Swedish University of Agricultural Sciences
Faculty of Veterinary Medicine and Animal Science

Investigation of genetic correlation among traits using massive SNP genotype in German Holstein population

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Summary

The aims of this study were to demonstrate the genomic architecture of quantitative traits using Illumina BovineSNP50 Beadchip as well as the identification of chromosomes or SNPs affecting multiple traits in German Holstein population. For this research, a total of 2333 German Holstein bulls were genotyped for 54,001 SNPs. Only SNPs with less than 5% missing genotypes and minor allele frequency greater than 3% were used. Finally, among 45181 SNPs distributed on 29 autosome and XY pseudo-autosomal chromosomes, 43,838 known position SNPs were selected. Total additive genomic variance were calculated by sums of chromosomal variances and covariances between them or SNP variance and covariances between SNPs for milk, fat, protein yield and somatic cell score traits. Chromosomal genetic correlations were estimated for six categories of traits: production (3 traits), udder health (1 trait), milkability (4 traits), fertility (6 traits), calving (4 traits) and body type (2 traits). SNP genetic correlations were calculated for fat and milk yield on BTA14 and BTA20 as well.

All bovine chromosomes contribute to construct the total additive genetic variance. Sums of the chromosomal additive genetic variances and covariance between chromosomes were equal with total additive genetic variance as well as sums of SNP variances and covariance between SNPs along the genome. Chromosomal additive genetic variance explain 54.49 to 69.9% of total additive genetic variance with higher additive genetic variance on BTA14 for milk and fat yields and BTA6 for protein yield and somatic cell score traits. Sum of SNPs variance explain 6.3 to 9.6% of total additive genetic variance with higher SNPs additive genetic variance on XY pseudo-autosomal. Results of chromosomal genetic correlations between analyzed traits showed negative and positive correlations between traits across chromosomes. e.g. BTA14 has strong negative correlation between fat with milk and protein yields. Higher positive correlations between milk, fat and protein yields with SCS have been seen on BTA26. In the other hand, correlations between traits across SNPs can exhibit chromosomal regions having positive or negative correlations for interested traits. It can help to design low density chip with high correlated SNPs for economical traits in genomic selection.

Key words: Additive genetic variance, chromosomal genetic correlation, low density chip, German Holstein population

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Abbreviations:

AI	Artificial Insemination
BCS	Body Condition Score
BTA	Bos Taurus Autosome
BW	Body weight
CEBV	Chromosomal EBV
CEd	Direct Calving ease
CEm	Maternal calving ease
CFc	Interval from calving to first insemination cow
CI	Calving Interval
DFS	Days to first service
DGAT1	Dacylglycerol O-acyltransferase
DOc	Days open
FKG	Fat yield
FSC	First-service conception
FSc	Interval from first to successful insemination cow
FSh	Interval from first to successful insemination heifer
GEBVs	Genomic estimated breeding value
INS	Number of inseminations per conception
MAS	Marker assistant selection
MFR	Milk flow rate
MKG	Milk yield
MSP	Milking speed
MTP	Milking temperament
NRc	Non-return rate to 56 d cow
NRh	Non-return rate to 56 d heifer
PKG	Protein yield
QTL	Quantitative trait loci
RAN	Rump angle
RWI	Rump width
SBd	Direct stillbirth
SBm	Maternal stillbirth

SCC	Somatic Cell Count
SCS	Somatic Cell Score
SNP	Single Nucleotide Polymorphism
VIT	Vereinigte Informationssysteme Tierhaltung

1. Introduction:

Historically humans have tried to breed animals to increase their production value. Animal production is increased by improvement of environmental factors such as housing, feed composition, feed strategies, health status and farm management (Rauw et al., 1998); as well as, animals with adequate genetic capacity can improve the production level of interesting economical traits. This gene capacity is transferable to the next generation which is the main black box of animal breeding. Data collection from populations, computational progress, molecular genetic success and use of statistical formula provide main material to estimate accurate breeding values. The estimation of breeding values is an integral part of most breeding programs for genetic improvement. In population the genetic parameters, heritability, additive genetic variance and genetic correlation, are the base knowledge of selection in quantitative genetics (Dekkers and Hospital, 2002). Subsequently, mating assortment is a supplementary process with selection for genetic improvement in animals.

Selection has been based on two traditional types of data, pedigree and phenotypes. Recently, a third type of data has been developed based on DNA markers (Hayes, 2008). The information of markers can be used early in life, by producing more offspring than required for testing in later life and by selecting progeny with the most favorable alleles at the quantitative trait loci (**QTL**). The later method combines with pedigree and phenotype information is called genomic selection. This can improve selection before phenotypic information from animal or its progeny arise and reduce the generational intervals. Since 2001, this method has been replacing classical selection methods in dairy cattle industry. According to this method, single nucleotide polymorphism (**SNP**) effects are estimated using genotyped individuals that are phenotyped for quantitative traits, and then genomic estimated breeding value (**GEBV**s) are predicted for any individual by using only its SNP genotypes and estimated SNP effects (Meuwissen et al., 2001).

In economic species the value of a potential replacement individual is usually a function of several quantitative characters (Rutledge et al., 1973). Selection for a certain trait can lead to genetic changes in other traits (Falconer, 1989) because traits in an organism are not isolated from each other. Individuals are made up of genetically, functionally, developmentally, and physiologically interconnected traits. To understand the genetics and for evaluating groups of traits, breeders use phenotypic, genetic, and environmental correlations among traits simultaneously. Knowledge of genetic correlations among important traits, permit the breeder

to predict what will happen to an indirect trait, if this trait is ignored completely and selection is performed for the direct trait.

Dairy selection programs are now global and a key priority in breeding programs should be to identify those traits that really affect cost of production. Many traits that affect dairy cattle profit can be included in a selection index. More traits provide more information about profit, but too many could confuse breeders and distract attention away from those with highest value. It is important to identify SNP, QTL or genomic regions influencing two or more traits of interest and traits of secondary importance. Due to economical view of genomic selection policy, it is not justifiable for farmers to genotype all individuals using high density chips. Hence, it is a solution of designing small chip with high correlated SNPs for economical traits for widely usage. The aim of this study was to demonstrate the genomic architecture of quantitative traits using Illumina BovineSNP50 Beadchip. Moreover, the identification of chromosomes or SNPs affecting multiple traits in German Holstein population was part of the investigation.

2. Literature review:

2.1. What is the correlation between traits?

Correlation between two traits is the covariance normalized by the standard deviations of each trait; it has a range from 1 to -1. It is also necessary to have reliable estimates of the covariance components. At the genetic level, a covariance between traits is generated when alleles affecting both traits tend to be found within the same individual. Two causes of genetic covariance (and thus correlation) are pleiotropy and linkage disequilibrium (Falconer, 1989). Pleiotropy is defined as one locus affecting more than one trait. It is the main cause for the existence of a genetic correlation between traits in outbred population. Some pleiotropic genes can cause positive and others negative pleiotropy on investigated traits; the balance determines the genetic correlation of the two characters. In the other hand, linkage disequilibrium can cause genetic correlation between traits as well. It is defined as a non-random relationship between the alleles present at two or more loci. Roughly in QTL level, Pleiotropic effects of QTL, or closely linked QTL, each affecting a different trait, can affect the value of individual QTL for marker assistant selection (**MAS**) (Schrooten et al., 2004). It is assumed that most eukaryotes have thousands of genes linked together in no more than several dozen chromosomes (Lande, 1980). Linkage between loci (or between genetic elements within genes), contribute to genetic correlations because these linked effects tend to be inherited together.

The correlation between traits can be favorable or unfavorable; therefore consideration of correlated responses suggests that it might sometimes be possible to achieve more rapid progress under selection for a correlated response than from selection for the desired character itself. We call this indirect selection. Selection applied to some character other than the one it is desired to improve. Indirect selection cannot be expected to be better than direct selection unless the secondary character has a substantially higher heritability and the genetic correlation is high. There are practical considerations that may make indirect selection preferable. Three such practical matters are:

1. If it is difficult to measure the direct trait. Due to this difficulty as the error of measurement increases the indirect selection becomes advantageous.
2. If the desired trait is measurable in one sex only but the secondary trait is measurable in both, then a higher intensity of selection will be possible by indirect selection.
3. The desired trait may be costly to measure, then it may be economically better to select for an easily measured correlated trait (Falconer, 1989).

Recently, molecular genetic selection can lead to much higher genetic gains than traditional quantitative genetic selection, especially for traits with low heritability, phenotypes that are difficult to record, unfavorable genetic correlations, and genotype * environmental interactions (de Roos et al., 2007). Further information provided from denser markers and/or a larger number of generations may reveal the presence of linked loci or proof that correlation between traits is due to pleiotropy. It is shown that the covariance between contrasts from separate single trait regression analysis can be used to identify pleiotropic or closely linked QTL (Schrooten and Bovenhuis, 2002). Estimation of genetic correlation between traits has done by availability of data from progeny-parent measures on both traits. This study tries to estimate genetic correlation between traits using SNP effects on each trait of individual's genome.

2.2. Genetic correlation between production traits with others:

2.2.1. Production traits:

There is an abundance of published evidence on the genetic correlation of milk production traits in the breeding of cattle. The main focus of dairy selection has been on increasing milk yield. Milk, fat and protein yields are the biological and main economical interesting traits in dairy cattle (Freyer et al., 2003). Different researches have shown that genetic correlations among yield traits were strongly positive, ranged from 0.49 to 0.92 (Harris et al., 1992; Montaldo et al., 2010). The highest genetic correlation is between milk and protein production (0.83 – 0.92), and the lowest is between milk and fat production (0.80 – 0.41) (Harris et al., 1992; Veerkamp et al., 2001). Though, genetic correlation for protein yield showed some lack of consistency between the beginning and the end of lactation (Silvestre et al., 2005). Correlation between milk and protein are more similar from study to study, than correlation between milk and fat (Van Vleck and Dong, 1988). This means, milk is more associated with protein than fat yield. Genetic correlation for milk and fat percentage and milk and protein percentage was negative, although it was positive for fat and protein percentage (Schutz et al., 1990).

Genetic correlation across the parities showed variable result. Carlen et al., (2004) estimated genetic correlations between milk production traits in Swedish Holstein cows. They indicated that the strength correlations between production traits declined with increasing parity especially between milk and fat. Conversely, other study reported that genetic correlations between milk and fat and fat and protein yields increased from lactation one to lactation two and later lactations (Al-Seaf et al., 2007).

Identification of QTLs could help to better understand the structure of the genetic correlation. Thus, it is reasonable to assume that a QTL may often act on related traits. Several chromosomes, particularly *bos taurus autosome* (**BTA**) 3, 6, 9, 14, 20 and 23 have been reported to harbor QTLs with pleiotropic effects on multiple milk production traits (Khatkar et al., 2004). Study on US Holstein population revealed a significant marker effects for at least one QTL affecting fat percentage, protein yield and protein percentage in chromosome 3 (Heyen et al., 1999). A multiple QTL mapping study in German Holstein population revealed significant pleiotropic QTL on 68 cM of BTA6. This QTL affects on fat and protein yield with correlation coefficient of 0.651 ($P< 0.0001$) (Freyer et al., 2003). Although, In Norwegian dairy cattle a QTL close to marker FBN9 in the middle of chromosome 6 increases milk yield and reduces fat and protein percentages (Olsen et al., 2002).

A polymorphism in the centromeric end of bovine chromosome 14 of gene Diacyglycerol acyltransferase (***DGAT1***) in German and Fleckvieh (Thaller et al., 2003), Duch and New Zealand (Grisart et al., 2002), Israeli (Weller et al., 2003) Holstein populations was investigated for genetic correlation effect on milk production traits. In these populations the *DGAT1* allele with a lysine residue (denoted K), as opposed to alanine residue (denoted A), is associated with increased fat yield and fat and protein percent, and decreased milk and protein production.

2.2.2. Production traits with somatic cell count:

Somatic cell count (**SCC**) is routinely recorded in most milk recording systems. Although, information of SCC is easily available on a large scale (Koivula et al., 2005). Somatic cell count is used to monitor mastitis, and milk yield declines, even at relatively low levels of somatic cells (Schutz et al., 1990). High SCC in milk affects the price of milk in many payment systems that are based on milk quality (Rupp and Boichard, 1999).

Somatic cell score (**SCS**), which is the $\log_2$ transformation of SCC [$SCS= \log_2(SCC/100)+3$], corrects the problem of SCC and has accepted as a standard recording scale for SCC (Da et al., 1992). Montaldo et al., (2010) showed that genetic correlation between production traits and SCS score were generally close to zero for three lactations ranged from 0.19 to -0.27. Al-Seaf et al. (2007) used three models to estimate correlation among yield traits and somatic sell score. This study showed that the estimate of genetic correlation between milk yield and SCS were small and negative (-0.03). But it was small and positive between fat and protein yield and SCS for all three models (0.02 – 0.12. Subsequent studies indicated that the estimate of genetic correlations between production traits and SCS in the first lactation was highest (0.17

to 0.31), and decreased to about 0.1 and 0.2 for SCS and milk or protein, respectively. The correlation for SCS and fat was close to zero (Carlen et al., 2004; Samore et al., 2008). Hence, grater protein yield is associated with smaller SCS (Samore et al., 2008).

There are two opposing mechanisms that have been suggested to contribute to the genetic correlations between milk yield traits and SCC. First: cows with high milk yield may be more susceptible to mastitis resulting in a positive correlation in the first lactation. And then, mastitis causes high SCC and damage to the udder, which reduces the second lactation milk yield and causes a negative correlation (Koivula et al., 2005).

2.2.3. Production with Fertility traits:

Genetic correlations between production and fertility traits have been discussed intensively in the literature. Compared with the other trait groups, the fertility complex was considerably more heterogeneous in trait definition across countries (Liu et al., 2008). All in all, due to antagonistic correlation between production and fertility traits, selection for production traits have declined fertility in lasts decades (Rauw et al., 1998; Van Arendonk et al., 1989; Veerkamp et al., 2001). Thus a higher production is correlated with poorer fertility.

Some studies (e.g., Hoekstra et al., 1994) revealed that genetic associations between fertility traits with milk yield were weaker than those with protein yield. Days open had a larger genetic correlation with production traits (ranging from 0.63 to 0.86) than interval calving (0.55). Days open is a widely used fertility traits in most of the countries. Greater antagonism between production and days open may be due to voluntary management decisions for high-yielding cows, resulting in longer lactation lengths (Gonzalez-Recio et al., 2006). It has reported that high milk yield after calving is genetically correlated with a latter showing of the first heat. Genetic correlation between milk yield with NR56 and NR90 were -0.31 and -0.33 respectively (Konig et al., 2008). Different studies report that no genetic correlation was found between 100-day protein yield and NR56, (Van Arendonk et al., 1989) in virgin heifers but it was unfavorable in first lactation cows (-0.18) (Andersen-Ranberg et al., 2005).

2.2.4. Production traits with body weight:

The relationship between yield traits and body weight (**BW**) is complex largely dependent on both the frame size of a cow and BCS. It is stated that large cows give more milk than smaller cows (Harville and Henderson, 1966; Lin et al., 1985). So, there is a positive genetic correlation between size and production (Harville and Henderson, 1966). If there is positive correlation, then a cow's BW can add little information about her breeding

value for milk and milk fat production. Conversely, some studies found unfavorable genetic relationship between weight at first calving and milk, fat and protein yields. They indicated that genetically heavier cows after calving produce less milk, fat and protein but conceive earlier than smaller cows (Abdallah and McDaniel, 2000; Moore et al., 1991). Others, found genetic correlation of the range near zero in the first lactation to moderate negative in the second lactation between BW and milk production traits (Berry et al., 2003b; Clark and Touchberry, 1962). Selection for milk yield has a negligible progress on the BW of animal (Berry et al., 2003b). However, still potential exists to select animals with less BW loss at high levels of milk production, which is expected to improve cow health and reproductive performance (Toshniwal et al., 2008).

2.3. Genetic correlation between somatic cell score and udder type traits:

Mastitis is one of the most costly diseases in dairy industry which has a strong genetic correlation with somatic cell count. Thus, udder and teat confirmation traits, which have moderate to high heritability, and have the possibility to indirectly select for the incidence of mastitis (Chrystal et al., 1999; Seykora and McDaniel, 1986, 1985a). Estimated genetic parameters indicate a variable correlation between udder traits and SCC. It has been reported that teat-end shape was related to SCC. Cows with pointed teat ends have the lowest SCC and cows with flatter teat-ends have higher SCC (Seykora and McDaniel, 1985a, b), however result from Chrystal et. al., (2001 and 1999) did not support the previous research to find a relationship between SCS and teat-end shape. Several studies indicated that cows with higher udder, tighter fore-udder attachment, deeper cleft, and smaller teat diameter had lower lactation SCS and lower incidence clinical mastitis (Rogers et al., 1991; Rupp and Boichard, 1999; Seykora and McDaniel, 1986, 1985a, b). These results suggest that selection for higher udder, teat placement, length of fore udder and udder depth (tight udder) would have a positive effect on reducing SCC (DeGroot et al., 2002; Lund et al., 1994; Monardes et al., 1990). Genetic correlations between teat length and SCC were favorable. That means, longer teats were associated with higher SCC and clinical mastitis (Rogers et al., 1991; Rupp and Boichard, 1999).

2.4. Genetic correlation between Functional traits with others:

2.4.1. Longevity with locomotion type traits

Longevity is one of the functional traits that considerably affects overall profitably in dairy cattle. This means longevity is an indicator of overall health of the cow and satisfaction

of the owner. With increased longevity, the mean production of the herd increases. Decision to culling a proportion of cows in herd depends on production level and the proportion of mature cows, which produce more milk than do young cows (Sewalem et al., 2005). Related study showed that genetic correlation among feet and leg's, Foot angle, rear legs set were low (-0.10 to 0.05). They concluded that cows with higher feet and leg's scores and intermediate foot angle and rear legs set scores showed better performance in terms of production and longevity (Perez-Cabal et al., 2006).

2.4.2. Body condition score and production traits:

Body condition score (**BCS**) has been confirmed by the different literature as a management, visual or tactile evaluations tool for the farmers and breeders. Its main practical advantage is to assess the nutritional status and health status of producing cows during their productive cycle (Berry et al., 2003b; Domecq et al., 1997; Hady et al., 1994; Kadarmideen and Wegmann, 2003). BCS is an approximate way of judging the body lipid content of a live animal (Pryce and Harris, 2006) which is easy to measure on a large scale and accurate to indicate a major part of the variation in body reserves between the same breed of animals (Veerkamp et al., 2001). During each stage of the lactation cycle BCS should be optimal for maximal return.

In general genetic correlations between BCS and 305-d milk, fat, and protein yields were negative and unfavorable (Dal Zotto et al., 2007; Kadarmideen and Wegmann, 2003; Veerkamp et al., 2001). A biological reason for the negative genetic correlation between BCS and milk production is the apparent relationship between BCS with energy balance and tissue mobilization. Body tissue may be used in part to fuel milk production, a moderate to strong antagonistic genetic correlation between BCS and milk production is therefore expected (Berry et al., 2003b). It has been reported that there are genetic correlations between BCS change in early lactation and milk production (Berry et al., 2003b). This means, genetic correlation between BCS in early lactation and 305-d lactation fat yield was smaller than for BCS in latter lactation (Veerkamp et al., 2001). Genetic correlations between BCS and fat and protein yields estimated using the multivariate models were close to zero, while, using the Random Regrassion model, genetic correlations between BCS and fat and protein yields were positive at d 1 of lactation (Pryce and Harris, 2006).

Cows that are genetically superior milk producers tend to have genetically lower BCS in late lactation. If selection continues alone for high milk, fat and protein yields a genetic decline is to be expected in the long term selection program (Berry et al., 2002, 2003b; Dal Zotto et al., 2007; Kadarmideen and Wegmann, 2003). Study by Veerkamp et al., (2001) have been agreed that selection for a high-lactation fat yield has less effect on BCS during early lactation, and selection for a high-lactation protein yield decreased BCS especially at the end of lactation.

2.4.3. Body condition score and fertility traits:

Since, fertility traits have low heritability and are more difficult to record than BCS (Kadarmideen, 2004), results of different studies exhibit that BCS can serve as indicator for estimated breeding value for fertility traits (Berry et al., 2003a, b; Haas et al., 2007; Kadarmideen, 2004).

BCS is used in dairy cattle to assess body composition and energy balance, and besides that, fertility in dairy cattle is affected by both extent and the duration of negative energy balance (Haas et al., 2007). Cows that are in negative energy balance, particularly in early lactation, may be yielding milk at the expense of reproduction. Thus, mobilization of body tissue plays a role in the genetic control of fertility (Pryce et al., 2000). Most studies reported a moderate genetic correlation between average BCS and fertility traits (Berry et al., 2003b; Dechow et al., 2001; Kadarmideen and Wegmann, 2003). However, there is a tendency that BCS in mid lactation expressed the strongest genetic relationship with improve the fertility (Berry et al., 2003b; Haas et al., 2007). Body condition score for calving interval and days to first service showed a range between -0.4 and -0.6 and during early lactation it showed a stronger association with First-service conception (**FSC**) than BCS in later lactation (Veerkamp et al., 2001). Genetic correlations suggest that increasing BCS levels will increase the genetic merit for fertility (Haas et al., 2007) and cows with good body condition after calving have a shorter interval to insemination. Or the other way around, cows with low BCS may lack sufficient energy reserves to activate ovarian function, and are more likely to have a longer calving interval or display estrus (Dal Zotto et al., 2007; Pryce et al., 2000).

From a biological point of view, genetic correlation between BCS and fertility could lie through either 1) hormones such as insulin, growth hormone, and insulin like growth factors controlling intermediary metabolism having direct effect on ovarian function or 2) reproductive hormones regulating ovarian function having direct effects on intermediary

metabolism (Royal et al., 2002) or, genes associated with body tissue mobilization may have pleiotropic effects or be closely linked to genes controlling fertility in animals (Berry et al., 2003b).

2.4.4. Fertility traits:

After a successful increase in production traits with direct selectio, recently, focus on functional traits such as reproduction traits have received increased. Fertility is an economically important trait in the dairy industry, because it affects direct reproduction and influences calving interval (Boichard et al., 1997; Ranberg et al., 1997). From the economical view, better fertility decreases cost for inseminations, calving intervals, veterinary cost and finally lowers the percentage of infertility culling (Miesenberger et al., 1998). Fertility is based on both sexes which influences the process in different ways. Good cow fertility would be defined as an animal in lactation, which shows her heat in time and gets pregnant after the first insemination. The animal with these characters will have the desired calving interval. As a result, no waste of labour and semen occurred (De Jong, 1997). On the male side, dilution of semen before freezing, age of the sire when collected semen, and the Artificial Insemination (**AI**) technician all have large effects upon fertility as well as fertility on the female side (Jamrozik et al., 2005). Two aspects of the fertility complex are concerned with female fertility: First is the traits that the animal becomes pregnant as soon as possible after calving, that are calving interval, interval from calving to first or last insemination, intervals between first and last insemination and intervals between successive inseminations (Thaller, 1998). One of the most widely used interval traits is the interval from calving to first insemination, which describes the ability of a cow to show estrus after calving (Andersen-Ranberg et al., 2005).

Second is the ability of the animal to recycle after calving such as non-return rates, which are related to the capability of a heifer or a cow to conceive when inseminated. The advantages of the interval from calving to first insemination and 56-d non-return rate are that they are available earlier and are less biased because of selection than other fertility traits (Andersen-Ranberg et al., 2005; Thaller, 1998; Wall et al., 2003).

Heritability estimations are low for all fertility traits (Liu et al., 2008; Wall et al., 2003), but fertility can change with the age of the cow. Heifer fertility traits had higher heritability than cow traits (Jamrozik et al., 2005). Liu et al., (2008) reported high moderately genetic correlation between heifers and cows for the same traits non-return rate to 56 day (**NR**) or

interval from first to successful insemination (**FS**) in German Holstein population. They indicated a negative genetic correlation between NRc and FSc that exhibit a limited accuracy of using NR56 for projecting conception (Liu et al., 2008). There was shown a strong and favorable correlation of the calving interval (**CI**) with days to first service (**DFS**) and the number of inseminations per conception (**INS**) which suggests that improving 1 fertility trait would result in improving other correlated fertility traits (Wall et al., 2003). An unfavorable genetic trend was reported in Holstein German and United Kingdom for all fertility traits in recent years, thus CI, DFS, and INS increased and NR56 decreased (Liu et al., 2008; Wall et al., 2003)

2.4.5. Calving traits:

Calving ease and stillbirth are important complex traits which affect calving deaths, profitability of heard, and aspect of animal welfare, which is becoming important for proper strategies for genetic improvement (Dekkers, 1994). Both, calving ease and stillbirth are mainly influenced by two factors, maternal and fetal (or direct). Maternal effects refers mainly to the pelvic dimension of the dam and direct calving ease refers to calf size (Dekkers, 1994; Hansen et al., 2004). From a clinical point of view, in most cases size of the calf exceeds the pelvic opening hearupon difficult births can be seen in such parturition (Gutierrez et al., 2007). However, studies show three times higher calving difficulty and stillbirth in primiparous than multiparous dams (Carnier et al., 2000; Dekkers, 1994; Hansen et al., 2004), and that males calves were more likely to be stillborn (Cole et al., 2007).

In most studies, estimated heritability for maternal and direct calving ease were low and a negative genetic relationship has been found between direct and maternal calving ease in dairy and beef cattle (Carnier et al., 2000; Cue and Hayes, 1985; Eaglen and Bijma, 2009; Gutierrez et al., 2007). This negative correlation reflects a genetic antagonism between direct and maternal calving ease effects. From a genetic point of view, female calves born more easily are expected to exhibit greater difficulties when giving birth as dams (Carnier et al., 2000). However some studies (i.e., Luo, Boettcher et al. 2002) reported a positive genetic correlation between all combinations of one maternal and one direct genetic component of calving ease which is in contradiction with many other conclusions estimated in the literature. Carnier et, al., (2000) reported a strong genetic correlation between direct effects for first and second and for first and third parity, which suggests that the same genes are involved in the

control of direct calving ability of heifers and cows in piemontese population (Carnier et al., 2000; Cue and Hayes, 1985).

Estimated genetic correlations are varied between studies for stillbirth, some of them (e.i., Eriksson, Nasholm et al. 2004) estimated negative genetic correlation between direct and maternal stillbirth while some others found a small, close to zero genetic correlation between these two effects (Hansen et al., 2004; Heringstad et al., 2007). It would be expected that very few chromosome regions affect both direct and maternal effects of stillbirth. Following this hypothesis Thomasen et, al., (2008) reported a pleiotropic QTL on chromosome BTA12 and a two linkage QTL on chromosome BTA26 affecting both direct and maternal stillbirth. The later studies imply that selection on, e.g., the direct effect of stillbirth would not have an affect on maternal effects of stillbirth therefore it is recommended to evaluate bulls as sires and maternal grand sire to decrease stillbirth (Heringstad et al., 2007).

3. Materials and Methods:

3.1. Genotyped animals and SNP Data:

In this project, DNA was extracted either from frozen semen, leukocyte pellets or full blood samples of 2333 German Holstein Friesian bulls. The BovineSNP50 Beadchip (Illumina, San Diego, CA) was used to genotype 54,001 SNPs distributed over the whole genome for all bulls. SNP effects were estimated for 44 traits by Vereinigte Informationssysteme Tierhaltung (**VIT**) which is responsible for genetic evaluations of dairy breeds in Germany. Only SNPs with less than 5% missing genotypes and minor allele frequency greater than 3% were used. Finally among 45181 SNPs distributed on 29 autosome and XY pseudo-autosomal chromosomes, 43,838 known position SNPs were selected for subsequent analysis. Maximum numbers of SNPs were detected on BTA1 and minimum on XY pseudo-autosomal chromosome. Numbers of SNPs per each chromosome are shown in table 1.

Table 1: Distribution of numbers of SNPs per each chromosome

Chromosome	Number of SNP	Chromosome	Number of SNP
1	2816	16	1342
2	2286	17	1355
3	2169	18	1141
4	2117	19	1154
5	1807	20	1363
6	2140	21	1147
7	1883	22	1076
8	1999	23	923
9	1701	24	1080
10	1838	25	845
11	1903	26	903
12	1391	27	840
13	1477	28	811
14	1442	29	890
15	1421	XY	578

3.2. Selected traits for analyze:

In this research, twenty dairy traits were analyzed (Table 2). These traits are consisted of three production traits, somatic cell score, four milkability traits, six female fertility traits, four calving traits and two body type traits.

Table 2: selected traits were used for genetic correlation.

	Traits	Abbreviation
Production trait	▪ Milk yield	MKG
	▪ Fat yield	FKG
	▪ Protein yield	PKG
Milkability	▪ Milk flow rate	MFR
	▪ Milking speed	MSP
	▪ Milking temperament	MTP
	▪ RZD	RZD
Udder health	▪ Somatic cell score	SCS
Reproduction traits		
Fertility	▪ Non-return rate to 56 d heifer	NRh
	▪ Interval from first to successful insemination heifer	FSh
	▪ Non-return rate to 56 d cow	NRc
	▪ Interval from first to successful insemination cow	FSc
	▪ Interval from calving to first insemination cow	CFc
	▪ Days open	Doc
Calving	▪ Direct calving ease	CEd
	▪ Maternal calving ease	CEm
	▪ Direct stillbirth	SBd
	▪ Maternal stillbirth	SBm
Body type traits	▪ Rump angle	RAN
	▪ Rump width	RWI

3.3. Estimation of additive genetic variance:

3.3.1. SNP additive genetic variance:

Since allele's frequency and SNP effects were provided for each SNP. Additive genetic variance for each SNP (σ^2_{SNP}) on the population was calculated using:

$$\sigma^2_{SNP_i} = 2p_i(1-p_i)\alpha_i^2$$

Where $\sigma^2_{SNP_i}$ is SNP additive genetic variance, p_i is the frequency of the ith allele on a locus, and α_i is the substitution effect of the ith allele on the locus. Total σ^2_{SNP} for each trait was counted by the sum of individual SNP additive genetic variances along the genome.

3.3.2. Chromosomal additive genetic variance:

There are two approaches to calculate chromosomal additive genetic variance on the population.

First: chromosomal EBV (**CEBV**) was calculated as the sum of individual SNP effects on each chromosome for each bull. Then chromosomal additive genetic variance was constructed by calculate the variance between chromosomal EBV across the population.

$$\sigma^2_{g_c} = \frac{1}{n-1}\sum_{i=1}^{n}(x_i - \bar{x})$$

Where $\sigma^2_{g_c}$ is chromosomal additive genetic variance, n is the number of animals which their chromosomal additive genetic variance were investigated, x_i is CEBV of each animal and $\bar{x}$ is mean of each chromosome across population.

Second: In the second approach it was calculated by sums of SNP additive genetic variance and covariances between SNPs on each chromosome across the population as

$$\sigma^2_{g_c} = \sum_{i=1}^{n_{SNP}}\sigma^2_{SNP_i} + 2\sum_{i=1}^{n_{SNP}-1}\sum_{j=i+1}^{n_{SNP}}\mathrm{cov}(SNP_i, SNP_j)$$

Where $\sigma^2_{g_c}$ is chromosomal additive genetic variance, n_{SNP} is the number of SNPs on each chromosome, $\sigma^2_{SNP_i}$ is the genetic additive variance of ith SNP on chromosome, and $\mathrm{cov}(SNP_i, SNP_j)$ is the covariance between ith and jth SNP on the chromosome.

3.3.3. Total additive genomic variance:

To estimate the total additive genetic variance, three approaches were used.

First: **GEBV** was calculated as the sum of individual SNP effects for each bull. Then total additive genetic variance was constructed by calculating the variance between EGBV across the population.

$$\sigma^2_{G_{tot}} = \frac{1}{n-1}\sum_{i=1}^{n}(x_i - \bar{x})$$

Where $\sigma^2_{G_{tot}}$ is total additive genetic variance, n is the number of investigated animals, x_i is EGBV of each animal and $\bar{x}$ is the mean EGBV population.

Second: Total additive genetic variance was calculated with sums of chromosomal additive genetic variance and all covariance combinations between chromosomes as

$$\sigma^2_{G_{tot}} = \sum_{i=1}^{n_c}\sigma^2_{g_i} + 2\sum_{i=1}^{n_c-1}\sum_{j=i+1}^{n_c}\mathrm{cov}(g_i, g_j)$$

Where $\sigma^2_{G_{tot}}$ is the total additive genetic variance, $\sigma^2_{g_i}$ is the variance in the i th chromosome, $\mathrm{cov}(g_i, g_j)$ is the covariance between i th and the j th chromosome and n_c is number of bovine chromosomes (29 autosomes and xy pseudo-autosomal chromosomes).

Third: also it is possible to calculate total additive genetic variance with sums of SNP additive genetic variances and all covariance combinations between SNPs along the genome without pay attention to chromosomal divisions as

$$\sigma^2_{G_{tot}} = \sum_{i=1}^{n_{SNP}}\sigma^2_{SNP_i} + 2\sum_{i=1}^{n_{SNP}-1}\sum_{j=i+1}^{n_{SNP}}\mathrm{cov}(SNP_i, SNP_j)$$

Where $\sigma^2_{G_{tot}}$ is the total additive genetic variance, $\sigma^2_{SNP_i}$ is the variance in the i th SNP, n_{SNP} is the number of investigated SNP along the genome, and $\mathrm{cov}(SNP_i, SNP_j)$ is the covariance between i th and j th SNPs. Due to computational space limit, we were not able to calculate covariance between all SNPs simultaneously.

3.4. Genetic correlation between traits:

Estimation of genetic correlation between two traits in chromosomal level was calculated using CEBV for each trait and each bull. That means, correlation between two groups of data, one was the bull's CEBV for trait one and second was the bull's CEBV for trait two. The main formula for calculating correlation between traits is:

$$r_{g_{i,j}} = \frac{\mathrm{cov}(t_i, t_j)}{\sigma_{t_i} . \sigma_{t_j}}$$

Where $r_{g_{i,j}}$ is the genetic correlation between i th and j th trait, $\mathrm{cov}(t_i, t_j)$ is the covariance between i th and j th trait, and $\sigma_{t_i} . \sigma_{t_j}$ are standard deviations for i th and j th trait respectively.

In the chromosomal level the result was a matrix of numbers. On the matrix diagonal are correlations between traits on the same chromosomes and numbers above and below the diagonal are correlations between traits between of different chromosomes.

After getting correlation matrices, results were plotted to illustrate the positive and negative genetic correlations between traits between chromosomes. Positive and negative correlations were displayed with green and red colors respectively. Moreover, correlations ranging from 0.1 to -0.1 were shown in white. Genetic correlations were calculated between milk and fat for BTA14 and BTA20.

Finally, genome wide correlations were calculated using bull's EGBV between first and second traits as chromosomal genetic correlations.

3.5. Software Use:

All manipulations, calculations and graphical displays in this research were performed by R version 2.10.0 (http://cran.r-project.org).

4. Results:

4.1. Additive genetic variance:

Total chromosomal and SNP additive genetic variance were calculated for Milk, Fat, Protein yield and Somatic cell score. A summary of sums and percentages of $\sigma^2_{g_c}$ and σ^2_{SNP} for selected traits were given in table 3. As it is shown, chromosomal genetic variance explain 62.50%, 69.90%, 56.49%, and 63.26% of $\sigma^2_{G_{tot}}$ for analyzed traits. Sums of σ^2_{SNP} were explained 9.5%, 9.6%, 9.0%, and 6.3% of $\sigma^2_{G_{tot}}$ for analyzed traits respectively. Regarding to covered variance percentage by chromosomes and sums of SNP, covariance between chromosomes should explain a range of 30% to 43% and covariance between SNPs along the genome range of 90.4% to 93.7% of the $\sigma^2_{G_{tot}}$.

Table 3: Total additive genetic variance ($\sigma^2_{G_{tot}}$), Sums and percentage of $\sigma^2_{g_c}$, and sums and percentage of σ^2_{SNP}

Trait	$\sigma^2_{G_{tot}}$	Sums of $\sigma^2_{g_c}$	Percentage of $\sigma^2_{g_c}$	Sums of σ^2_{SNP}	Percentage of σ^2_{SNP}
Milk (kg)	306442.1	191540.3	62.5%	29092.25	9.5%
Fat (kg)	445.31	311.28	69.9%	42.75	9.6%
Protein (kg)	272.6143	153.98	56.49%	24.55	9.0%
SCS	0.1581837	0.100062	63.26%	0.01	6.3%

Furthermore, amount and percentage of additive genetic variance explained by each chromosome are shown in appendix I (Table 1-4). Sums and percentage of σ^2_{SNP} expressed within each chromosome were reported as well. The results indicate that BTA14 can explain higher $\sigma^2_{g_c}$ in milk and fat yield compared to other chromosomes: while the minimum part of additive genetic variance is expressed by XY pseudo-autosomal and BTA29 for milk and fat yield, respectively. In protein yield and somatic cell score BTA6 explains more variance than other chromosomes. Minimum $\sigma^2_{g_c}$ were expressed by BTA27 and BTA25 for protein yield and somatic cell score, respectively. Notably, sums of σ^2_{SNP} within XY pseudo-autosomal are higher than the sums for other chromosomes in considered traits. While, sums of σ^2_{SNP} within BTA9 and 14 in milk and fat yield and BTA6 in protein yield and somatic cell score have minimum of σ^2_{SNP} within the chromosome.

4.2. Genetic correlation:

4.2.1. Production traits and somatic cell score:

Genome wide correlation among production traits and SCS were given in table 4. Estimate of genome wide correlations among milk production traits were positive. Estimates for milk with fat and protein were 0.41 and 0.86, respectively, and 0.61 for fat and protein yield. Genome wide correlations between production traits and SCS were positive (unfavorable) and generally close to zero ranging from 0.019 to 0.087.

Table 4: Genome wide correlation between production traits and somatic cell score

Trait	Milk	Fat	Protein	SCS
Milk yield	-	0.41	0.86	0.069
Fat yield		-	0.61	0.019
Protein yield			-	0.087
SCS				-

Results of chromosomal genetic correlations between production traits and SCS were illustrated in figure 1-6. Genetic correlations were positive for all same chromosomes between fat yield with milk and protein yields except BTA14 (figure 1 and 3). The BTA14 has revealed strong to moderate negative correlations for fat with milk and protein yields (-0.873 and -0.53, respectively). This unfavorable correlation confirms the effect of correlated QTLs for fat with milk and protein yield on BTA14. The maximum positive chromosomal genetic correlations were 0.836 and 0.91 in BTA28 for both combinations, respectively. However majority of the correlations between these traits in different chromosome combinations ranged from -0.1 to 0.1 (white) but there are still some correlations out of range. Chromosomal genetic correlations between milk and protein yield were positive in same the chromosomes (figure 2). Maximum positive correlations were 0.924 on BTA24. Some slight negative correlations were visible between fat and protein in different chromosome combinations. The lowest correlation revealed between BTA18 protein and BTA21 milk (-0.14). Genome wide correlations revealed a slight positive and close to zero correlation between milk, fat, protein yields and somatic cell score. But in chromosomal level correlations between these traits were a range from -0.55 to 0.528. The BTA26 showed moderate positive correlation between milk, fat, and protein with SCS (0.388, 0.528, and 0.462, respectively).

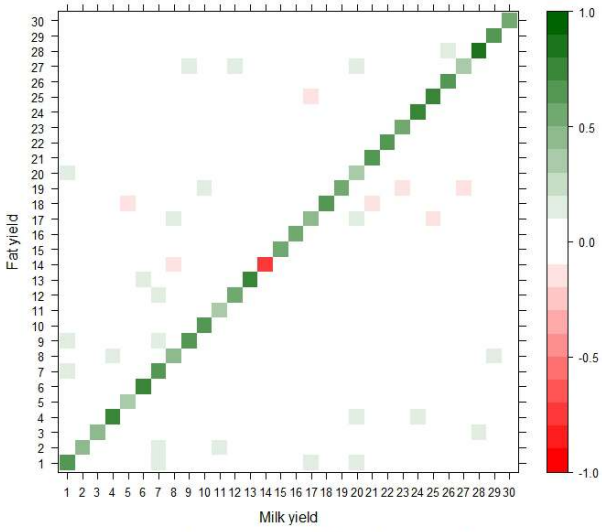

Figure 1: Correlation between Milk yield and Fat yield

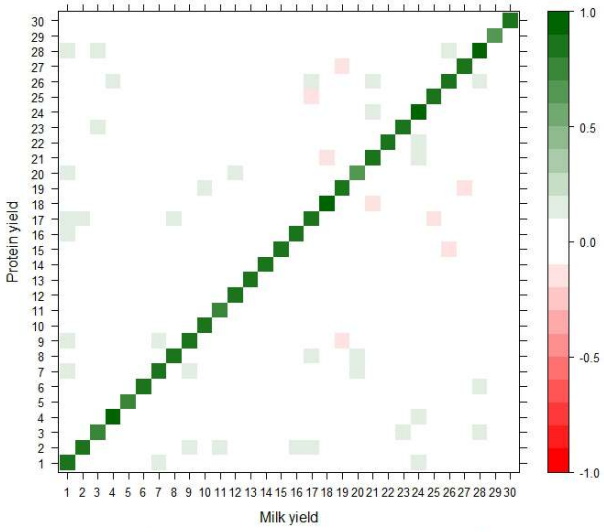

Figure 2: Correlation between Milk yield and Protein yield

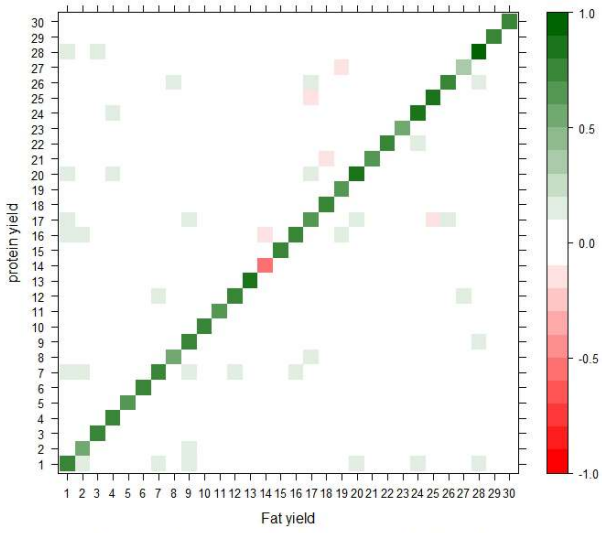

Figure 3:Correlation between Fat yield and Protein yield

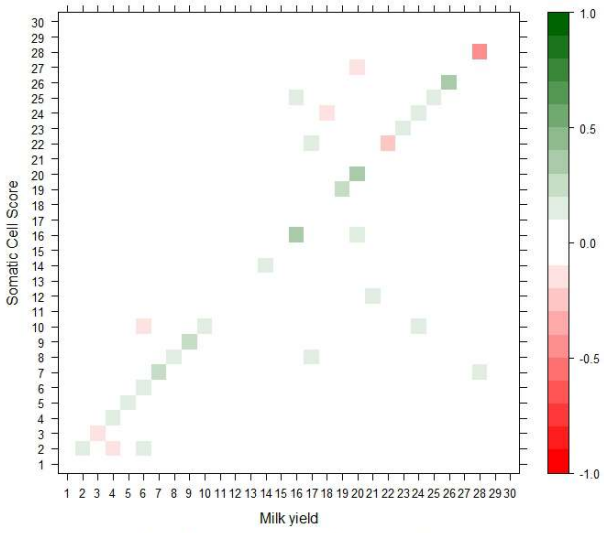

Figure 4:Correlation between Milk yield and Somatic Cell Score

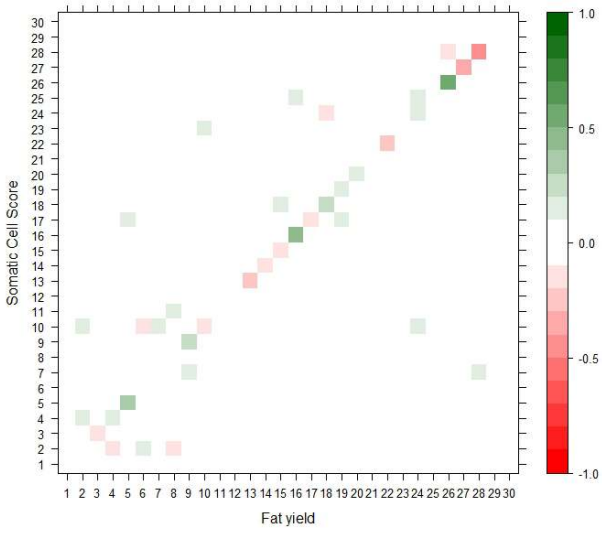

Figure 5:Correlation between Fat yield and Somatic Cell Score

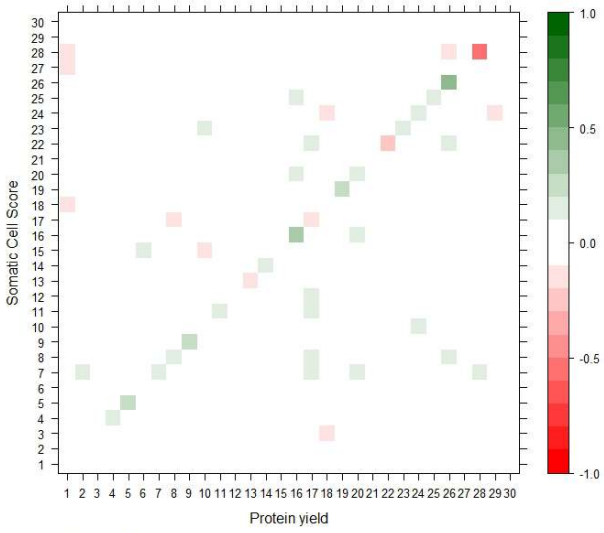

Figure 6:Correlation between Protein yield and Somatic Cell Score

Conversely, BTA28 has moderate negative correlations, -0.434, -0.46, -0.55, between milk, fat, protein yields and SCS, respectively. Notably, BTA16 and BTA21 have shined positive and negative correlations for correlations between these three production traits and SCS. The numbers of same chromosomes with negative correlation between fat yield and SCS were more than other two traits.

4.2.1.1. BTA14, 20 milk and Fat yield

Particularly, genetic correlations between SNPs on BTA14 and BTA20 for fat and milk were shown in figure 7 and 8. In the chromosomal level BTA14 shows strong negative correlation between milk and fat production but BTA29 shows positive correlation. As it is inferred from these two figures, SNPs in the beginning of the chromosomes has fewer correlations from one trait with the SNPs in the end of chromosome for second trait. Some regions of the chromosomes are very green or very red, which are the locations of QTLs laying on the chromosome with the positive and negative correlations between these two traits.

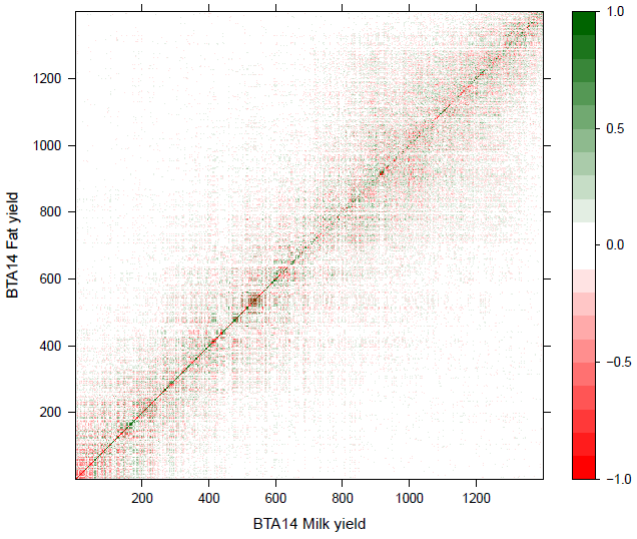

Figure 7: Correlation between BTA14 Milk yield and BTA14 Fat yield

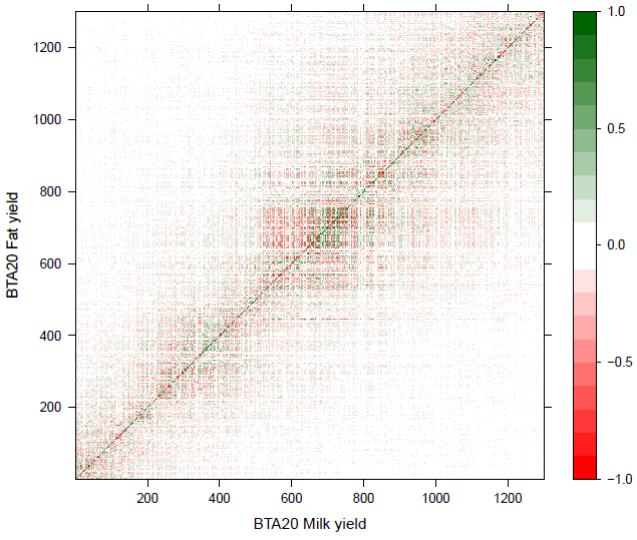

Figure 8: Correlation between BTA20 Milk yield and BTA20 Fat yield

4.2.2. Milkability traits and somatic cell score:

Estimate of genome wide correlation between milkability traits are positive between these traits (table 5). Strong genome wide correlations are between Milk flow rate (**MFR**), milking speed (**MSP**) and RZD (0.94 – 0.98). These three traits have shown positive close to zero correlations with milking temperament (**MTR**) (0.059 – 0.083). Estimation of genome wide correlation among MFR, MSP, RZD and SCS are moderately positive but unfavorable, ranging from 0.27 to 0.33. These correlations indicate that more milking flow rate and milking speed increase milk somatic cell score. As correlation between other traits with MTP, somatic cell score has showed positive but very low correlation with MTP as well.

Table 5: Genome wide correlations between milkability traits and somatic cell score

Trait[1]	MFR	MSP	RZD	MTP	SCS
MFR	-	0.94	0.98	0.059	0.33
MSP		-	0.98	0.083	0.27
RZD			-	0.073	0.31
MTP				-	0.019
SCS					-

1: MFR= Milk flow rate, MSP= Milking speed, MTP= Milking temperament

Chromosomal genetic correlation among RZD with MFR and MTP were shown in figure (9 and 10). Since RZD is a trait combined of MFR and MSP, chromosomal genetic correlation between them shows similar patterns. We did not show plots of MTP with MFR and RZD. Maximum chromosomal genetic correlations, close to unity, between MFR, MSP and RZD were on BTA19 (0.98, 0.99 and 0.995, respectively) (figure 9). Correlation between BTA7 MFR and BTA18 MSP and RZD has lower negative chromosomal genetic correlation (-0.149). Correlation among BTA18 MSP and BTA25 RZD was negative between these two traits. Chromosomal genetic correlations among MFR, MSP and RZD with MTP have similar patterns ranging from -0.383 to 0.430 (correlation between RZD and MTP was shown in figure 10). The lower negative chromosomal genetic correlation between those three traits and MTP were seen in BTA29 (-0,383, -0.295 and -0.366, respectively). On the other hand, BTA2 revealed maximum positive correlation between MSP, RZD and MTP (0.43 and 0.373, respectively) and BTA5 for MFR and MTP (0.381).

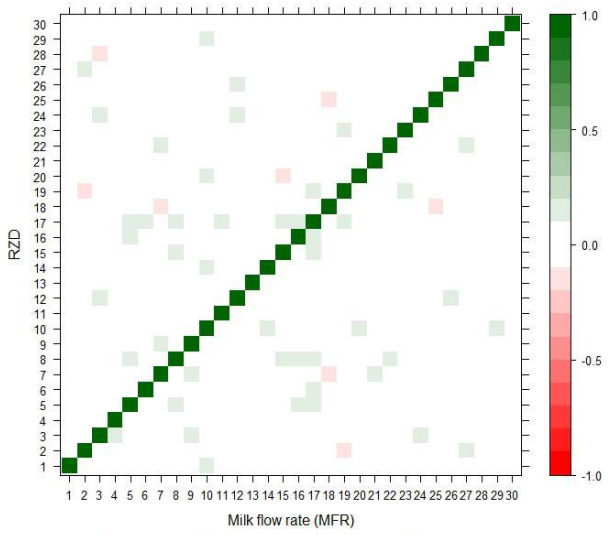

Figure 9:Correlation between Milk flow rate (MFR) and RZD

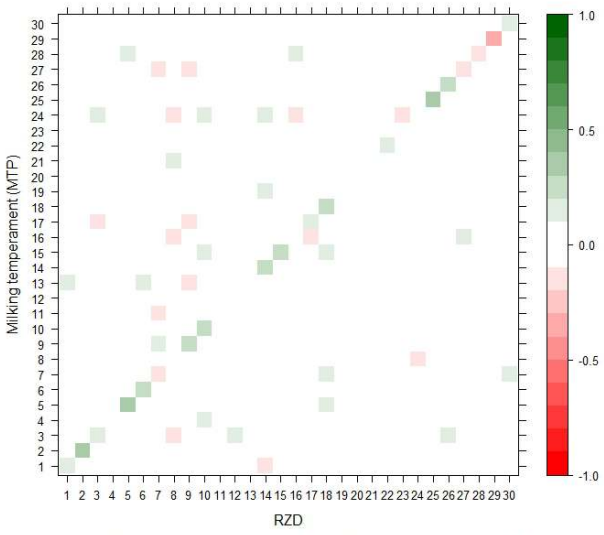

Figure 10:Correlation between RZD and Milking temperament (MTP)

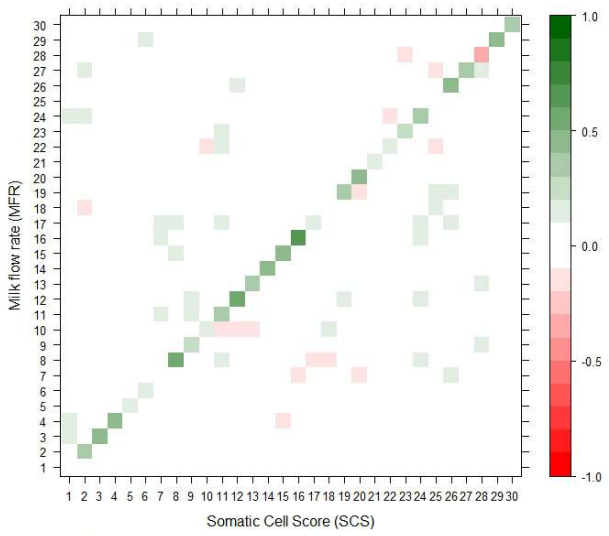

Figure 11:Correlation between Somatic Cell Score (SCS) and Milk flow rate (MFR)

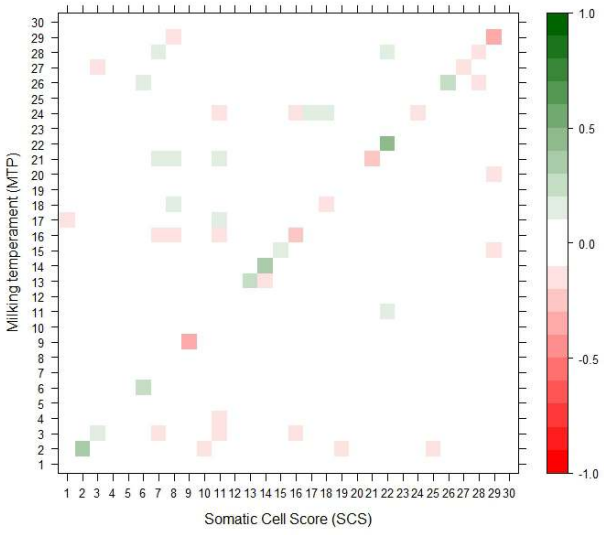

Figure 12:Correlation between Somatic Cell Score (SCS) and Milking temperament (MTP)

Chromosomal genetic correlations between MFR, MTP and SCS were illustrated in figure 11 and 12. We did not show the plots of correlations between MSP and RZD with SCS, since they have similar patterns as MFR and SCS. Lowest negative chromosomal genetic correlations between MTP, MSP, RZA and SCS revealed by BTA28 (-0.3, -0.321, -0.306, respectively). The BTA16 has positive chromosomal genetic correlations between these combinations (0.606, 0.622 and 0.629). Chromosomal genetic correlation between MTP and SCS (Figure 12) ranging between -0.376 to 0.431. The lower negative correlation between these two traits were showed by BTA29 (-0.376) as combination between MFR, MSP, RZD and MTP. Conversely, BTA22 has more positive chromosomal genetic correlation for MTP and SCS.

4.2.3. Fertility traits:

Estimate of genome wide correlations were shown in table 6. Genome wide correlation was moderately high between heifers and cows for the same trait FS (0.44) or NR (0.78). The FS traits and NR were found to have negative correlation, however the correlation between FSh with NRh and NRc is more negative (-0.68 and -0.53 respectively) than correlation between FSc with NRh and NRc (-0.31 and -0.40). Genome wide correlations between CFc with NRh and NRc were positive but low (0.10 and 0.22). Genome wide correlation between DOc and NR56 in heifers and cows were moderately negative but DOc with FS and CF traits revealed a positive correlation.

Table 6: Genome wide correlation among fertility traits

Traits[1]	FSh	NRh	CFc	NRc	FSc	DOc
FSh	-	-0.68	0.26	-0.53	0.44	0.56
NRh		-	0.10	0.78	-0.31	-0.21
CFc			-	0.22	0.28	0.86
NRc				-	-0.40	-0.23
FSc					-	0.51
DOc						-

1. FSh and FSc= interval from first to successful insemination in heifer and cow respectively, NRh and NRc= nun-return rate to 56 in heifer and cows respectively, CFc= interval from calving to first insemination cow, DOc= Days open.

Chromosomal genetic correlation were illustrated between heifers' fertility traits, FSh and NRh, (Figure 13) and cow's fertility traits, FSc, NRc, and CFc (Figure 14-16). The majority of correlation combinations between FS and NR traits in heifers and cows were negative. Heifer's chromosomal genetic correlation between FS and NR is stronger than the cow's correlations do. Thus, BTA17 explains the strong negative correlation in heifers but negligible correlation in cows. The strong negative correlation between these two traits were on BTA6 (-0.812) for heifers and BTA10 (-0.71) for cows. Chromosomal genetic correlation between CFc and NRc (figure 15) were slight positive with maximum correlation in BTA26 (0.66). There are some negative correlations close to zero between combinations of chromosomes and traits. Similar patterns have been seen for CFc and FSc with moderately high positive correlation on BTA18 (0.79) (Figure 16).

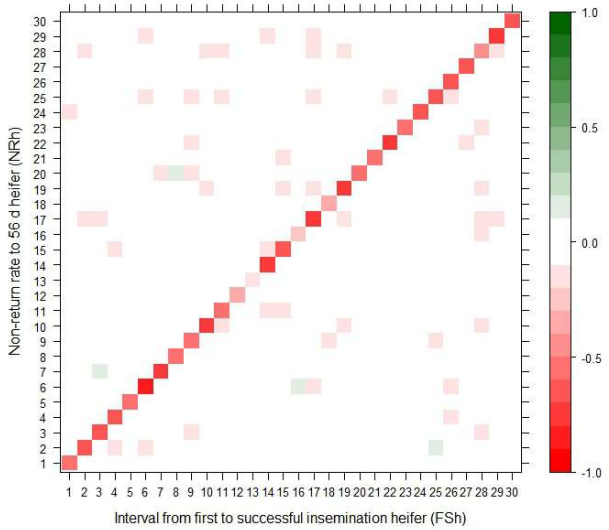

Figure 13:Correlation between Interval from first to successful insemination heifer (FSh) and Non-return rate to 56 d heifer (NRh)

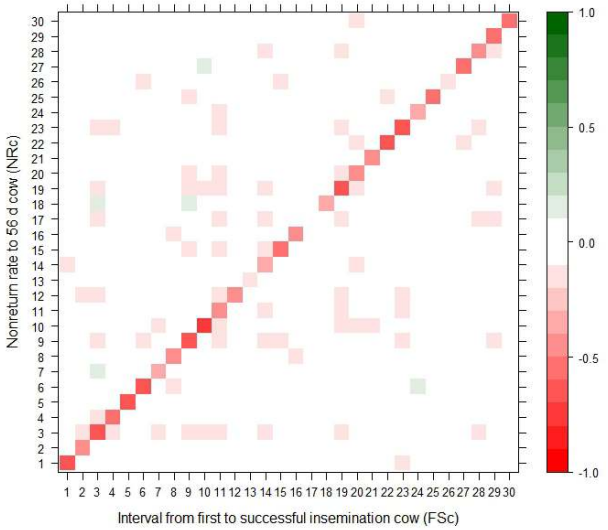

Figure 14:Correlation between Interval from first to successful insemination cow (FSc) and Nonreturn rate to 56 d cow (NRc)

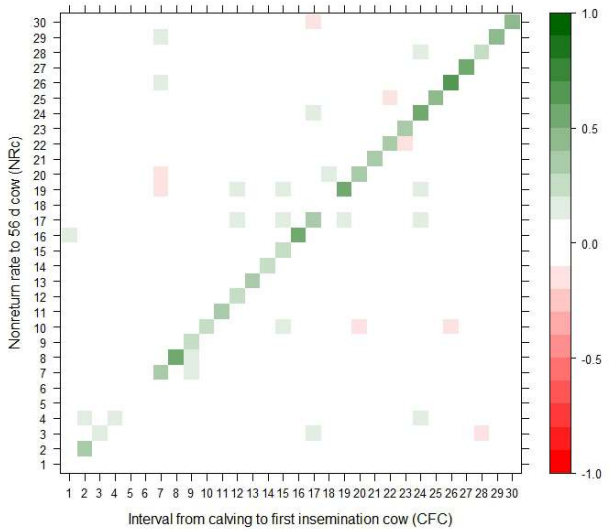

Figure 15:Correlation between Interval from calving to first insemination cow (CFc) and Nonreturn rate to 56 d cow (NRc)

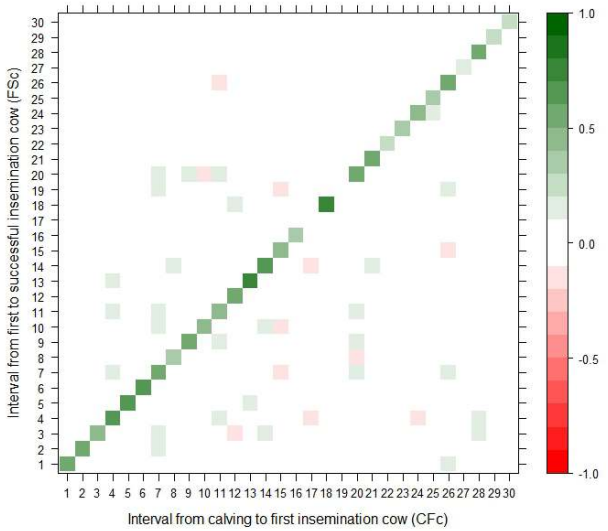

Figure 16:Correlation between Interval from calving to first insemination cow (CFc) and Interval from first to successful insemination cow (FSc)

Chromosomal genetic correlation between heifers and cows fertility traits were illustrated in figures 17-22. Chromosomal genetic correlation between FSh and NRh with CFc revealed a major positive correlation between chromosomes and traits. Maximum correlations were in BTA18 (0.626) and BTA23 (0.556) for FSh and NRh with CFc respectively. The correlations between same trait of NR and FS in heifers and cows were strongly positive (figure 19 and 20). Maximum chromosomal correlations were 0.923 (BTA25) for NRh with NRc and 0.894 (BTA9) for FSh with FSc. Conversely, chromosomal genetic correlation between FS and NR were shown as negative genetic correlation in the majority of chromosomal combinations (figure 21 and 22). Lower negative chromosomal correlations were -0.726 (BTA9) for FSh with NRc, and -0.68 (BTA10) for NRh with FSc.

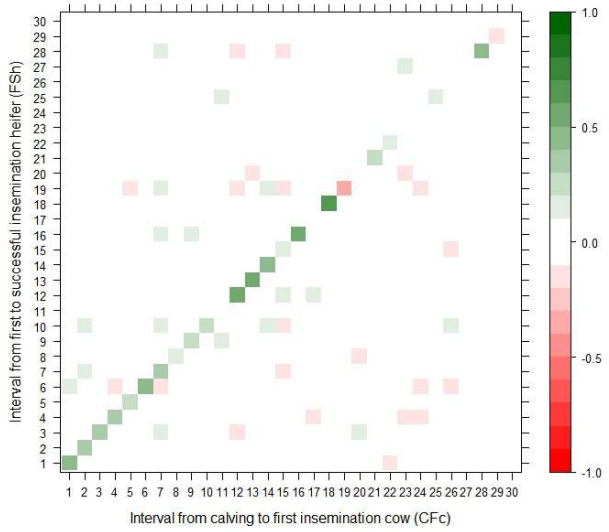

Figure 17:Correlation between Interval from calving to first insemination cow (CFc) and Interval from first to successful insemination heifer (FSh)

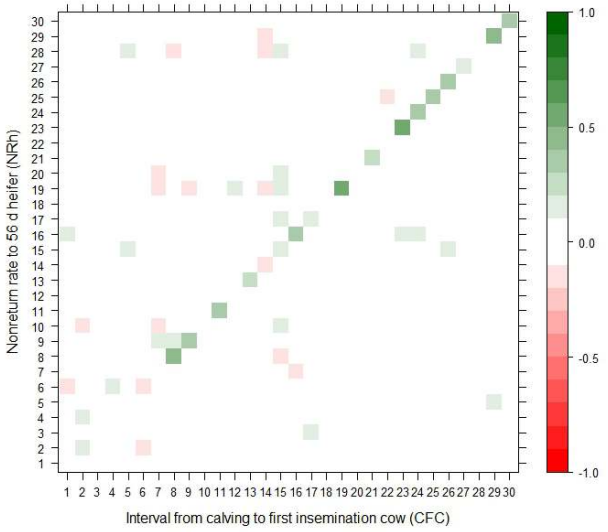

Figure 18:Correlation between Interval from calving to first insemination cow (CFc) and Nonreturn rate to 56 d heifer (NRh)

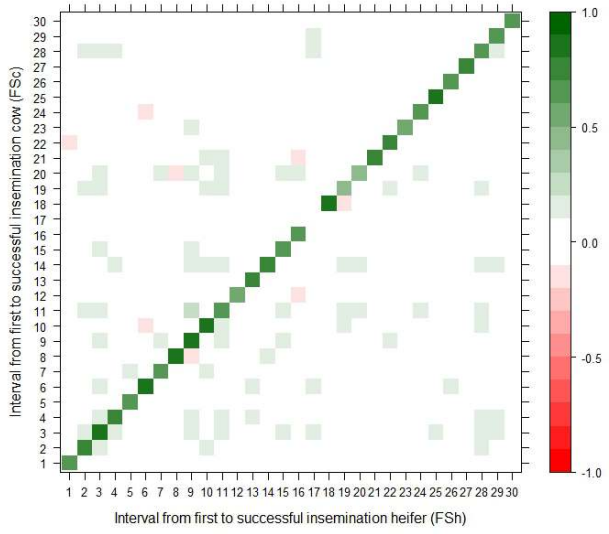

Figure 19:Correlation between Interval from first to successful insemination heifer (FSh) and Interval from first to successful insemination cow (FSc)

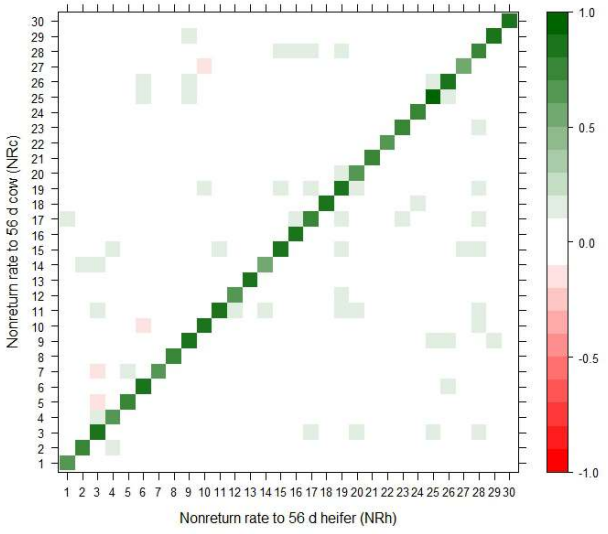

Figure 20:Correlation between Nonreturn rate to 56 d heifer (NRh) and Nonreturn rate to 56 d cow (NRc)

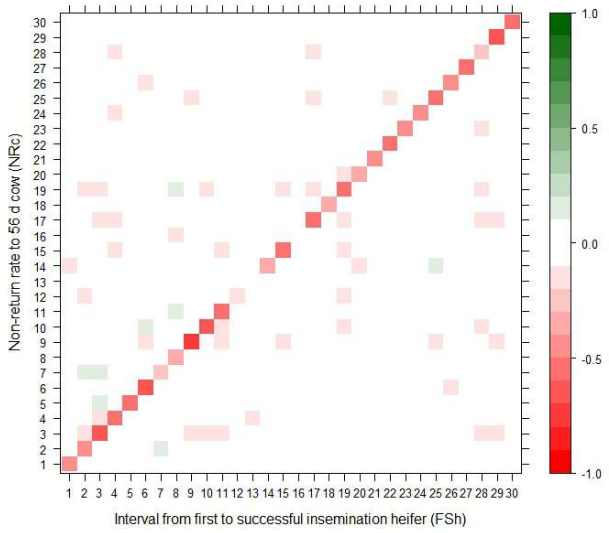

Figure 21:Correlation between Interval from first to successful insemination heifer (FSh) and Nonreturn rate to 56 d cow (NRc)

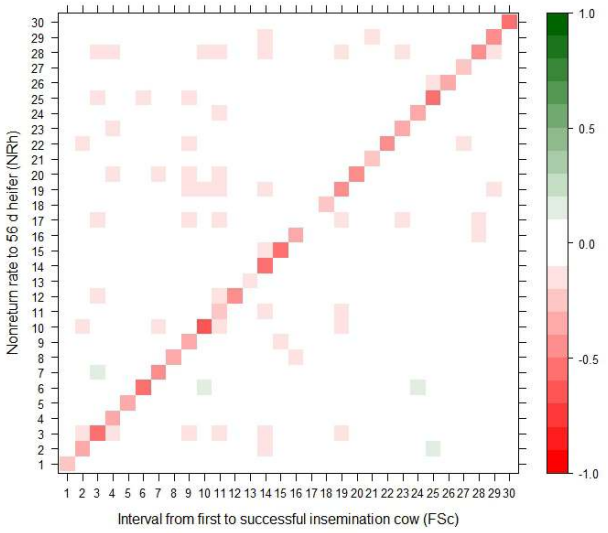

Figure 22:Correlation between Interval from first to successful insemination cow (FSc) and Nonreturn rate to 56 d heifer (NRh)

Combinations of chromosomal genetic correlations between days open and other fertility traits in cows and heifers were illustrated in figures 23-26. Chromosomal genetic correlations between DOc with FSh and FSc (figures 23 and 24) show similar patterns with strong positive correlations in the same chromosome. Maximum positive correlations between both combinations were on BTA18 (0.74 for Doc and FSh, 0.92 for Doc and FSc). The chromosomal genetic correlations between DOc with NR traits in heifers and cows (figures 25 and 26) showed that all chromosomes do not contribute on genetic correlation. Lower chromosomal genetic correlation could be seen on BTA14 (-0.35) and BTA5 (-0.40) between DOc with NRh and NRc, respectively.

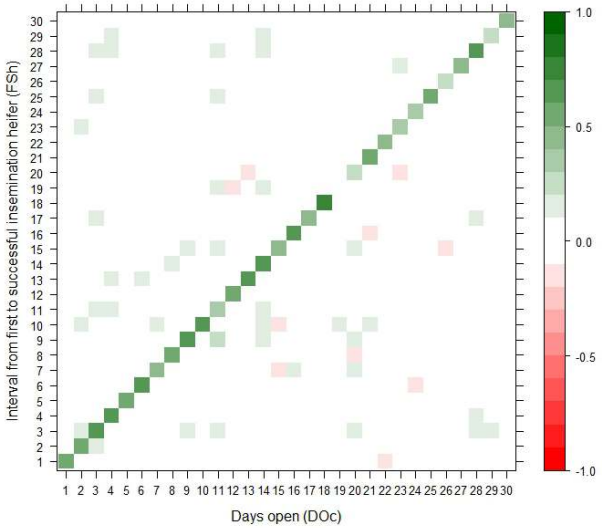

Figure 23:Correlation between Days open (DOc) and Interval from first to successful insemination heifer (FSh)

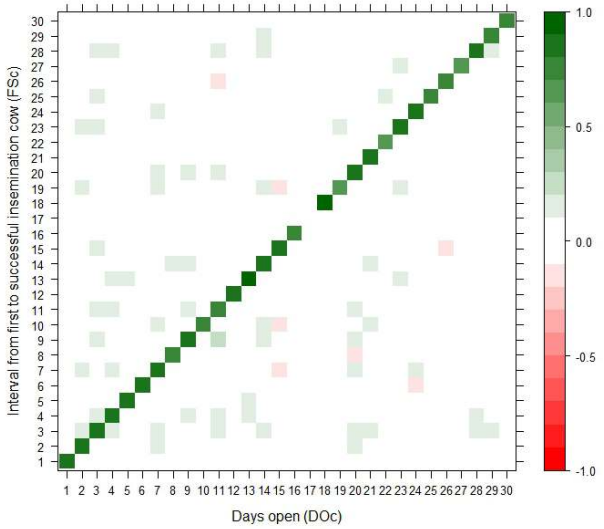

Figure 24:Correlation between Days open (DOc) and Interval from first to successful insemination cow (FSc)

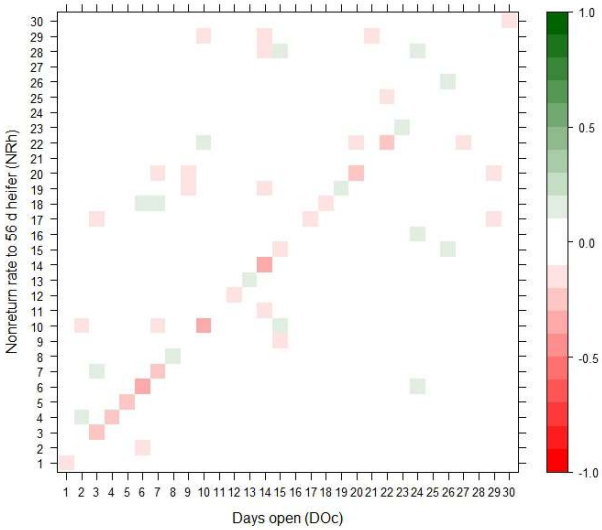

Figure 25:Correlation between Days open (DOc) and Nonreturn rate to 56 d heifer (NRh)

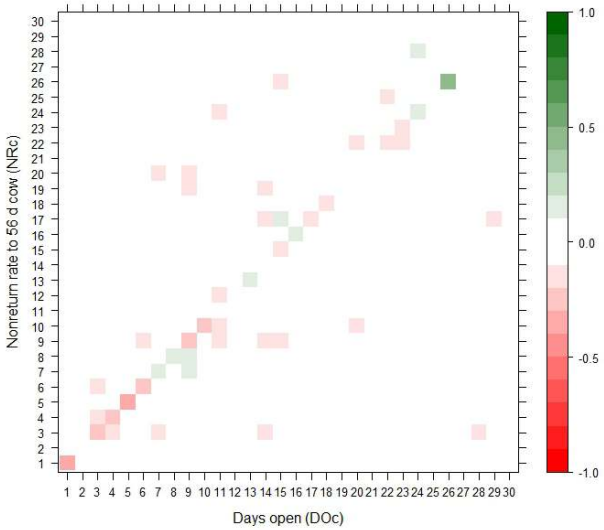

Figure 26:Correlation between Days open (DOc) and Nonreturn rate to 56 d cow (NRc)

4.2.4. Calving traits with rump angle and rump width:

Genome wide correlations between calving traits with rump angle and rump width were shown in table 7. Genome wide correlations among these traits were somewhat close to zero, except correlation between direct and maternal calving ease with direct and maternal stillbirth (0.371 and 0.39), respectively. Correlations between maternal and direct for same traits indicated that selection for direct of these traits can not help to progress of maternal traits and vice versa. There were slight negative (-0.0018, -0.0027) correlations between rump angle with direct and maternal calving ease.

Table 7: Genome wide correlation among calving traits with rump angle and rump width

Trait[1]	CEd	CEm	SBd	SBm	RAN	RWI
CEd	-	-0.0233	0.371	0.07	-0.0018	-0.16
CEm		-	0.085	0.39	-0.0027	0.086
SBd			-	0.07	0.0075	0.115
SBm				-	-0.011	0.082
RAN					-	0.04
RWI						-

1: CEd= Calving ease direct, CEm= Calving ease maternal, SBd= Stillbirth direct, SBm= Stillbirth maternal, RAN= Rump angle, and RWI= Rump width

Chromosomal genetic correlation between calving ease (**CEd**) with direct stillbirth (**SBd**) and calving ease (**CEm**) with maternal stillbirth (**SBm**) were illustrated in figure 27 and 28. Majority of correlations between these traits in the same chromosomes were positive. Maximum positive correlation between CEd and SBd were shown on BTA18 (0.83) and that for CEm and SBm showed by BTA23 (0.723). Illustration of chromosomal genetic correlation between rump angle (**RAN**) with CEd and SBd were shown in figure 29 and 30. However, gnome wide correlations between these combinations were not high but BTA18 and BTA27 show moderate positive (0.64 and 0.6) and negative (-0.35 and -0.40) correlations between RAN with CEd and SBd respectively. Chromosomal genetic correlations between rump width (**RWI**) with CEd and SBd were comparable (figure 31 and 32). BTA18 has a lower negative chromosomal genetic correlation for both of the combinations. The correlation between RWI and CEd explained by BTA18 was -0.53 and -0.50 for RWI and SBd, respectively. Maximum positive correlations between these two combinations were calculated for BTA21 (0.23 and 0.29, respectively).

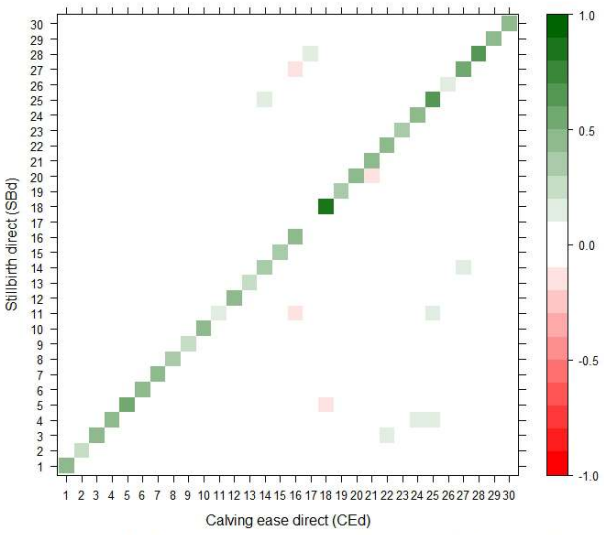

Figure 27:Correlation between Calving ease direct (CEd) and Stillbirth direct (SBd)

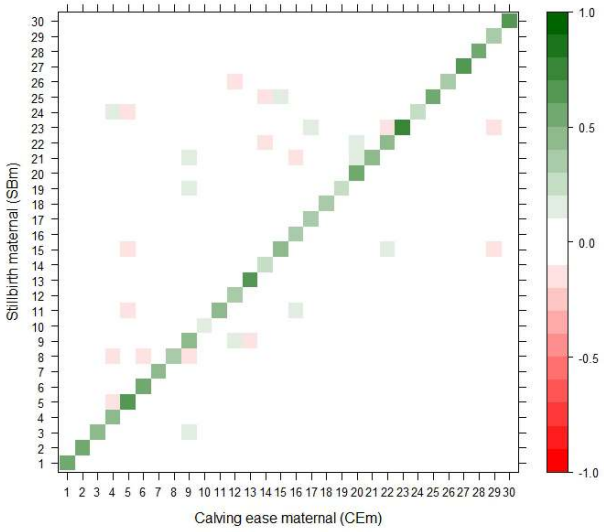

Figure 28:Correlation between Calving ease maternal (CEm) and Stillbirth maternal (SBm)

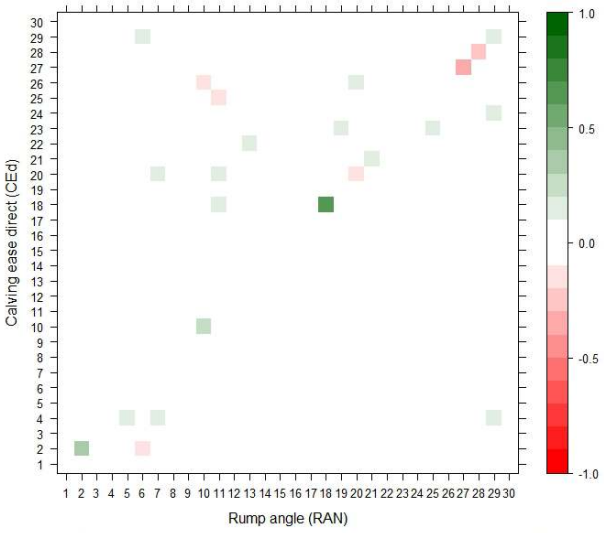

Figure 29:Correlation between Rump angle (RAN) and Calving ease direct (CEd)

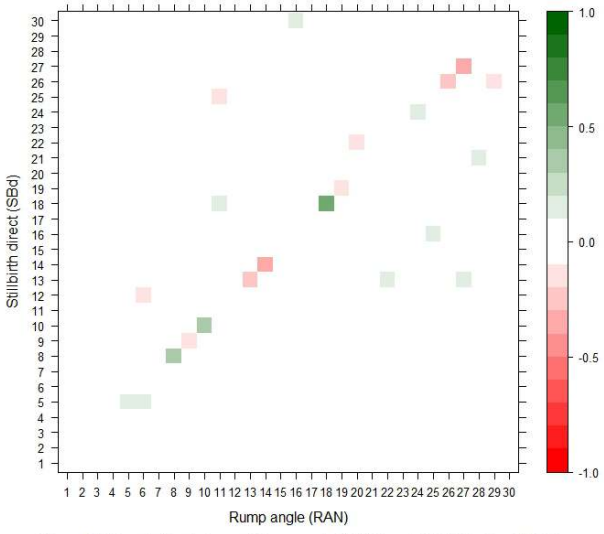

Figure 30:Correlation between Rump angle (RAN) and Stillbirth direct (SBd)

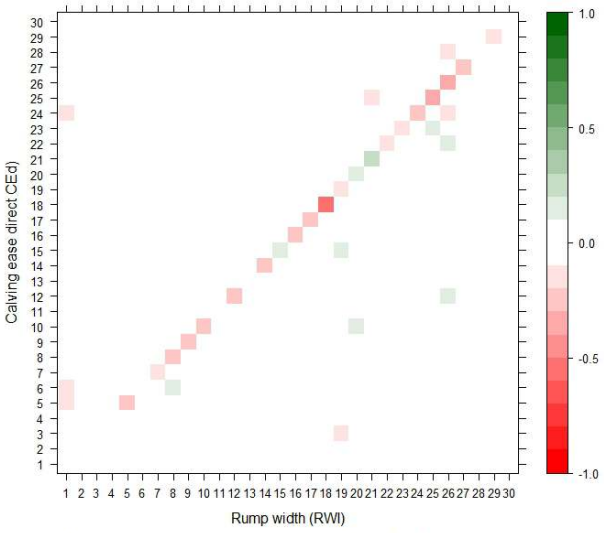

Figure 31:Correlation between Rump width (RWI) and Calving ease direct (CEd)

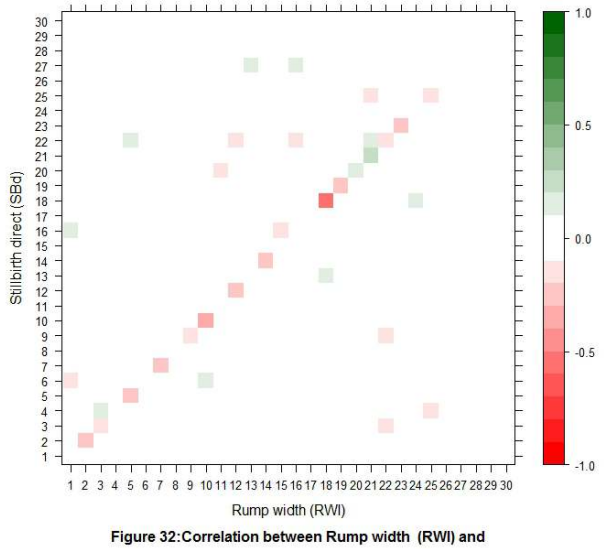

Figure 32:Correlation between Rump width (RWI) and Stillbirth direct (SBd)

5. Discussion:

5.1. Additive genetic variance:

In this study we have shown that all chromosomes contribute to construct the total additive genetic variance for milk, fat, protein yields and SCS traits. We have reported that sum of chromosomal additive genetic variances and covariance between chromosomes is equal with total additive genetic variance. Moreover, we have shown that in a high-density genome scan, SNP's variances adding with covariances between SNPs along the genome can construct total additive genetic variance. Sums of variance of SNPs within chromosomes count ranging from 5.41 to 32.07% of chromosomal additive genetic variance. The rest of the chromosomal variance is covered by covariance between SNPs. As a result, summation of SNPs variance can not be a good measure to explain the $\sigma^2_{G_{tot}}$. It can only count 6.27 to 9.6% of $\sigma^2_{G_{tot}}$ in milk, fat, protein yields and somatic cell score.

It was expected that proportions of genetic variance for each trait accounted for by SNP on a chromosome were calculated based on chromosomal lengths, assumed that all markers had equal effects (Cole et al., 2009). BTA1, 2, 3, 5, 6, 14 and 20 explain more $\sigma^2_{g_c}$ than other chromosomes for milk, fat, and protein yield (appendix I table 1-4). Notably, milk and fat yield chromosomal additive genetic variance of BTA14 (16.5%, 16.41%) is almost 2.5 times higher than other chromosomes which show more additive genetic variance. This result confirms the existence of some QTLs on reported chromosomes. These QTLs are associated with milk and fat production traits in dairy cattle (Grisart et al. 2002). There are different reports of association between QTLs on BTA14 with fat, protein and milk yield (Wibowo et al., 2008). Regarding to review by Khatkar et al., (2004) QTL affecting milk yield have been identified on 20 of the 29 bovine chromosomes. Significant QTL for fat yield have been reported on BTA14, 3, 5, 6, 9, 20 and 26. There is an abundance of studies (e.g. Olsen et al., 2002) have been detecting QTL related to milk, fat and protein yield on BTA6 and BTA5.

In the case of SCS, maximum chromosomal genetic variance was found on BTA6, 3 and 20. A study on five chromosome confirmed that QTL on BTA9, 11, 14 and 18 were affected SCS in Finish Ayrshire, Swedish Red and White and Danish Red cattle breeds (Lund et al., 2007). Danish Holstein cattle exhibited of some regions affect SCS on chromosomes 5, 6, 8, 13, 22, 23, 24, and 25 (Lund et al., 2008). Markedly, in the four analyzed traits, chromosomes which show more $\sigma^2_{g_c}$ have fewer sums of σ^2_{SNP} within chromosomes. Conversely, XY pseudo-autosomal shows maximum sums of σ^2_{SNP} within the chromosomes than others.

5.2. Genetic correlation:

5.2.1. Production traits and somatic cell score:

Positive genome wide correlations between production traits were exhibited in table 4. The correlation between milk and protein yield and fat and protein yield were higher than correlation between milk and fat yield (0.81, 0.61 and 0.41, respectively). These results agree with estimates reported for production traits of first lactation in Mexican Holstein cows (Montaldo et al., 2010), Black-and-White cows that had at least 50% Holstein genes (Veerkamp et al., 2001) and Swedish Holstein cows (Carlen et al., 2004). But the results are lower than the estimate reported by Van Vleck and Dong, (1988) and Harris et al., (1992).

Genome wide correlations between production traits and SCS were positive which indicate unfavorable relationship (0.069, 0.019 and 0.087 for milk, fat and protein yields with SCS respectively) (Table 4). The sign of our result agree but the values were lower than estimates reported by Rupp and Boichard, (1999) (0.15, 0.11, and 0.27 for fat and protein yields with SCS respectively) and Carlen et al., (2004) for three lactation of Swedish Holstein cow. The results of this study were inconsistent with result in second and third lactation of Mexican Holstein cows (Montaldo et al., 2010). Schutz et al., 1990 reported positive estimated genetic correlation between production traits with SCS in first lactation (0.13, 0.13, 0.29), but moderate negative correlation for second lactation (-0.21, -0.31 and -0.14 for fat and protein yields with SCS, respectively).

Chromosomal genetic correlations between production traits (figures 1-3) confirm positive genome wide correlations between these traits. As it was exhibited in figure 1 and 3, BTA14 has negative correlation between fat with milk and protein yields. Therefore, it would be the reason which genome wide correlations between these two combinations are fewer than correlation between milk and protein yields. Identification of a locus on the centromeric end of bovine chromosome 14 was reported with increasing milk and protein yield and decreasing fat production (Coppieters et al., 1998). This is consistent with study by Thaller et al., (2003) where the lysine-encoding variant of *DGAT1* on chromosome 14 has favorable effect on milk and protein yields and unfavorable effect on fat yield in Fleckvieh and German Holstein populations. In particular case as it was shown in figure 7. Clear negative correlation between milk and fat yield was shown in the centromeric end of BTA14. Several chromosomes, particularly BTA3, 6, 9, 14, 20 and 23 have been reported to harbor QTL with pleiotropic effects on multiple milk production traits (Khatkar et al., 2004). QTL mapping in Fleckvieh breed confirmed a QTL located on BTA5 which increases milk, fat and protein yields (Awad et al., 2010). The multivariate analysis of three bivariate trait combinations supported the

presence of a significant pleiotropic QTL for fat and protein yields on BTA6 in German Holstein population (Freyer et al., 2003). SNP genetic correlations explain positive correlation between milk and fat yield ob BTA20 (Figure 8). Attempt of researchers on BTA20 found a phenylalanine to tyrosine substitution in the transmembrane domain of the growth hormone receptor gene associated with effect on fat percentage and modest influence on the yield traits (Blott et al., 2003).

According to figures 4-6, correlations between production traits and SCS on BTA3, 22 and 28 are more negative than other chromosomes which show negative correlation. As well as correlation in BTA20 and 26 are positive between production traits and SCS than other chromosomes. Regarding our knowledge, no reports of pleiotropic or close linkage between QTLs for production traits and SCS on BTA3, 20, 22, 26 and 28 were found in the literature. Two QTLs affecting SCS were reported at opposite ends of BTA26 in US Holstein (Ashwell et al., 2004). QTLs affecting SCS reported by Lund et al., (2008) mapped on BTA5, 6, 8, 13, 22, 23, 24, and 25 in Danish Holstein population. Also in other study (Lund et al., 2007) they confirmed QTLs affecting SCS on BTA9, 11, 14, and 18 in Finish Ayrshire, Swedish Red and White and Danish Red cattle breeds.

5.2.2. Milkability traits and somatic cell score:

Positive close to unity genome wide correlation between MFR, MSP and RZD (table 5) indicate that there are no differences between these traits. Actually, both traits MFR and MSP are combined into one MSP index with equal weights for one genetic standard deviation. This index is called RZD a relative breeding value with average 100 and a genetic standard deviation of 12 (Rensing and Ruten, 2005). Estimated genetic correlations between milk flow rate, maximum milk flow and milking time in a research farm were near unity with r_g= 0.98 between average and maximum milk flow, r_g= -0.89 between average milk flow and milking time and r_g= -0.86 between maximum milk flow and milking time (Gäde, 2006). Genome wide correlations between MFR, MSP and RZD with MTP were favorable positive but close to zero (0.059, 0.083 and 0.073). it was reported that milking speed and milk temperament are completely independent traits with genetic correlation close to zero (Rensing and Ruten, 2005). Conversely, genetic correlation between temperament and ease milking estimated slightly high (0.56) in Irish Holstein-Friesian cows (Berry et al., 2004). Genome correlations between MFR, MSP, RZD and MTP with SCS are unfavorable positive. Although correlation among MTP and SCS is lower than other combination and close to zero (0.019). It was reported that faster milking is associated with increased SCS (Boettcher et al.,

1998). Genetic correlation between milking speed and SCS was 0.41 and 0.25 first and second lactations of their study. Unfavorable genetic correlation (0.44) was found between milking ease and SCS in French Holstein population (Rupp and Boichard, 1999). In a study by Gäde, (2006), genetic correlation between average milk flow rate, maximum milk flow, and milking time with SCS estimated as 0.35, 0.38, and -0.24 respectively. Genetic correlation was estimated to be slightly positive (0.27) between SCC and milking speed in Danish Holsteins (Lund et al., 1994). An unfavorable genetic correlation (0.23) was reported between RZD and relative EBV SCS in the study of Rensing and Ruten, (2005). Also, Berry et al., (2004) estimated a negative genetic correlation (-0.42) between temperament and SCC that may be attributed to elevated levels of blood cortisol.

The chromosomal genetic correlations between MFR, MSP, and RAZ emphasize the definite similarity between them. Chromosomal genetic correlation between these three traits and MTR show a strong negative correlation between them on BTA29 and strong positive genetic correlation on BTA2 and BTA5 compare to other chromosomes. Analysis of chromosomal genetics correlation between MFR, MSP and RZD with SCS showed more negative correlation on BTA28 and conversely BTA16, 20, 26 and 29 have more positive correlation between these traits than other chromosomes. When it comes for correlation between MTR and SCS, BTA2, 14 and 22 have more positive and BTA9, 16, 21 and 29 have more negative genetic correlation than other chromosomes. In a QTL mapping study for behavior in cattle QTL for temperament on BTA29 exceeded the experiment-wise significant threshold at the 5% level and for milking speed approached at the 10% significant level (Hiendleder et al., 2003). They showed QTLs with correlations between temperament and milking speed on BTA5 at 136/136 cM, on BTA18 at 105/109 cM, on BTA29 at 20/20 cM, and on chromosome X/Y at 9/9 in German Holstein population. Schrooten et al., (2004) reported positive correlations between milking speed with udder confirmations and fat percentage (0.44 to 0.56) and negative correlation with milk yield (-0.46) on BTA14. In resent research, they detected seven SNP with significant effects on milking speed at chromosome-wise level ($p<0.05$) on BTA1, 10, 19, 24, 26 and 27 (Kolbehdari et al., 2008). Also, they detected 9 SNP with a significant effect on milking temperament at the chromosome-wise level ($p< 0.05$) on BTA4, 13, 19, 22, 23, 26 and 29.

5.2.3. Fertility traits:

Favorable positive genome wide correlations between same fertility traits, FS (0.44) and NR56 (0.78), in heifers and cows (table 6) indicated that NR56 are more correlated

genetically than FS traits in heifers and cows. Liu et al., (2008) reported same estimation for FS (0.48) traits but a little bit lower genetic correlation for NR56 (063). Definite genome wide negative correlation between FS traits and NR56 combinations in heifers and cows (table 10) indicated that cows with long interval from first to successful insemination need more insemination service after 56 days of showing heat. However, genome wide correlation between NRc and FSC (-0.39) is similar with correspondence combination in research by Liu et, al., (2008), but correlations between FSh with NRc (-0.56) and FSc with NRh (-0.31) in our study are twice the correspondence in Liu et al., (2008) (-0.25 and -0.15 respectively). Lower positive genome wide correlations were seen between CFc and other traits which agreed with the results of other studies in German and Spanish Holstein populations (Gonzalez-Recio and Alenda, 2005; Liu et al., 2008).

Days open has negative correlations with NR56 traits and positive correlations with FS traits in cows and heifers. These results are not agreed with the result estimated by Liu et al., (2008). They estimated positive genetic correlations for DOc with NRh (0.09) and lower genetic correlation between DOc and NRc (-0.18). Maximum correlation among fertility traits were seen between CFc and Doc (0.86) which was similar with the estimated result by Liu et al., (2008) and Gonzalez-Recio and Alenda, (2005). Due to farm management farmers like to inseminate cows with high production milk later, and that cause longer days open in the genetic correlation estimate.

Chromosomal genetic correlation between FS and NR56 were showed negative genetic correlations in all chromosomes in heifers and cows (figures 13, 14, 21 and 22). Notably, except correlation between FSh and NRh, BTA17 has negligible, close to zero correlations between NR and FS traits in heifer and cows. Chromosomal genetic correlations between FS and NR56 traits indicated that negative correlations between these traits distributed on all chromosomes except BTA17 for the mentioned traits and also BTA14 for FSh and NRc. Lower negative chromosomal genetic correlation between FSh with NRc and FSc expressed by BTA9 and that for FSh and NRh expressed by BTA6. A highly significant QTL were reported for length in day of interval from first to last inseminations in heifers and cows that is correspond with FS (Hoglund et al., 2009a; Hoglund et al., 2009b). Markedly, BTA18 showed maximum chromosomal genetic correlation between Doc with FSh and FSc and also between CFc and FSc and FSh. BTA26 has maximum positive correlations between NRc with DOc and CFc and also between NRh and DOc. Minimum chromosomal negative correlations between NRh with CFc and DOc is on BTA14. Attempts to find QTLs affecting fertility traits have exhibited of QTLs for NRc on BTA1, 2, 11, 12, 15, 18, 20 and 29 (Hoglund et al.,

2009a; Hoglund et al., 2009b; Holmberg and Andersson-Eklund, 2006). Different study (e.g, Holmberg and Andersson-Eklund, 2006) found QTLs on BTA2, 9, 19, 22, 25 and 26 which influencing NRh. Hoglund et al., (2009a and b) detected QTLs on BTA4, 9, 10 and 26 in Danish and Swedish Holstein cattle that affecting FSh. QTLs reported to affect CFc is located on BTA1, 2, 3, 6, 10, 11, 13, 15, 24, 25 and 29 (Daetwyler et al., 2008; Hoglund et al., 2009a). Finally, QTLs affecting DOc are located on BTA1, 2, 5, 12, 20, 25 and 29 in finish Ayrshire cattle (Schulman et al., 2008).

5.2.4. Calving traits with rump angle and rump width:

Genome wide correlation between direct and maternal calving ease was negative (-0.0233) (Table 7). However, our result agreed in sign with the estimated results by Eaglen and Bijma, (2009) (ranging from -0.4 trough -0.44), Cue and Hayes, (1985) (-0.40), and Carnier et al., (2000) (-0.219) but lower than reported estimates. Estimation of maternal and direct calving ease genetic correlation were negative (-0.16) in Canadian Holstein cattle (Luo et al., 1999). Genome wide correlations were definitely against direct and maternal calving ease correlation estimated (ranging between 0.24 to 0.40) in different parities of Canadian Holstein (Luo et al., 2002). Genome wide correlation among sire (SCE) and daughter (DCE) calving ease in US Holstein were 0.58 (Cole et al., 2009).

Genome wide correlation between direct and maternal stillbirth was positive but close to zero (0.007). This result is in agreement with result of Hansen et al., (2004) (0.03-0.06). Heringstad et al., (2007) estimated close to zero (-0.02) correlation between maternal and direct stillbirth. Our result is strongly against estimated results by Eriksson, Nasholm et al. (2004) (-0.58 to -0.60) and Luo et al., (1999) (-0.24). A correlation close to zero implies that selection on e.g., the direct effect of stillbirth or calving ease would not influence the maternal effect of stillbirth or calving ease. Positive genome wide correlations between direct and maternal SB and CE are given in table 7. Moderate positive correlation between direct CE and direct SB (0.371) and between maternal CE and maternal SB (0.39) state that selection for one of the traits would result in a favorable response for the second trait. However sign of our result are in agreement with the estimated result in Norwegian Red cows (Heringstad et al., 2007), but these result are lower than reported estimations. Luo et al., (1999) estimated negative genetic correlation between CEd and SBd (-0.59) and CEm with SBm (-0.34) that were inconsistent with result of this study. Instead, genetic correlations between CEd and SBm (0.06) and between CEm and SBd (0.4) were close to the results of this study. Chromosomal genetic correlation between CEd and SBd and between CEm and SBm (figures

27 and 28) showed the contribution of positive correlation of all chromosome between CE and SB. Maximum positive chromosomal genetic correlation between CEd and SBd were expressed by BTA18. It was located a QTL on BTA18 with a pleiotropic effect on the direct calving traits and linked to maternal stillbirth in Danish Holstein cattle (Thomasen et al., 2008).

Genome wise correlations between rump angle with SB and CE, which were given in table 7, were negative except RAN and SBd, and close to zero. Therefore, selection for rump angle has no such effect on SB and CE. Genome wide correlations between RAN with CEd and SBd (figure 29 and 30) revealed maximum positive correlation on BTA18. Minimum negative genetic correlation between RAN and CEd expressed on BTA27 and 28. Also, BTA14, 27 and 29 showed minimum negative correlations between RAN and SBd.

Genome wide correlations between rump wide with CE and SB (table 7) were positive except RWI and CEd. Correlations between RWI with CEd and SBd were grater than others combinations (-0.16 and 0.115 respectively). Opposite to correlations between RAN with CEd and SBd, BTA18 express lower negative correlations between RWI with CEd and SBd. Conversely, BTA21 express more positive chromosomal genetic correlations between RWI with CEd and SBd. Attempt to find QTLs along cattle genome have been undertaken to identify the genomic regions that affect CE and SB. Study on German Holstein indicated QTL affecting calving traits on BTA7 and BTA10 and fertility traits on BTA7 (Seidenspinner et al., 2010). Subsequent study confirmed microsatellite marker DIK4234 in telomeric region on BTA18 was associated with SBm, CEd and body depth (Brand et al., 2010). Although, Hiendleder et al., (2003) found QTLs on BTA1, 6, 22 and xy affecting rump wide and on BTA17 that affecting rump angle in German Holstein population. Kolbehdari D. et al.(2008) detected 13 SNPs on BTA3, 6, 7, 8, 11, 18, 25 and 27 with significant effect on overall rump, nine SNPs on BTA4, 6, 8, 11, 18, 21 and 23 with significant effect on direct calving ease, and seven SNPs on BTA7, 9, 23, 24, 28, and 29 with significant effect on maternal calving ease. It was reported that putative QTL on BTA18 is associated with calf growth rate (Cole et al., 2009). They emphasized that the QTL on BTA18 affects calf size and that selection for extreme confirmation (larger body size) has resulted in large calves and increased rate of dystocia. Therefore this QTL reported to has largest effect on both sire and daughter stillbirth (Cole et al., 2009).

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7. Appendix I

Amount and percentage of additive genetic variance counted by each chromosome are shown

Table 1: Milk chromosomal and percentage of additive genetic variance ($\sigma^2_{g_c}$), sums and percentage of σ^2_{SNP} expressed within each chromosome

Chromosome	$\sigma^2_{g_c}$	Percent of $\sigma^2_{g_c}$	σ^2_{SNP}	Percentage of σ^2_{SNP}
1	9757.52	5.09	1383.526	14.18
2	6012.97	3.14	1124.119	18.69
3	8338.273	4.35	1355.789	16.26
4	6152.125	3.21	1134.262	18.44
5	11384.40	5.94	1446.566	12.71
6	9996.718	5.22	1288.470	12.89
7	5761.67	3.01	1121.617	19.46
8	4261.267	2.22	965.1052	22.65
9	6328.077	3.31	581.5525	9.19
10	5687.913	2.96	1054.485	18.54
11	6533.386	3.41	1071.605	16.41
12	4024.352	2.10	845.0949	20.99
13	6348.78	3.31	989.7921	15.60
14	31599.46	16.50	2999.746	9.49
15	6969.279	3.63	944.6438	13.55
16	4327.211	2.26	699.4584	16.16
17	4813.991	2.51	803.2739	16.68
18	5721.751	2.99	1026.823	17.95
19	5753.997	3.01	873.2733	15.18
20	8137.122	4.25	913.4082	11.23
21	3351.891	1.74	676.6149	20.19
22	3470.976	1.82	680.2853	19.60
23	3665.096	1.92	609.8235	16.64
24	4048.368	2.11	664.5529	16.42
25	3876.383	2.02	694.1646	17.91
26	3035.746	1.59	536.6591	17.68
27	2102.544	1.10	523.9326	24.92
28	4297.804	2.25	782.5752	18.21
29	3661.435	1.92	621.1561	16.97
XY	2119.775	1.11	679.868	32.07

Table 2: Fat chromosomal and percentage of additive genetic variance ($\sigma^2_{g_c}$), sums and percentage of σ^2_{SNP} expressed within each chromosome

Chromosome	$\sigma^2_{g_c}$	Percent of $\sigma^2_{g_c}$	σ^2_{SNP}	Percentage of σ^2_{SNP}
1	14.06284	4.52	1.994684	14.18
2	13.20165	4.24	1.794792	13.60
3	9.371772	3.01	1.774379	18.94
4	11.28458	3.62	1.653388	14.65
5	21.72584	6.98	2.643351	12.17
6	12.47554	4.01	1.56327	12.53
7	11.56252	3.71	1.464759	12.67
8	9.389346	3.02	1.449006	15.43
9	8.25256	2.65	1.365630	16.55
10	8.76557	2.82	1.434334	16.36
11	9.945134	3.20	1.663785	16.73
12	11.42976	3.67	1.515648	13.26
13	6.718333	2.16	1.280168	19.06
14	51.05667	16.41	4.354778	8.53
15	13.19053	4.24	1.480277	11.22
16	8.751384	2.81	1.180264	13.49
17	6.087822	1.96	1.143690	18.79
18	11.28000	3.62	1.352571	11.99
19	8.974364	2.88	1.413476	15.75
20	8.572196	2.75	1.109344	12.94
21	5.01132	1.61	0.9598125	19.15
22	5.202495	1.67	0.9253598	17.79
23	4.716164	1.52	0.8606213	18.25
24	4.436556	1.42	0.8413257	18.96
25	6.103289	1.96	0.9783203	16.03
26	8.543983	2.75	0.8635952	10.11
27	5.357839	1.72	0.825753	15.41
28	7.080685	2.28	1.090555	15.40
29	3.909375	1.26	0.7834589	20.04
XY	4.813877	1.54	0.979849	20.35

Table 3: Protein chromosomal and percentage of additive genetic variance ($\sigma^2_{g_c}$), sums and percentage of σ^2_{SNP} expressed within each chromosome

Chromosome	$\sigma^2_{g_c}$	Percent of $\sigma^2_{g_c}$	σ^2_{SNP}	Percentage of σ^2_{SNP}
1	8.98865	5.84	1.179961	13.13
2	5.106877	3.32	1.012998	19.84
3	6.401327	4.16	1.191580	18.62
4	6.62821	4.31	1.027538	15.50
5	7.538214	4.90	1.191888	15.81
6	10.11632	6.57	1.128052	11.15
7	5.782684	3.75	0.9692023	16.76
8	3.988066	2.60	0.8318364	20.86
9	5.100123	3.31	0.8483167	16.63
10	6.164268	4.01	0.940984	15.26
11	5.044164	3.27	0.9158102	18.16
12	4.426609	2.88	0.8176056	18.47
13	5.350124	3.47	0.9104773	17.02
14	8.485574	5.51	1.082657	12.76
15	4.666248	3.03	0.7854665	16.84
16	4.900984	3.18	0.6702795	13.68
17	4.699632	3.05	0.7288164	15.51
18	7.263619	4.72	1.019984	14.04
19	4.345813	2.81	0.7380958	16.98
20	5.942631	3.86	0.7117459	11.98
21	3.762512	2.45	0.6199674	16.48
22	3.54912	2.30	0.6297366	17.74
23	2.618043	1.70	0.5159798	19.71
24	3.796364	2.47	0.5853532	15.42
25	4.088137	2.66	0.6451231	15.78
26	3.530347	2.29	0.4945047	14.01
27	2.069806	1.34	0.4806208	23.22
28	4.645391	3.01	0.7338024	15.79
29	2.818290	1.83	0.5348858	18.98
XY	2.155577	1.40	0.6066958	28.15

Table 4: Somatic cell score chromosomal and percentage of additive genetic variance ($\sigma^2_{g_c}$), sums and percentage of σ^2_{SNP} expressed within each chromosome

Chromosome	$\sigma^2_{g_c}$	Percent of $\sigma^2_{g_c}$	σ^2_{SNP}	Percentage of σ^2_{SNP}
1	0.00430646	4.30	4.303804	10.87
2	0.004187921	4.18	4.185338	9.71
3	0.005375831	5.37	5.372517	9.55
4	0.003624394	3.62	3.622159	11.60
5	0.004442316	4.44	4.439576	10.01
6	0.008729612	8.72	8.724229	5.78
7	0.002808845	2.81	2.807113	12.55
8	0.003084699	3.08	3.082797	10.93
9	0.003505704	3.51	3.503542	10.29
10	0.004138860	4.13	4.136308	10.15
11	0.004055539	4.04	4.053038	10.36
12	0.003768344	3.77	3.76602	8.99
13	0.0032816	3.28	3.279576	9.95
14	0.00471315	4.71	4.710243	8.01
15	0.003633785	3.63	3.631544	9.51
16	0.004515698	4.52	4.512914	5.41
17	0.001848014	1.85	1.846874	15.56
18	0.003104134	3.10	3.102220	10.78
19	0.003416055	3.42	3.413949	11.82
20	0.005039948	5.04	5.03684	6.24
21	0.002203862	2.22	2.202503	13.02
22	0.001995208	1.99	1.993977	10.93
23	0.002767947	2.76	2.766240	9.25
24	0.002655585	2.66	2.653948	10.15
25	0.00127388	1.27	1.273094	16.25
26	0.001694897	1.70	1.693852	10.84
27	0.001586212	1.59	1.585234	12.70
28	0.0012938	1.29	1.293002	14.86
29	0.001447378	1.45	1.446485	14.61
XY	0.001562063	1.56	1.5611	17.44

Appendix II