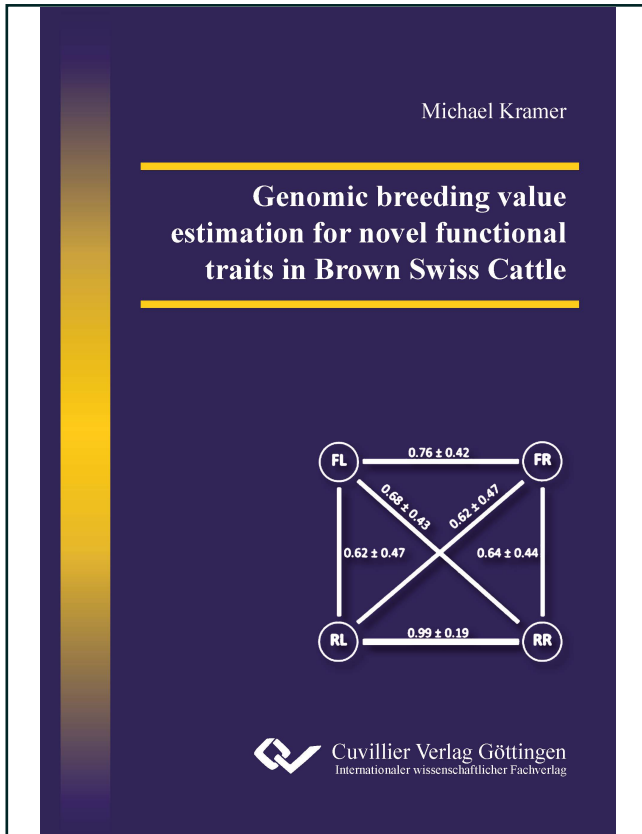




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Genomic breeding value estimation for novel functional traits in Brown Swiss Cattle



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daughters. With decreasing genotyping cost it might also be possible to estimate SNP effects from genotyped cows (possible in cooperator herds) and on basis of their phenotypic records. The SNP information generated from these animals is afterwards used to estimate GEBV for young genotyped bulls. The reliability of GEBV is much higher than the reliability of conventional EBV and so these young bulls can be bred to the complete population without any restrictions as soon as semen can be collected. This reduces generation interval on the bull sire path from 5 - 6 years to just one year. In this scheme, bull dams and bull sires might be preselected on the basis of SNP information, on basis of pedigree, on basis of phenotypic records or on basis of a mixture of these three sources of information.

In recent years, GEBV became well implemented in dairy cattle breeding all over the world and for most economically important breeds. In German Holstein breeding e.g. GEBV became official in August 2010. The last three years showed that GEBV are unbiased (Rensing, 2012). Table 1 gives a comparison between reliabilities (r_{TI}^2) of GEBV and r_{TI}^2 of conventional EBV from pedigree index for the German Holstein population.

Table 1: Reliability (r_{TI}^2) of pedigree index (PI), and genomic breeding value (GEBV) and daughter equivalent for different traits of the German RZG in German Holstein (Rensing 2012).

Breeding value	r_{TI}^2 PI (%)	r_{TI}^2 GEBV (%)	Daughter equivalent
Milk yield (RZM)	31	73	ca. 50, 3 MS ¹
Somatic cells (RZS)	31	76	ca. 85, 3 MS
Conformation (RZE)	28	57	ca. 25
Productive life (RZN)	26	52	ca. 100 1. La ² + 70 2. La
Daughter fertility (RZR)	25	43	ca. 80, 1. La
Calving ease paternal	33	53	ca. 40 calvings
Calving ease maternal	28	43	ca. 40 calvings
Milking speed (RZD)	24	61	ca. 30
Total merit (RZG)	29	65	

¹ Milk Sample

² Lactation

The pedigree index includes all information available from the pedigree for a young bull without daughter records and without SNP information. The GEBV at this stage does not contain information from daughter records either, but it does have pedigree information and additionally SNP information. Table 1 shows that the r_{TI}^2 of pedigree index varies between 25% and 30% for most of the traits. In contrast to this, r_{TI}^2 of GEBV varies on a



higher level between 40 and 76%. This is close to the r_{TI}^2 values which 6 year old bulls with their first daughters in milk achieve, although these young bulls with SNP information are just one year of age (Rensing, 2012). The highest gain in r_{TI}^2 is realized for milk yield and somatic cells (difference of 42% and 45% between r_{TI}^2 of GEBV and EBV). The smallest benefit is realized for daughter fertility and maternal calving eases (difference of 18% and 15% between r_{TI}^2 of GEBV and EBV). The gain of SNP information for breeding value estimation is better described by the number of daughter records which are needed to achieve the same r_{TI}^2 than from genomic information. To get an r_{TI}^2 of 73% (like the GEBV) for milk yield from progeny testing, milk records from three different test days from 50 daughters of a bull are required. This might be possible in short time after the first daughters of a young bull have calved. To get an r_{TI}^2 of 52% for productive life just from daughter records 100 daughters in first lactation and additionally 70 daughters in second lactation are required. This will take a long time and might be actually impossible for some sires. If SNP information is available, an r_{TI}^2 of 52% for productive life is already achieved for a young born bull calf. In this context it has to be mentioned that a GEBV always combines SNP information and several traditional sources of information. For a young sire this is SNP information and information from pedigree, with most weight on SNP information. With an increasing number of daughters in milk, more and more information from daughter records contribute to the GEBV and weight on information from daughter records increases. If just SNP information is considered (Chapter 4) the notation direct genomic value (**DGV**) will be correct.

The possibility to collect data for traits that are difficult to measure with reasonable accuracy within cooperator herds and the potential of genomic selection to estimate breeding values with high r_{TI}^2 for traits with low heritability and for young animals offer the chance to combine these two techniques in a modern breeding program. So in the past several years work was done to assess if there was economic benefit in the use of genomic selection at all, to assess this benefit within cooperator herds, and to develop strategies for finding the best suitable cooperator herds.



COOPERATOR HERDS IN DAIRY CATTLE BREEDING

Functional traits concerning health have become more and more important in dairy cattle breeding in recent years. Data recording on basis of the complete population delivered good results for production traits, but for functional traits an additional assessment of phenotypes is necessary (Bergfeld and Klunker, 2002). This could be done in a system of cooperator herds. Cooperator herds (or test herds) are herds that are contracted to breed cows to young sires and to collect numerous data with high accuracy. The majority of a population in a breeding program with cooperator herds is inseminated by proven bulls. Cooperator herds can thus basically be seen as a pool of nucleus herds. Swalve and König (2007) mention several advantages of cooperator herds. One of these advantages is that the capacity for testing can be ensured even if the proportion of AI decreases. The authors also think that additional phenotypes can be assessed if measurement is very time consuming or cost intensive such as feed intake, energy balance, the level of reproduction hormones or incidences of claw disorders. In a different study, König and Swalve (2006) found that the accuracy of breeding values for the low heritable trait laminitis ($h^2 = 0.14$) could be more than doubled if diagnostics of claw disorders from 50 daughters of a bull were available. This would be much easier in cooperator herds. Another advantage mentioned by Swalve and König (2007) is the fact that less doses of semen are required to ensure a specific number of daughters with records because herds are contracted to the breeding organization and so farmers are not allowed to sell a cow unless e.g. first lactation is finished. The authors also mention that young sires can be distributed to the herds very efficiently and that there is a better chance to implement methods of molecular biology such as QTL analysis or SNP technique in cooperator herds. There is also a positive marketing aspect if cooperator herds are visited by foreign customers of the breeding organization. Swalve and König (2007) also mention that there might be some concerns, such as a risk of genotype by environment interactions between cooperator herds and the majority of a population and that there is no independent organization for data recording. Nevertheless Swalve and König (2007) state that a system of cooperator herds is essential to use genomic selection efficiently.

As stated by König et al. (2008), herds where additive genetic variance and heritability of the traits under selection are highest should be chosen as cooperator herds. In these herds genetic differences between sires are most obvious. The authors found that heritability and additive genetic variance are significantly positively correlated to herd size and average milk yield of the herd. Heritability and additive genetic variance are further significantly



negatively correlated to average age at first calving and amount of unknown sires. Thus the authors conclude that large farms with high average milk yield and good management (low age at first calving and low amount of unknown sires) should be chosen as cooperator herds. In these herds, the best environments predominate and all cows have the chance to show their full genetic potential.

Estimation of variance components is a very time consuming method and genetic parameters on herd level have to be calculated separately. So Schierenbeck et al. (2011) propose a method to identify cooperator herds by clustering of daughter yield deviations (**DYD**). DYDs are defined as the average phenotypic yield of the daughters of a bull corrected for all fixed environmental effects and for all random genetic effects. They accrue as a co-product in routine breeding value estimation (VanRaden and Wiggans, 1991) and so no extra effort is need for calculation. Schierenbeck et al. (2011) found that daughters with extreme contribute to their sires DYD (either a very high DYD or a very low DYD) belong to herds with high average protein yield, low age at first calving, and low average SCS. Daughters with extreme DYD contribute are also often found in large herds, whereas the number of cows in the herd is not the only criterion if a herd should become cooperator herd. Schierenbeck et al (2011) also state that the low age at first calving reduced generation interval of the breeding program and that large cooperator herds have logistical advantages e.g. in terms of conformation classification or for DNA sampling.

As mentioned above, genotype by environment interactions might be a problem in a system of cooperator herds. König et al. (2005) found drastic differences between residual and permanent environment variance of milk production traits, but also high additive genetic correlations between 0.90 and 0.95 between herds in western and eastern Germany. This is a sign that genotype by environment interactions are small and thus could be neglected. Gernand et al. (2007) analyzed variance components for milk production traits in large and small herds with a focus on cooperator herds and also found no signs for genotype by environment interaction between large and small herds.



IMPLEMENTATION OF GENOMIC PREDICTION IN DAIRY CATTLE BREEDING PROGRAMS

Shortly after the theoretical basis for genomic selection was established by Meuwissen et al. (2001) and after the first SNP chips became available, Schaeffer (2006) examined from a theoretical point of view how genomic selection might influence dairy cattle breeding programs in regard to changes in genetic gain, generation interval, and economical aspects. For the Canadian Holstein industry, Schaeffer (2006) assumed costs of \$25 million per year for progeny testing of 500 young Holstein bulls in a conventional AI breeding program. This includes all costs for housing, feeding, semen production, and data recording. Assumed that 20 of these 500 bulls will return to AI, each of these bulls is burdened with costs of \$1.25 million. Selection intensity and generation interval on the four different pathways for the Canadian Holstein industry are shown in table 2.

Table 2: Selection intensity (i), accuracy (r_{TI}), and generation interval (L), as well as genetic gain in standard deviations (SD) on the four different pathways for conventional (conv) and genomic (genom) Holstein breeding programs in Canada (Schaeffer, 2006).

Pathway	Selection	i	r_{TI}		L		$SD (i \cdot r_{TI})$	
			conv	genom	conv	genom	conv	genom
Sire of bull	5%	2.06	0.99	0.75	6.5	1.75	2.04	1.54
Sire of cow	20%	1.04	0.75	0.75	6	1.75	1.05	1.05
Dam of bull	2%	2.42	0.60	0.75	5	2	1.45	1.82
Dam of cow	85%	0.27	0.50	0.50	4.25	4.25	0.14	0.14
Total					21.75	9.75	4.68	4.55

In total, a genetic gain of 4.68 genetic standard deviations (SD) is made within one generation, with a sum of generation intervals from all four path ways of 21.75 years in a conventional breeding scheme. So the genetic gain is 0.215 SD per year and costs per SD are \$116 million. Due to the high selection intensity and due to the high accuracy of estimates, the sire of bull path has the highest contribution to the genetic gain, but also the longest generation interval. The contribution of dams of cows is the smallest due to low selection intensity and due to low accuracy of EBV.

With the use of genomic selection, the values change fundamentally. The sum of generation intervals on the four pathways decreases from 21.75 years to 9.75 years, because GEBV of good accuracy are available at birth and so animals can be mated with onset of sexual maturity. The genetic gain per generation for a genomic breeding program also decreases slightly from 4.68 SD in a conventional breeding program to 4.55 SD , due



to the lower r_{TI} of genomic breeding values of 0.75 in contrast to 0.99 for conventional breeding values in the sire of bull path. On the other hand, the genetic gain on the dam of bull path increases from 1.45 SD to 1.82 SD in a genomic breeding program. Nevertheless a genomic breeding program will end up with a genetic gain of 0.467 SD per year, which is 2.17 times greater than the genetic gain of 0.215 SD from a conventional breeding program. Schaeffer (2006) calculates the annual costs for a genomic breeding program with \$1.95 million, which is just 7.8% of the annual costs of a conventional breeding program. This includes the costs for genotyping young bulls ($n = 500$) and elite dams ($n = 2,000$), buying the 20 best young bulls (\$100,000 each) and housing these bulls. Schaeffer (2006) also calculated costs of \$1.25 million for genotyping an initial sample of 2,500 which is essential for estimation of SNP effects. These costs can be depreciated for several years. In addition, a genomic breeding program causes fewer costs than the annual costs of \$25 million of a conventional breeding program, even if the initial sample has to be genotyped every year. Further advantages which Schaeffer (2006) mentioned are the higher quality of semen of young bulls which will result in a lower non return rate and less inbreeding because there is more weight on the dam of bull path. The dams of bulls should also be selected from completely genotyped cooperator herds, where additional phenotypes could be measured. This very early work of Schaeffer (2006) showed that genomic selection has a large potential for increasing genetic gain per year and for reducing costs of dairy cattle breeding.

In contrast to Schaeffer (2006), who estimated the benefit of genomic selection based on the formula of Rendel and Robertson (1950), König et al. (2009) evaluated economic gain of genomic breeding programs for different scenarios based on the gene flow method proposed by Hill (1974). König et al. (2009) also use a more sophisticated model which accounts for two traits (production trait and functional trait) with negative correlation and different heritability in the breeding goal. The scenarios represent different proportion of cows being inseminated by young bulls without daughter records, in order to simulate situations in which not all milk producers might be willing to use bulls without daughters in milk. Results of König et al. (2009) are mostly in line with Schaeffer (2006) concerning the selection response. In both studies selection response is almost doubled. But in contrast to Schaeffer (2006), König et al. (2009) did not find a reduction of costs by 92%, but rather by only 22.4% in the most advanced scenario for genomic selection. The authors also state that genomic selection has an economic advantage in contrast to conventional breeding schemes only if at least 20% of the cows are inseminated by young sires without daughter



records and that costs for genotyping have a minor impact on discounted profit per cow. König et al. (2009) state that the most crucial point for implementation of genomic selection will be whether farmers are willing to inseminate cows with semen of young bulls without any daughter records. König and Swalve (2009) found that the selection response can be increased especially for low heritable functional traits, if additional phenotypic records are available from daughters of young sires coming from cooperator herds.

SCOPE OF THIS THESIS

At the present time functional traits are becoming more and more important in dairy cattle breeding. Great hopes are being placed in the recent developments of genomics for finding economically feasible methods to estimate breeding values for these traits with low heritability. For this reason, it was the overall aim of this work to develop a method of genomic breeding value estimation for some novel functional traits in dairy cattle breeding. This was done using the example of the Brown Swiss population of Switzerland.

In chapter 2, genetic parameters, conventional breeding values and accuracies of conventional breeding values for novel traits concerning behavior/workability, conformation and fertility are estimated in order to deliver input data for a genomic breeding value estimation of these traits.

In chapter 3, genetic parameters for milk content traits on the udder quarter level are estimated in order to identify quarters of higher heritability for some traits, which should thus be given more weight in breeding value estimation or for finding an early indicator for mastitis.

In chapter 4, genomic breeding values were estimated on the basis of 777k SNP information for the traits examined in chapter 2. Commonly used methods to assess the accuracy of gEBV are said to lead to an overestimation of accuracy. So an advanced method that is based on the correlation between conventional breeding value on the one side and the correlation between genomic breeding value and conventional breeding value on the other side was implemented for some of the traits.



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