variation in milk, fat, and protein yield, fat and protein content and milk somatic cell count.
- 2) to assess genetic and phenotypic correlation between milk production, milk compositional and somatic cell count traits
- 3) to estimate the effective population size and to assess the current genetic state of the WFC using the pedigree information to understand the overall state of genetic variation and potential for genetic improvement.

4 MATERIAL AND METHODS

4.1 Materials

Data and traits

Data for this study were provided by the Finnish Cattle Breeding Organization, Faba Coop. A total of five data sets for the Finncattle cows were made available from the cow database. The 305-day production data contained 69,083 cows of all Finncattle breeds which had calves in the period 2002–16. A data set containing among others the animal identity and breed information was used to extract Western Finncattle records from the previous dataset with production records and resulted in 21,987 WFC cows. The calving data contained the animal identity, calving date and parity number (related to calving date) of Finncattle cows. This data was used to arrive at a data body of WFC cows with first calving in the period of 2002–16. Further, the days open intervals for the cows were from the Finncattle dataset containing animal identity, parity, calving date, last insemination date after calving and the length of days open interval. The herd data contained animal identity, parity, calving date and herd. The data was merged with the previous data to add the herd identity to the data. As a result of the data management the total number of WFC cows calving the first time in 2002–16 were 5,455 distributed across 2512 herds (Table 5).

Table 5. The number of WFC cows and herds for the cows having first calving in the period 2002 - 2016

Calving years	No of cows	No of herds
2002	302	150
2003	306	151
2004	344	160
2005	400	188
2006	373	176
2007	380	170
2008	437	216
2009	350	172
2010	371	178
2011	417	190
2012	354	177
2013	386	164
2014	344	152
2015	354	143
2016	337	125
Total	5455	(2512)

Pedigree data

The original pedigree data set received from Faba contained dam and sire information on 78,880 Finncattle individuals including the cows with phenotypic records in the WFC dataset. Pruning of the pedigree data with phenotypic data of the WFC cows was done to provide the additive relationships for the genetic analyses. Applying a restriction of at least of two cows per herd gave 3743 cows for which the distribution of sires' daughter group size is in Figure 1.

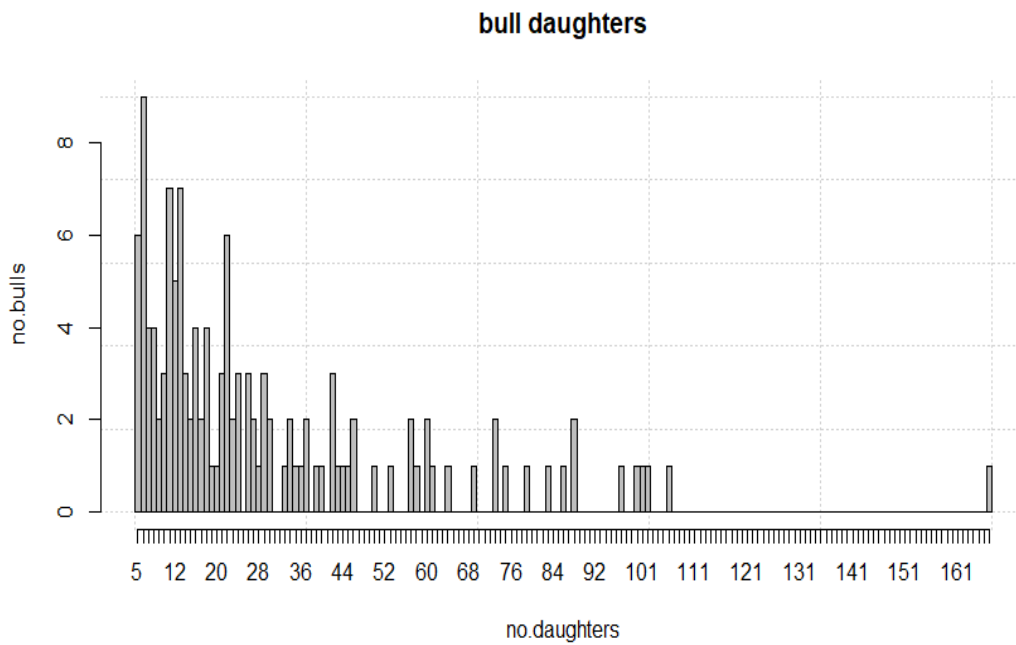
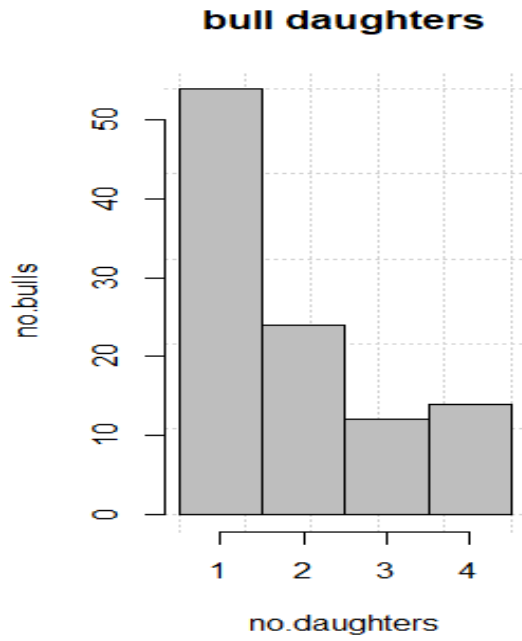


Figure 1. The distribution of sires of cows with phenotypic record for 1, 2, 3 or 4 daughters (top figure) and for ≥ 5 daughters.

4.2 Traits

4.2.1 Milk yield traits

The final dataset had 305-day yield records for milk, fat and protein yield for each cow. The cows with milk yield less than 500 kg were excluded from the data, also cows with fat and protein yield less than 50 kg were removed and so were cows with missing records. As per these data edition criteria, records of 741 animals were deleted from the dataset.

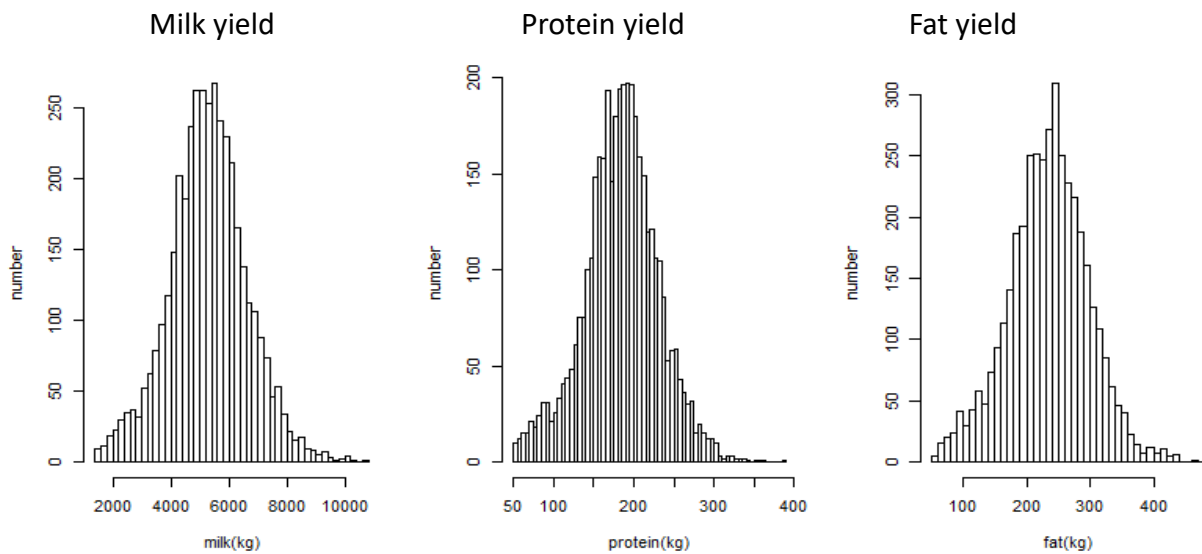


Figure 2. Distribution of WFC cows in milk, protein and fat yield (1st lactation cows calved in the period 2002-16)

4.2.2 Milk content traits

The content traits which are fat and protein percentage, were calculated by dividing fat or protein yield with milk yield multiplied by 100, e.g.

$$\text{protein\%} = 100 \times \text{protein yield} / \text{milk yield}$$

4.2.3 Somatic cell count records

The logarithm of SCC record was calculated to make the distribution of observations more normal. Cows with logSCC less than 1 were deleted from the dataset. There were 5364 WFC individuals remaining in the dataset after the cows with outliers and missing values were

excluded.

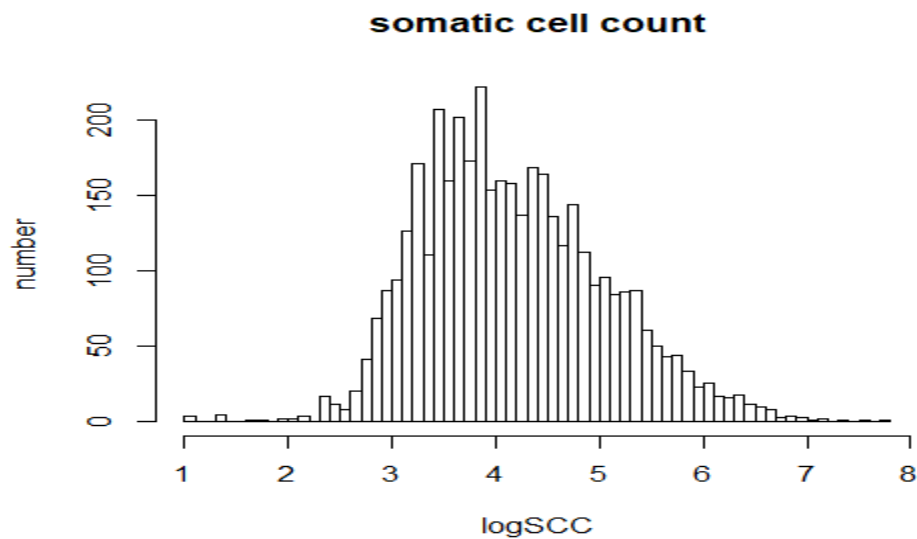


Figure 3. Phenotypic distribution of logSCC in Western Finncattle data.

The mean, standard deviation and coefficient of variation for the traits are given in Table 5. The coefficient of variation for yield traits (almost 30%) and log SCC (about 20%) were very high and lower for content traits, especially for protein%. The values differ somewhat from the full lactation record means of Table 2 as they are only from 1st lactation cows and standardized for the 305-day production.

Table 6. The summary statistics of milk, fat, protein, SCC, protein/fat ratio in the 1st lactation cows in the WFC data on the 305-day production basis.

Traits	Mean	Standard Deviation	Coefficient of Variation
Milk (kg)	5246	1356.42	25.86
Protein (kg)	183.1	47.64	26.02
Fat (kg)	233.1	64.26	27.57
Fat%	4.46	0.62	13.82
Protein%	3.50	0.32	9.00
Protein/fat	0.80	0.10	12.26
logSCC	4.19	0.90	20.98

4.3 Statistical Analysis

The data quality was very good and only a small fraction (<2%) of cows had to be left out in removing the outliers.

4.3.1 Fixed effects

To find out the effect of non-genetic factors on the variation of the traits the fixed effect model was fitted. The significance of the effects was tested using ANOVA, i.e. assuming the (random) residual effect followed normal distribution with mean 0. Herd, year of calving and season of calving were fitted as classified effects while calving age (days) and days open were fitted as a linear or quadratic covariate. The calving age was calculated by subtracting cow's birth date from her first calving date. The herd and calving year interaction were tested. Calving season had three levels: January – April, May – August, September – December. The interaction of season and year was also considered in the analyses. With requiring at least 5 cows in each herd-year subclass in the estimation, the data size was reduced to 1763 cows in 233 herds.

To find the statistical models for variance component estimation, different sets of fixed effects were tested. Initially the model for the variance component estimation had the interaction term for herd \times calving year \times calving season as a random effect. Such models were tested with the data requiring herd size ≥ 2 . The variance components with the model and the data gave very high (0.55 - 0.60) heritability estimates for the yield traits. The data was reduced with the constraint for herd \times calving year subclass size ≥ 5 . Even then the heritability estimate stayed high (around 0.50). It was only when the fixed interaction effects were included that the heritability estimates were at a reasonable level.

There were observable differences in the significance of the tested fixed effects for all traits analyses that were carried out with the WFC data with the standard significance level of p-value < 0.05 (Table 7).

Table 7. The outcome from testing the classified fixed effects herd, year of calving, season of calving and the covariates age of calving and days open in the WFC data with herd size ≥ 5

Trait \ Factor	Days open	(Days open) ²	Calving age	Calving year \times Season	Calving Year \times Herd
Milk	***	***	***	o	***
Protein	***	***	***	o	***
Fat	**	***	***	*	***
Protein%	ns	ns	o	ns	***
Fat%	ns	ns	**	*	***
LogSCC	ns	ns	ns		***
Protein/fat	ns	ns	*	***	***

Fixed effect significant at p-value <0.001 (***), at p-value <0.01 (**), at p-value < 0 (*), non-significant at p-value >0.10 (o) or p-value > 0.10 (ns).

The models that gave statistically sound outcome for each trait, had the following fixed effects in the variance component estimation (analysed phenotype record y and μ the mean):

Milk, protein and fat yield

$$y = \mu + b_1 \text{ days open} + b_2 (\text{days open})^2 + b_3 \text{ calving age} + \text{calving year} \times \text{season} + \text{herd} \times \text{calving year} + \text{residual}$$

Protein %

$$y = \mu + b_3 \text{ calving age} + \text{herd} \times \text{calving year} + \text{residual}$$

Fat% and protein/fat ratio

$$y = \mu + b_3 \text{ calving age} + \text{calving year} \times \text{season} + \text{herd} \times \text{calving year} + \text{residual}$$

logSCC

$$y = \mu + \text{calving year} \times \text{season} + \text{herd} \times \text{calving year} + \text{residual}$$

The regression coefficients are marked with b_i .

4.3.2 Estimation of genetic parameters

The variance component analyses were performed with the data applying the restriction on the subclass size for the herd \times year interaction effect being ≥ 5 . The data was reduced to 233 herds

and 1763 cows after the restriction. The pedigree information in WFC runs back more than hundred years. The variance component estimation was done restricting the pedigree depth to four generations which is customary in such statistical analyses. The size of the pedigree data after pruning and the four-generation depth was 3743 individuals.

First, a univariate animal model with Bayesian procedure (Gelman et al. 2004) was applied to estimate variance components for yield and content traits and SCC. In this analysis, a non-informative (flat) prior was used, i.e. avoiding any influence on the estimated posterior distribution. We assumed that the animal's additive genetic effect follows normal distribution with mean 0 and variance $\mathbf{A} \sigma_a^2$ where \mathbf{A} is the relationship matrix of all the individuals in the analysis providing the covariances between them. The residual effect is following also normal distribution with mean 0 and variance $\mathbf{I} \sigma_a^2$ where \mathbf{I} is the identity matrix indicating identical and independent variation among the residual effects. The flat prior was inverse gamma with $V = 1$ and $\eta = 0.002$ giving the shape parameter value $\frac{\eta}{2}$ and the scale parameter $\frac{\eta V}{2}$. Heritability was computed as the ratio of additive to phenotypic (additive + residual) variance. The point estimates (mean of distribution) and the 95% credibility area (or highest density probability HPD) are obtained from the posterior distribution. The posterior distribution was obtained by iteration where the output from the first rounds is ignored (burn-in period) and the posterior distribution values are picked from the rounds minimizing possible correlation values between the values of consecutive rounds (picking interval is called thin). The target is to have a sufficient number of independent values for the posterior distribution or an effective sample size of the values (ESS). Usually ESS >100 is required.

Multi-variate animal model was used to estimate the genetic and environmental (residual) covariance components and from them the genetic and phenotypic correlations for all the traits. The model for individual traits was the same as in the respective single trait analyses.

The genetic covariance between traits i and j is $\sigma_{a(i,j)}$ and the respective genetic correlation was computed as

$$r_{a(i,j)} = \frac{\sigma_{a(i,j)}}{\sigma_{ai} \sigma_{aj}}$$

The environmental covariance is denoted as $\sigma_{e(i,j)}$ and phenotypic correlation is computed as

$$r_{p(i,j)} = \frac{\sigma_{a(i,j)} + \sigma_{e(i,j)}}{\sigma_{pi} \sigma_{pj}} \text{ where phenotypic standard deviation for trait } i \text{ is } \sigma_{pi} = \sqrt{\sigma_{ai}^2 + \sigma_{ei}^2}$$

4.3.3. Genetic trend

The EBV's are obtained from MCMCglmm with an option `pr=TRUE` giving the list of solutions for both fixed and random effects. genetic trend is expressed as the mean of cows' EBV's by birth year. The trend is given as the mean of cow EBV's for a birth year class. The respective standard deviation is computed by taking a square root of the weighted variance of the EBVs developed in the following way $Var\left(\frac{\sum w_i EBV_i}{\sum w_i}\right) = \frac{1}{(\sum w_i)^2} Var(\sum w_i EBV_i) =$

$$\frac{\sum w_i^2}{(\sum w_i)^2} \sigma^2 Var(EBV)$$

The weight prediction error variance of EBV is approximated from squared value of four times the interval HPD95% for EBV in the MCMCglmm output.

4.3.4 Estimation of effective population size (N_e)

First inbreeding coefficients (F) were obtained by R software ('`calcInbreeding`' of the package `pedigree`). The effective population size is $N_e = 1/2 \Delta F$ where ΔF is the rate of inbreeding per generation. The rate of inbreeding is defined as

$$\Delta F = \frac{F_t - F_{t-1}}{1 - F_{t-1}}$$

where F_t is the average inbreeding coefficient of individuals in generation t (Falconer & Mackay 1996).

Estimating the rate of inbreeding using population averages is misleading when there are overlapping generations (e.g. Strandén & Peura 2007). The rate of inbreeding can be computed with regression (b) of inbreeding coefficient on individuals' birth year (Gutierrez et al. 2003). If the average generation interval is l , then the increase between two generations $F_t - F_{t-1}$ is $l b$ and $F_{t-1} = F_{last} - l b$ where F_{last} is the inbreeding coefficient in the last studied age class. Then we can write

$$\Delta F = \frac{l b}{1 - F_{last} + l b}$$

4.3.4 Software packages

R statistical software package version 3.2.0 was used for data preparation and to produce summary statistics. Significance of fixed effects were analysed by analysis of variance (ANOVA) and computed with `lm` function in R. The pedigree data for the WFC cows was obtained by pruning the whole Finncattle pedigree data with the WFC phenotypic data (with R

function *prunePed* of the R package *MasterBayes*). The pedigree records were ordered so that parents occur before their progeny (with R function *ordered* from library package *Kinship2*). The variance component analyses were performed with Bayesian methods explained above and using R software *MCMCglmm* (Hadfield, 2010). See the Appendix A for the command details of *MCMCglmm*.

5 RESULTS

5.1 Fixed effects

There was a curvilinear relationship between the milk, protein and fat yield with respect to the number of days open. All the yield traits reached the maximum when the days open interval was 250 d.

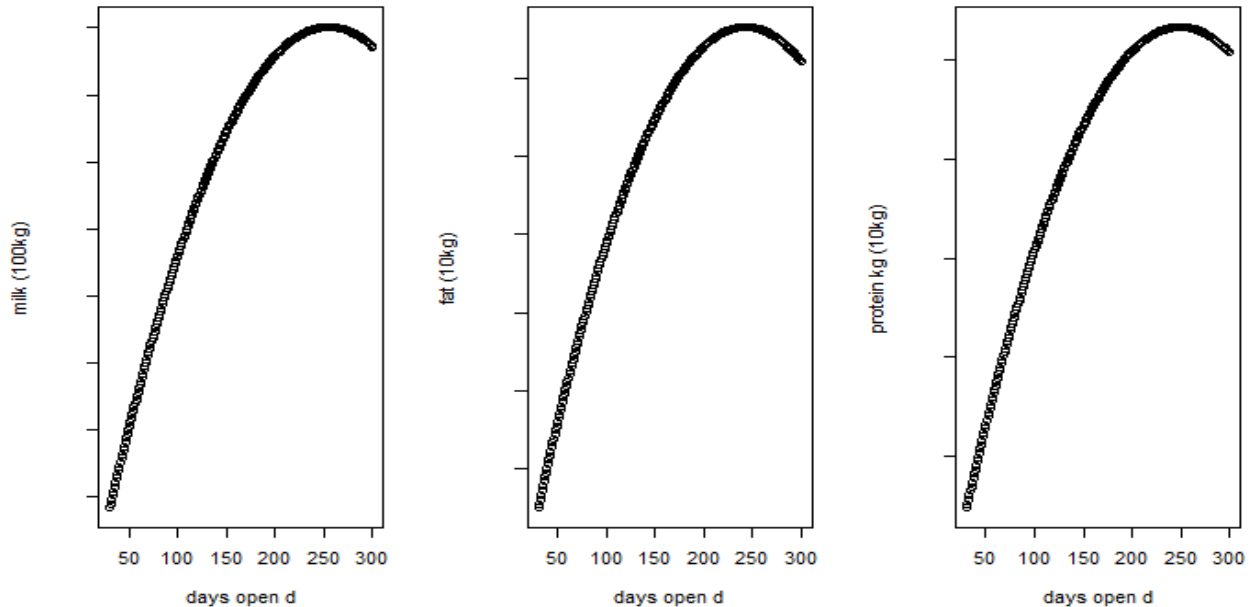


Figure 4. Curvilinear regression of milk, protein and fat yield on days open in Western Finncattle (vertical axis indicates the yield ranges for milk, fat and protein on the scale intervals of 1000, 10 and 10 kg, respectively).

5.2 Estimates of variance components and heritability

Table 8. gives the mean, the standard deviation and the highest posterior density interval (95%) of the posterior distribution, the number of iterations and ESS in the estimation of heritability. To reach the ESS > 100 steered the variance component analyses with the number of iteration rounds in the MCMCglmm analyses being 20000 – 40000, except 1200000 for the analysis on logSCC. The posterior distributions were symmetric, on which Fig 5 presents an example for milk yield. The content traits had very high (around 0.5) heritabilities, somewhat lower (0.20-0.35) in yield traits. The heritability of logSCC was very low (0.06). The standard deviation and HPD95% of the estimates were mostly 0.06-0.08 and around 0.3, respectively, and 0.033

and 0.12 for the low estimate of logSCC heritability. All the HPD95% intervals were above 0 indicating ‘significant’ estimates in a conventional sense.

Table 8. The heritability (h^2) estimate of milk traits and SCC in Western Finncattle from single trait analyses.

Traits	h^2	post SD	HPD 95%	No. of Iterations	ESS
Milk	0.35	0.079	0.20 – 0.53	20000	105.1
Protein	0.22	0.059	0.09 – 0.34	40000	119
Fat	0.28	0.064	0.17 – 0.41	30000	124
Protein%	0.52	0.066	0.39 – 0.66	20000	175.9
Fat%	0.52	0.068	0.39 – 0.66	20000	153.8
LogSCC	0.06	0.033	0.0018 – 0.12	120000	100.9
protein/fat	0.39	0.057	0.28 – 0.51	20000	155.9

post SD: standard deviation of the posterior density; HPD 95%: highest posterior density interval at 95%; ESS: effective sample size; P/F: protein-fat ratio

The posterior distributions were unimodal and symmetric for which the outcome from the analysis on milk yield, protein yield and logSCC is shown in Figure 5,6,7.

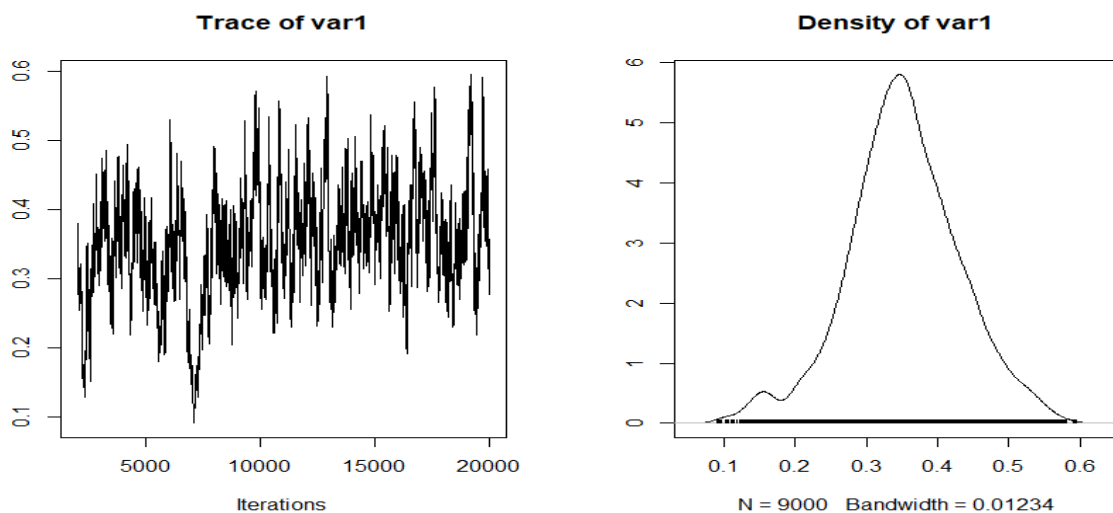


Figure 5: The posterior distribution densities of sampled values from the (20 000) rounds of iteration in computing the estimate of heritability for milk yield using MCMCglmm.

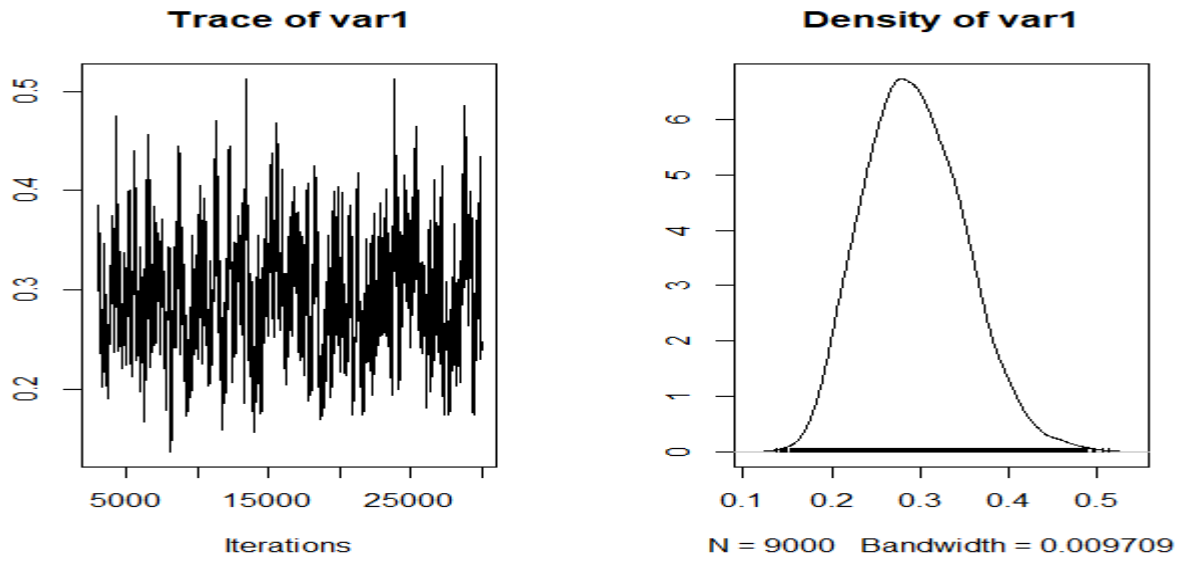


Figure 5: The posterior distribution densities of sampled values from the (40 000) rounds of iteration in computing the estimate of heritability for protein yield using MCMCglmm.

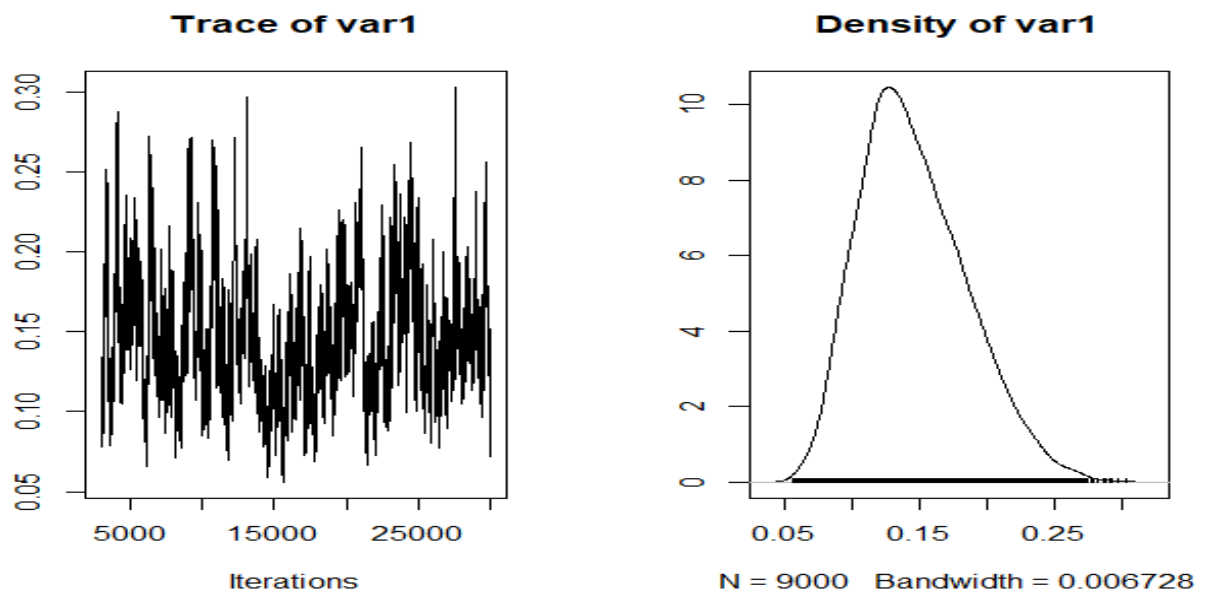


Figure 6: The posterior distribution densities of sampled values from the (120 000) rounds of iteration in computing the estimate of heritability for logSCC using MCMCglmm.

5.4 Genetic and phenotypic correlations

The seven-trait analysis was done with 30,000 rounds of iteration yielding ESS ranging from 99 (for logSCC) to 425. There were high genetic (0.76 – 0.91), environmental (residual) (0.91 –

0.96) and phenotypic (0.86 – 0.94) correlations among the yield traits found in the multivariate analysis (Table 9). There was positive correlation (0.59) between the two contents traits. The protein and fat content were negatively correlated with milk yield and had positive environmental correlation both with fat and protein kg. Correlations between logSCC and all traits were practically zero with the exception on environmental correlations: negative for milk and positive for protein content. The protein-fat ratio was not correlated with the other traits, except the negative correlation with fat yield and fat%, most likely due to fat being in the denominator of the ratio. The posterior distribution may be skewed and therefore the HPD95% is not necessarily symmetric with respect to the mean of the posterior distribution (see Appendix B for details).

Table 9. Genetic, environmental and phenotypic correlations among the milk traits and logSCC in Western Finncattle. Heritabilities (bold) are across the diagonal. The genetic correlations are above the diagonal, phenotypic (top of the two figures) and environmental (bottom) correlations are below the diagonal. The SD of posterior distribution is in brackets. The dimmed values indicate non-significance.

Traits	Milk(kg)	Protein kg	Fat kg	Protein %	Fat %	LogSCC	P/F
Milk(kg)	0.37 (0.06)	0.91 (0.02)	0.76 (0.05)	-0.48 (-0.10)	-0.39 (0.11)	0.003 (0.18)	0.097 (0.09)
Protein kg	0.94(0.003) 0.96(0.01)	0.30 (0.06)	0.82 (0.04)	-0.19 (0.12)	-0.21 (0.12)	-0.03 (0.18)	0.092 (0.10)
Fat kg	0.86(0.01) 0.91(0.01)	0.89(0.01) 0.92(0.01)	0.30 (0.06)	-0.15 (0.12)	0.22 (0.12)	-0.08 (0.18)	-0.33 (0.08)
Protein %	-0.17(0.03) 0.04(0.06)	0.10(0.03) 0.27(0.05)	-0.16(0.03) 0.20(0.05)	0.43 (0.05)	0.59 (0.06)	-0.06 (0.13)	-0.042 (0.08)
Fat %	-0.10(0.03) 0.12(0.07)	0.06(0.03) 0.25(0.06)	0.37(0.03) 0.48(0.05)	0.57(0.02) 0.56(0.04)	0.49 (0.061)	-0.11 (0.15)	-0.65 (0.04)
LogSCC	-0.09(0.03) -0.12(0.05)	-0.05(0.03) -0.06(0.04)	-0.07(0.03) -0.06(0.04)	0.16(0.02) 0.25(0.04)	0.08(0.03) 0.15(0.05)	0.15 (0.04)	0.072 (0.12)
P/F	-0.018(0.03) -0.10(0.05)	-0.011(0.03) -0.077(0.05)	-0.35(0.02) -0.37(0.04)	0.02(0.03) 0.08(0.05)	-0.65(0.02) -0.65(0.30)	0.03(0.03) 0.01(0.04)	0.49 (0.03)

The coefficient of variation was in the range 0.10 – 0.15 for yield traits, while there was less variation in the somatic cell count, the content traits and protein/fat. The coefficient of variation was lowest (0.05) for protein content.

Table 10: Additive genetic standard deviation σ_a and coefficient of additive genetic variation CV_a of production traits in WFC

Traits	σ_a	CV_a
Milk	708.94	0.14
Protein	20.32	0.11
Fat	30.51	0.13
logSCC	0.20	0.07
Protein%	0.19	0.05
Fat%	0.39	0.09
P/F	0.05	0.06

5.5 Genetic trend

The mean (weighted standard deviation) of EBV's for milk and protein(kg) of the cows by birth year is demonstrating a modest genetic trend in milk yield. The vertical axis is given as deviation from the population mean. For comparison, the additive genetic standard deviation for milk ~700 kg and for protein yield ~20kg. The irregularities in the may be related to the low number (100-150) of cows per year class.

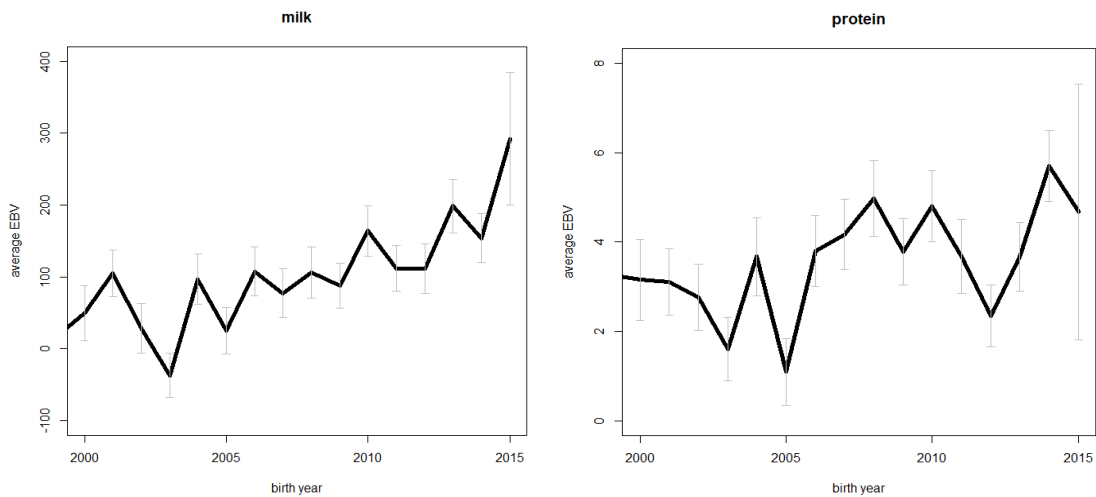


Figure 6. Genetic trend expressed as weighted mean and standard deviation of cows' EBV's for milk yield and protein yield with the weight being an approximated prediction error variance.

5.6 Effective population size of cows

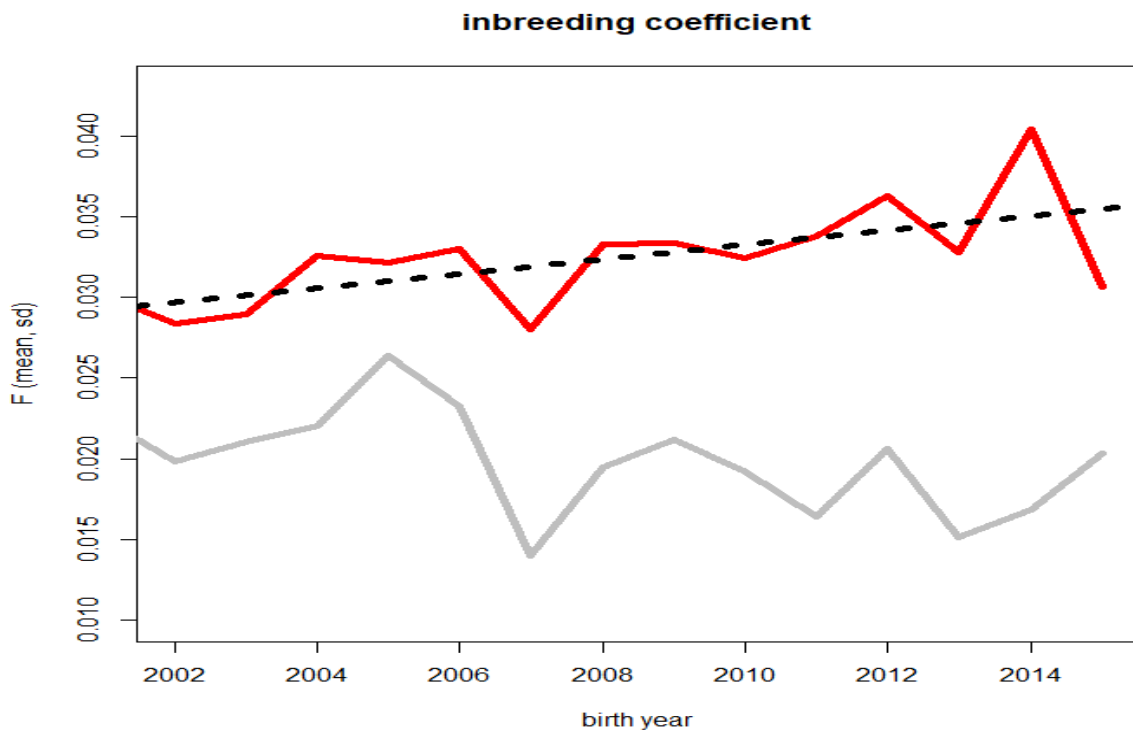


Figure 7: The average (red graph) and standard deviation (gray) of inbreeding coefficient by birth year (2002-15) of the cows with the linear regression (dashed black line) of the coefficient on birth year.

The effective population size was computed from the linear regression of the cows' inbreeding coefficient on their birth year (Figure 7). Assuming that the generation interval was 4, 6 or 8 years gave $N_e = 269, 179$ and 134 , respectively.

6 DISCUSSION

The Western Finncattle is one of the old local dairy breeds in Finland. WFC cows have evolved over the last century with a production level comparable to other remaining local breeds in Europe. WFC has not had recent studies on the genetic variation in milk production traits. The thesis research was set to estimate the heritability of milk, fat and protein yield, fat%, protein%, protein-fat ratio and somatic cell count (logSCC) and the genetic correlation amongst them. The heritability of milk, protein and fat yield, protein%, fat% and logSCC was in single (and in brackets for multi-traits analysis 0.36 (0.37), 0.27 (0.30), 0.32 (0.30), 0.61 (0.43), 0.52 (0.49) and 0.06 (0.15), respectively. The only noticeable difference in the heritability estimates was in logSCC, probably due to increased information via environmental correlations with milk yield and protein content. Amongst yield traits and also between the content traits the genetic correlation was high, 0.73 - 0.94 and 0.43 – 0.59, respectively. While the WFC population size is rather small for a dairy cattle breed, the effective population size (estimates 130-270) is well above the critical value of 50. The genetic progress is, however, very modest.

6.1 Production performance of Western Finncattle and effect of non-genetic factors

Among the Finncattle breeds the WFC cows produce the highest milk yield. The milk yield (6872kg) produced by Western Finncattle (ProAgria, 2017) is comparable to the production level of other local breeds like Montbeliarde of France producing 7090 kg milk per cow in 2017). The content traits were 3.47% for protein and 4.5% for fat, these results were higher than the estimates of Montbeliarde (3.45% and 3.86%). The milk yield estimates of WFC is high compared to Estonian red cattle which have an average milk yield of 3784 kg per cow and content traits 3.30% for protein and 3.98% for fat (Table 1 and ICAR.org).

The analysed smaller data set had mean milk yield (and standard deviation) was 5242 (1407.39), 4.27 (0.34) for fat%, 3.44(0.15) for protein% and 4.17 (0.90) for logSCC. which are comparable to those reported by the official data recording (ProAgria 2017).

The phenotypic coefficient of variation of yield traits were over 20% except for content traits (8.03%, 14.13%) and protein/fat ratio (13.39%) in WFC cows. These estimates could be compared to the coefficient of variation of Ayrshire cows by Torniainen (1991) which are a little less than 20% for yield traits and around 10% for content traits and protein/fat ratio (6.5%, 10.3%, 9.6%). The genetic coefficient of variation found in this present study for the traits were a little higher than in the previous study of Ayrshire (Torniainen 1991).

All the traits had herd-calving year interaction in the statistical model. Calving year x season was used in all the models except for protein% and the covariate calving age in all but for logSCC. Only the yield traits had days open as linear and quadratic covariate with all of the traits reaching the maximum at 250 days after calving. Similar models have been used for the traits in analysing the variation in the traits of the Finnish Ayrshire cows, e.g. by Mäntysaari et al. 2005. Even though some fixed effects – like of year of calving, age of calving and season of calving – included in the models were not significant in some traits (protein% and logSCC), these were not excluded from the models for reasons of consistency. These effects may be more significant with a larger sample size. In addition, the sample sizes appeared large enough and were not affected by loss in degrees of freedom.

6.2 Estimates of genetic parameters

The variance components were estimated with single and multi-trait animal model using a Bayesian approach and R studio package MCMCglmm. The method was flexible enough in performing the analysis simultaneously for seven traits with allowance for different fixed effects among the traits. The available phenotype and pedigree data gave satisfactory results and reliable estimates (e.g. short HPD95% intervals) even for low heritability traits and for environmental and genetic correlations. The single and multi-trait estimates for heritability were close to each other. The only noticeable difference – 0.07 vs 0.15 – was in the heritability estimate of logSCC.

6.2.1 Heritability Estimates

Yield traits

The heritability from the single trait analysis was 0.36 and was very similar to that (0.37) in the multivariate analysis.

Lindström (1969) found a heritability value of 0.29 - 0.24 for the joint Finncattle breeds' population. The study was done before the REML method was developed and the estimate was based on half-sib analysis without utilizing the pedigree information preceding the cow generation with phenotypic records. The recording quality has also improved since the studied period of 1960's and also the average herd size has increased, which both should result in better accuracy of statistical estimates.

This is a study estimating the variance components in the WFC breed in long while. Hence there are not too many earlier estimates for the breed and in the Finnish production conditions, the results can be compared only with e.g. the estimates on the Finnish Ayrshire cows.

We can compare the current results with the estimates obtained in Finland for the Ayrshire cows. Juga (1992), Luttinen and Juga (1997) reported a very similar figure of 0.37 in the Finnish Ayrshires; and Pösö et al. (1997) found heritability of 0.38. After that most of the studies have focussed on the use of test-day records instead of the whole lactation yield.

A heritability estimates of 0.32 was found for fat yield in the single trait analysis and in the multivariate analysis the estimate was 0.30. Torniainen (1991) reported a heritability estimate of 0.21 in the Finnish Ayrshire population while Luttinen and Juga (1997) found a much higher value (0.43) in their study. The heritability for protein yield in WFC cows was 0.27 in the single trait analysis and 0.30 in the multivariate analysis. In the Finnish Ayrshires, Torniainen (1991) found an estimate of 0.17, Juga (1992) found 0.27 while Luttinen and Juga (1997) reported a value of 0.37.

Content traits

Heritability for protein and fat% were 0.61 and 0.52, respectively, in the single trait analysis and 0.43 and 0.49 in the multivariate analysis. Lindström (1969) reported almost similar result (0.55) for fat% for the joint Finncattle breeds' population. Protein recording started in the late 1970s so there are no previous Finncattle heritability estimate for protein%. The Ayrshire heritability estimates of protein and fat% found were 0.52 and 0.43 (Torniainen 1991) while Juga (1992) found an estimate of 0.64 and 0.71.

Somatic cell count

The heritability estimate for the logSCC in univariate analyses was low (0.06) whereas a much higher estimate of 0.15 was found in the multivariate analysis. The HPD interval was 0.12 in the single trait and 0.14 in the multi-trait analysis, hence in relative terms much lower in the latter. The heritability values found generally fell within the range of those reported for the Finnish Ayrshire cows. Pösö et al. (1997) found a heritability of 0.13; Luttinen and Juga (1997) and Pösö and Mäntysaari (1996) both reported a similar value of 0.15 while Koivula et al. (2005) found a lower value of 0.07.

6.2.2 Genetic and phenotypic correlations

The genetic, environmental and phenotypic correlation estimates between the yield traits are high in WFC cows. This result was in agreement with the correlation estimates found by Torniainen (1991) in Finnish Ayrshire population. In contrast to this result, findings from Juga (1992) showed no correlations between milk yield and protein yield.

Content trait were negatively correlated with milk yield which is similar to previous result found in Ayrshire breed (Torniainen 1991, Juga 1992).

The genetic correlation between protein yield and protein% was not significant. A similar observation was made in the earlier studies of the Ayrshire population (Torniainen 1991, Juga 1992).

For the Western Finncattle, there are no earlier correlation estimates of yield traits and SCC. The correlation between SCC and other traits were not significant except the environmental correlations: negative with milk yield and positive with fat and protein%. Koivula et al. (2005) observed an unfavourable (positive) genetic correlation between milk yield and SCC in first lactation Finnish Ayrshires. The correlation estimates differ a bit from the previous study of Ayrshire by the genetic, environmental and phenotypic and correlation among the yield were slightly higher compared to the Ayrshire estimates. In contrast to findings from Torniainen (1991), protein% was negatively correlated to protein yield and no correlation exist between milk, protein and protein/fat ration.

6.3 Effective population size

The WFC population size is rather small and in a small population the effective population size is often small. Small effective population size would lead to reduced genetic variance. The effective population size of WFC is still over 100 and therefore the reductions would be very small which explains how the genetic variation has stayed stable over decades and heritability in the traits is of the same level as in main stream breeds. Some ten years ago the estimate of N_e was of the same size (Toro et al. 2011). Hence despite the continued decline in the number of WFC animals, the prospects for sustainable maintenance of variation are maintained.

The WFC pedigree has always been closed as there has been no introgression of genetic material from outside, in contrary breeds like the Ayrshire (Holma 1982). This should have a positive effect on the prediction of genomic EBV's in the future.

7 CONCLUSIONS

The genetic variation in milk traits resembles the level seen earlier in Finncattle and is in line with the most recent estimates on the Finnish Ayrshire cow population. There are now additional traits recorded, in particular protein and somatic cell count. Compared to the earlier times, the quality of recording and the methodology for variance component estimation have improved and herd size has increased, which all jointly enhance the efficiency and accuracy of estimation of the genetic parameters and prediction of breeding values. Our estimates of variance components for WFC cows somewhat similar to those estimates from the Finnish Ayrshire data. For genetic analysis, WFC cows have a big advantage compared to Ayrshire breeds because its population has been closed for decades. The results of this study provide relevant information about the current genetic state of WFC cows regarding the traits that were analysed. It also provides a foundation and a reference material for further future research in this area.

Finally, selection and breeding programs aim to change the genetic level in the subsequent generation for traits that are of interest to the breeder. This implies that the development and selection of WFC breeds would be rewarding.

8 ACKNOWLEDGEMENTS

This thesis work was done at the Department of Agricultural Sciences, University of Helsinki.

Firstly, I would like to thank my thesis supervisor, Prof. Asko Mäki-Tanila for steering me in the right direction whenever he thought I needed it throughout the whole period. I am grateful for the extra push which has given me a level of confidence in approaching future possibilities in research. I want to thank Jukka Pösö, FABA, for access to the data used in the study, for his guidance and quick responses to my questions.

I also want to thank my program supervisor, Dr Kari Elo, for providing assistance whenever I needed one.

During the thesis work, I sought the help of researchers that did not tire in responding to my many questions; many thanks to Dr Enyew Negussie, Prof. Pekka Uimari and Dr Jarmo Juga.

My gratitude also goes to the researchers at the Biometrical Genetics team of LUKE, where I learned to be more ambitious about research.

Finally, I must express my profound gratitude to my parents for providing me with unfailing support and continuous encouragement throughout my years of study and through the process of researching and writing this thesis. This accomplishment would not have been possible without them. Thank you.

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10 Appendices

10.1 MCMCglmm settings

The MCMCglmm settings contained a prior information defined for the residual variance ($R = \text{list}(V = 1, \text{nu} = 0.002)$, here nu stands for η) and for the genetic variance ($G = \text{list}(G1 = \text{list}(V = 1, \text{nu} = 0.002))$). Hence,

```
prior_1 = list ( R = list(V = 1, nu = 0.002), G = list (G1 = list (V = 1, nu = 0.002)))
```

The model used to estimate the additive and residual variances was:

```
MCMCglmm (phen ~ 1+ chosen fixed effects, random = animal, family = 'gaussian', prior =  
prior_1, pedigree = PED, data = name of data set, nitt = 5000, burnin = 500, thin = 5)
```

where

'phen' is the analysed trait value vector

'random = animal' indicates the random additive genetic effects following $N(0, \mathbf{A}\sigma^2)$

'family' sets the distribution to be used for the data and normal distribution ('gaussian') was assumed

'prior' calls the list of parameters for prior distributions which was stored in the variable prior_1

'nitt' is total number of iterations, with varying across the traits to arrive at ESS > 100.

'pedigree' is for the pedigree file (here PED) to create the relationship matrix \mathbf{A}

'burnin' is the number of iterations to be ignored at the beginning of the iterations. It was set to be 10% of nitt

'thin' gives the interval for picking the values from the iteration rounds for the posterior distribution.

option 'pr = TRUE' yields the list of EBV's with their HPD95% interval

10.2 HPD95% intervals for genetic parameters

Table 11. Genetic, environmental and phenotypic correlations (HPD95% in brackets) among the milk traits and logSCC in Western Fincattle. Heritabilities (bold) are across the diagonal. The genetic correlations are above the diagonal, phenotypic (top of the two figures) and environmental (bottom) correlations are below the diagonal. The dimmed values indicate non-significance.

Traits	Milk(kg)	Protein kg	Fat kg	Protein %	Fat %	LogSCC	P/F
Milk(kg)	0.37 (0.24 – 0.49)	0.91 (0.87 – 0.95)	0.76 (0.65 – 0.86)	-0.48 (-0.66 – -0.29)	-0.39 (-0.58 – -0.17)	0.003 (-0.33 – 0.35)	0.097 (-0.086 – 0.26)
Protein kg	0.94(0.93 – 0.95) 0.96(0.95 – 0.97)	0.30 (0.18 – 0.42)	0.90 (0.72 – 0.90)	-0.19 (-0.42 – 0.04)	-0.21 (-0.45 – 0.03)	-0.02 (-0.37 – 0.31)	0.092 (-0.10 – 0.26)
Fat kg	0.86 (0.84 – 0.87) 0.91(0.88 – 0.93)	0.89(0.88 – 0.80) 0.92(0.91 – 0.94)	0.30 (0.20 – 0.41)	-0.16 (-0.38 – 0.07)	0.22 (0.03 – 0.44)	-0.08 (-0.44 – 0.25)	-0.33 (-0.48 – -0.16)
Protein %	-0.17(-0.22 – -0.11) 0.04(-0.07 – 0.16)	0.10(-0.05 – 0.15) 0.27(0.17 – 0.38)	-0.16(-0.38 – 0.07) 0.20(0.09 – 0.30)	0.43 (0.33 – 0.53)	0.59 (0.46 – 0.72)	-0.06 (-0.31 – 0.18)	-0.042 (-0.19 – 0.12)
Fat %	-0.10(-0.16 – -0.04) 0.12(-0.001 – 0.25)	0.06(0.005 – 0.11) 0.25(0.12 – 0.37)	0.37(0.32 – 0.42) 0.48 (0.37 – 0.58)	0.57(0.53 – 0.61) 0.56(0.48 – 0.64)	0.49 (0.37 – 0.61)	-0.11 (-0.41 – 0.21)	-0.65 (-0.73 – -0.56)
LogSCC	-0.09(-0.14 – -0.03) -0.12 (-0.20 – -0.02)	-0.05(-0.11 – 0.0004) -0.04(-0.14 – 0.03)	-0.07(-0.12 – -0.01) -0.06(-0.15 – 0.02)	0.16(0.11 – 0.22) 0.26(0.18 – 0.34)	0.08(0.03 – -0.13) 0.15(0.05 – 0.25)	0.15 (0.08 – 0.22)	0.072 (-0.18 – 0.30)
P/F	-0.018(-0.072 – -0.035) -0.10(-0.21 – 0.0033)	-0.011(-0.062 – 0.04) -0.077(-0.16 – 0.022)	-0.35(-0.39 – -0.30) -0.37(-0.46 – -0.29)	0.02(-0.04 – 0.08) 0.08(-0.02 – 0.19)	-0.65(-0.68 – -0.62) -0.65(-0.71 – -0.59)	0.03(-0.03 – 0.08) 0.01(-0.08 – 0.098)	0.49 (0.42 – 0.56)