

**Estimation of Genetic Parameters and Evaluation of Breeding Program Designs with a
Focus on Dairy Cattle in Low Input Production Systems**

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SUMMARY

Due to restrictions on feeding and management on low input farms, there are vast differences between cattle on low input and conventional farms. Therefore, variance components of the same traits recorded in low input and conventional populations might be different. Even if the variance components were different, the necessities of setting up an overall breeding goal and implementing an own breeding program in organic production system are still open to further discussion. The first objective of this study was to estimate variance components of production, reproduction and health traits measured on Brown Swiss on low input farms in Switzerland. On the other hand, breeding strategies with consideration of genomic selection on both conventional and low input farms were compared by applying stochastic simulations.

Test-day data for milk yield (MY), fat percentage (Fat%), protein percentage (Pro%), lactose percentage (Lac%), somatic cell score (SCS), and milk urea nitrogen (MUN) were available on 1,283 cows kept in 54 small low input farms. For Gaussian distributed production traits mentioned above, a multi-trait random regression animal model (RRM) was applied with days in milk (DIM) as a time-dependent covariate. In general, daily heritabilities of production traits followed the pattern as found for high input production systems. Female fertility traits including number of inseminations (NI), stillbirth (SB), calving ease (CE), calving to first service (CTFS), days open (DO), and gestation length (GL) were analyzed with parity as a time covariate. Threshold methodology was applied for the first three traits. In most of case, heritabilities of reproduction traits were lower than 0.1. A threshold-linear sire model was applied to estimate daily correlations between MY, Fat%, Pro%, SCS, MUN and the binary distributed fertility trait conception rate (CR). Pronounced antagonistic relationships between MY and CR were in the range of -0.40 to -0.80 from DIM 20 to DIM 200. Estimated genetic parameters for reproduction traits were partly different from those estimated in high input production systems.

Phenotypic records for mastitis, metritis, retained placenta, ovarian cysts and acetonemia were available from the same cows as for production and reproduction traits, while the number of cows changed to 1,247. The five health traits were defined as binary data, categorical data and longitudinal binary data respectively. Binary data recorded between days in milk -1 and 120 were analyzed by linear models as well as threshold models with probit link function. Categorical data counted the total number of diseases during the same period and the data

were analyzed by linear models and Poisson mixed models respectively. The longitudinal binary data were analyzed by linear and threshold repeatability models and RRM respectively. Apart from moderate heritabilities for mastitis (0.32) and retained placenta (0.39), heritabilities were generally low for binary and categorical traits. Repeatabilities and heritabilities of longitudinal traits estimated from repeatability models were also low. The highest daily heritabilities for all health traits were found at the beginning of lactation and at the end of the defined interval. Generally, threshold models were favored by a low Bayesian information criterion except threshold RRM.

A stochastic simulation study was carried out with a focus on an application of genomic selection in dairy cattle breeding programs, to compare true breeding values (TBV) from a variety of selection schemes. Heritability of trait of interest was low (0.1) or moderate (0.3) and genomic estimated breeding value (GEBV) was imitated by the defined accuracy, which was between 0.5 and 0.9. Three breeding strategies were simulated in total, including selection of bull calves based on pedigree index, genotyped parents and genotyped bull calves themselves. A variety of scenarios were assumed within last two breeding strategies, indicating different pre-selection criteria for each strategy. Schemes of genotyping parents of the future bulls were similar with the classical young bull program, but TBV from these schemes were competitive or superior. The highest average TBV was found to be in scenarios of genotyping young male candidates. Only if the pre-fined accuracy of GEBV was greater than 0.5, TBV of the idealistic scenario, genotyping all male calves, was competitive with scenarios of genotyping pre-selected male calves based on estimated breeding values (EBV) of bull dams or the average GEBV of bull parents. Hence, genotyping young male candidates should be most suitable strategy for breeding organizations.

In the forth part of this thesis, another stochastic simulation was applied to compare TBV and inbreeding coefficients of organic breeding program designs. Basically, three breeding strategies were simulated: i) selection of sires from conventional population with consideration of genotype by environment (G x E) interactions, ii) selection of genotyped sires from the low input population for AI, iii) selection of genotyped nature service sires (NSS) in each of the organic herd. Heritabilities of the simulated traits were 0.05 and 0.3 respectively. The G x E interactions were realized by considering genetic correlations between traits of interest recorded in different environments ($r_g = 0.5$ to 1). GEBV were generated with accuracy (r_{mg}) between 0.5 and 1. The average TBV of the 5 best genotyped

AI sires from organic environment was always higher than selection of sires from conventional population on EBV. If the selection criterion was GEBV in both environments, $r_g \leq 0.80$ is the general threshold favouring selection in the organic population. Genotyped NSS were competitive with selection of sires based on EBV in conventional population, only if the significant G x E interactions ($r_g = 0.5$) was existed between two environments and accuracy of genotyped NNS was high ($r_{mg} \geq 0.9$). Inbreeding of selected sire and their progeny could be reduced when using genomic breeding program.

1st CHAPTER

GENERAL INTRODUCTION

Preface

The amount of animal products, i.e. milk and meat production, increased continuously in the past four decades. 305-d lactation milk yield was doubled from the middle of last century to 2008 for the Holstein, Ayrshire and UK Jersey cattle (CDI, 2011). However, because of the negative genetic relationship between production traits and functional traits, high intensive selection of milk production traits in the recent decades has resulted in a decline in female fertility and in dairy cattle's health status. Consequently, animal products with better quality and animals with higher welfare will probably meet the demands of customers in future. Low input or organic farming is a production system that strongly focuses on animal health and healthy products and in the meantime maintains a high level of animal welfare. Therefore, breeding goals and breeding strategies might be different compared to conventional dairy cattle breeding schemes. The pre-requisite for implementing an own organic breeding program and for evaluating different breeding program designs is the availability of genetic parameters for all traits of interest. Apart from definition of a breeding goal, breeding program design for organic farming also plays an important role and some particularities should be considered in the design, e.g. the importance of natural service sires. Another important part when defining breeding strategies is to control inbreeding and genetic relationships, because organic populations generally are characterized by a small population size.

Low input or organic farming

Due to a considerable number of crises of animal products from the 1980s, e.g. *Salmonella*, *Escherichia coli*, tuberculosis, swine fever, and foot and mouth disease (Kirk and Soffe, 2002), the concept of organic farming has become more and more popular. The increasing organic production is mainly based on consumers' demands, because consumers believe that animal products produced from organic production systems are more healthy. The demand for organic products increased dramatically after 1990, however the stability of the market has not been reached yet. The European Union statistics shown that the growth of organic farming has been consistently around 25% per year in the decade from 1990 to 2000 (Rosati and Aumaitre, 2004). A relatively fast increase of organic industry can be observed in the United States as well. For example, the organic industry grew to over \$28.6 billion and the growth rate of the industry was nearly eight percent in 2010 (U.S. Organic Industry Overview. 2011).

The basic rules of organic animal farming have been standardized in the guidelines of the Council Regulation (EC, 1999) and of the International Federation of Organic Agriculture Movements (IFOAM, 2000). Different from conventional production systems, organic farming has a high priority in maintaining genetic diversity of agricultural system and its surroundings. Animals should perform all kinds of their innate behavior in this production system. For example ruminants should be kept outside with access to pasture, and reproduction technologies are forbidden except artificial insemination. "Genetic modifications" of animals and their products are prohibited as well (von Borell and Sørensen, 2004). Additionally, local breeds with high disease resistance are prior to all the other breeds for feeding in organic farming. Antibiotic treatments and chemical applications are strictly restricted in organic farming systems.

In contrast to organic farming, low-input farming systems do not have any official definition. In the explanation by Parr et al. (1990), the low input farming systems are those who *“seek to optimize the management and use of internal production inputs (i.e. on-farm resources)... and to minimize the use of production inputs (i.e. off-farm resources), such as purchased fertilizers and pesticides, wherever and whenever feasible and practicable, to lower production costs, to avoid pollution of surface and groundwater, to reduce pesticide residues in food, to reduce a farmer's overall risk, and to increase both short- and long-term farm profitability.”* However, based on the report by Elbersen and Andersen (2007), specifications for the three types of "alternative farming" a) the low input system, b) the organic systems, and c) the high nature value system overlap (Figure 1). In this thesis, low input farming represents the organic farming to some extent.

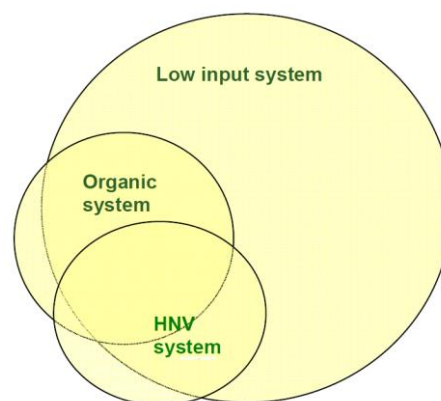


Figure 1. Impression for the overlapping elements between the low input system, the organic system, and the high nature value (HNV) system (Elbersen and Andersen, 2007).

Switzerland has about 4 million hectares land area, of which 1.7 million are grass. Among the grass land, 1 million hectares area is Alpine pastures and 0.7 million hectares are meadows and pastures. Therefore, increasing organic farming should be an economic alternative in Switzerland, because it can utilize the relatively remote mountainous area for producing high quality food. Figure 2 (Schmid et al., 2007) shows that there are two countries with more than 10% organic area in the whole cultivated land in Europe, which also demonstrates that organic farming is more important in Switzerland and Austria than in other European countries. All the raw data in this thesis were recorded on approximately 1200 Brown Swiss cows located in the mountainous region in Switzerland. The cows came from 50 farms characterized by small herd size. Parameters of the simulated low input population in Chapter 5 were also defined based on the characteristics of the Brown Swiss dairy cattle population.

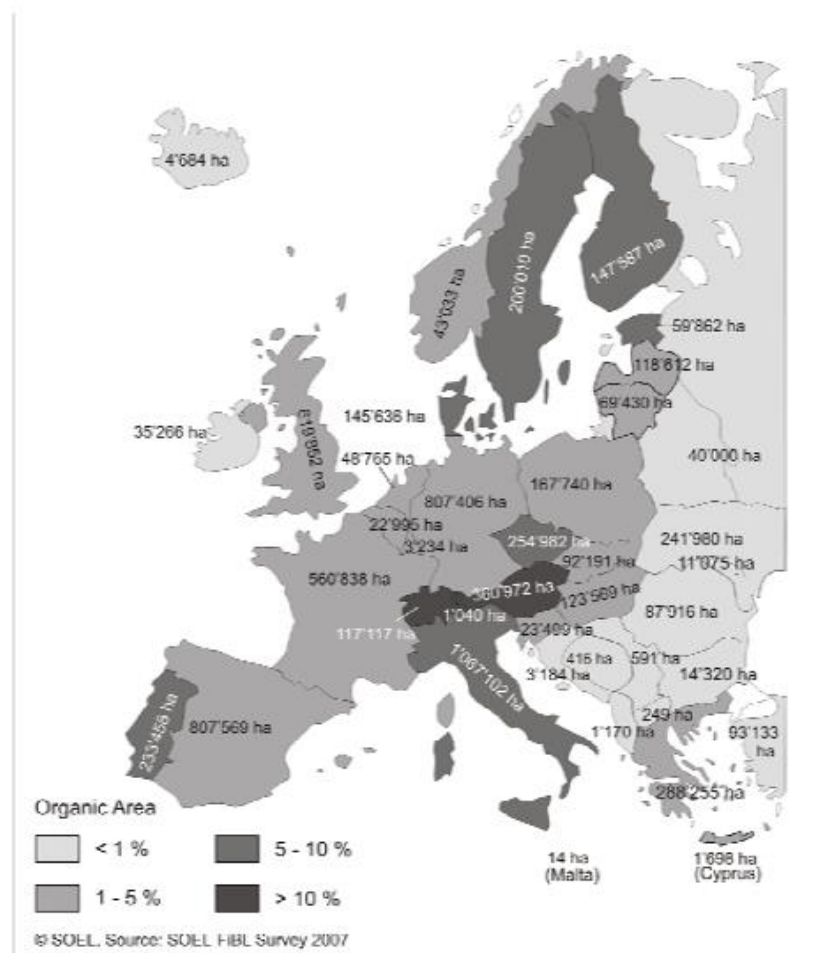


Figure 2. Area of organically cultivated land in Europe in 2005 (adopted from Schmid et al., 2007).

Organic breeding programs

Generally, fully developed breeding program designs based on artificial insemination are implemented in the conventional dairy cattle industry. Due to large daughter groups for progeny testing, milk and protein yield increased dramatically after a long term of breeding starting in the 1960s. However, no systematic breeding program has been built in organic dairy population. The first decision one has to make is whether to set up an own organic breeding program or using sires from the conventional population. Many questions and difficulties should be considered before making this final decision. For example, based on the regulations of organic farms, local breeds are preferred because they are more suitable for the local nature environment, however, a lot of the current organic farms converted directly from conventional farming by keeping the commercial genetic material and the same breeding strategies. Moreover, some farms use crossbreeds rather than just one pure breed, because hybrids have higher adaptability as well as production yield.

Embryo transfer is completely forbidden in organic production systems, while AI is allowed although it goes against the natural behavior of animals. Some farmers using AI recognized that it disobeys the naturalness of mating behavior, but there is no practical alternative available (Nauta et al., 2005). Because, on the one hand, keeping bulls in the farms is expensive and many farmers do not have enough knowledge on selection and kin-breeding in their own farms. On the other hand, completely abandoning AI service means organic farmers can not take advantage of a long and successful breeding achievement in conventional breeding programs. Even though a distinct breeding program was established in the organic production chain, with limited number of cows per farm and incomplete data recorded in organic farms, genetic components and estimated breeding values (EBV) could not reach the accuracy compared to the conventional dairy breeding programs. Therefore, it might be necessary to apply other selection criteria or new breeding technologies (such as genomic selection) in organic production systems.

Basically, there are three possible breeding scenarios for organic farmers. The first scheme is to use AI bulls from current world-wide breeding schemes as service sires in organic farms. Nevertheless, the re-ranking of sires might be caused by different breeding goals and the genotype by environment interactions (G x E) between conventional and organic populations, which means that sires selected based on data recorded in conventional population may not

meet the requirements in organic farms. Secondly, several AI bulls can be selected directly within the organic production systems on the base of organically data. Severely speaking, AI is also infringed by the spirit of naturalness advocated in organic farming. Therefore, an alternative can be selection of several natural service (NS) sires based on kin-breeding within each herd or a certain region, and to use these sires evenly to avoid mating of close relatives (Baars, 2002). Nauta et al. (2005) reported that the impact of NS sires in the organic cow population in The Netherlands is relatively low and should be extended. The authors focused on the necessity to formulate an own breeding goal and to implement specific breeding program designs for organic farming.

Breeding goals

The breeding goal is a main foundation for setting up breeding programs, and it is achieved by adding traits related to the overall breeding goal using weighting factors derived by applying selection index theory. Certainly, the importance of traits is determined by the value of relationship between the traits and the breeding goal (Falconer and Mackay, 1996). Over a long period, the breeding goals in conventional dairy farming systems focused on increasing outputs of dairy cows, which inferred higher income per cow. However, at the beginning of the 21st century, there has been a growing interest in broadening selection indices to include functional traits such as reproduction and health (Miglior et al., 2005). However, to improve functional traits by breeding is really difficult, because additive genetic variances and heritabilities for functional traits are low. For example heritabilities for female fertility traits ranged between 0.01 and 0.07, and for longevity from 0.02 to 0.18 (Mark, 2004). Additionally as a further problem, some of the functional traits are difficult to measure on farms in the whole population. Using a small number of phenotypic data collected from experimental stations only result in low accuracies of EBV. In some cases indirect selection is applied to improve functional traits, while physiological and genetic relationships between indicator and functional targeted traits should exist. For example, somatic cell count is an indicator trait for udder health, and in a limited number of studies food intake and body weight are collected to improve efficiency of feed utilization. Nevertheless, relatively low heritabilities combined with indirect selection for functional traits cause the genetic progresses in functional traits to be small and slow.

In general, organic farming is defined as an animal and environment friendly production system, so it focuses more on the functional traits than conventional production systems. From a survey conducted by Nauta et al. (2009) on 151 organic farms in The Netherlands, the overall breeding goal focused more on functional traits (43%) than on production (32%) and conformation traits (25%) in the overall breeding goal. Within the category of functionality, udder health was ranked in the first place, followed by fertility, animal behavior, and calving ease. However, there are conflicts within the organic farming systems as well. In order to meet the increasing demands for organic products from consumers, some organic farmers also expect that their organic cows produce more milk. Other farmers prefer dual purpose breeds and increased milk quality, because they switched into "a niche" such as cheese production, establishing farm gate shops (i.e. milk and meat products), or natural development and conservation (Nauta, 2009). Although health and fertility have a high priority in organic farming, the health and fertility status of cows in organic farms (Hovi et al., 2003; Vaarst et al., 2003) is almost the same as cows kept in conventional farms (Sandoe et al., 1999). This might result from the extreme limitation on the use of pharmaceuticals and chemicals which help problematic cows cure health diseases (Nauta, 2009).

Genotype by environment interactions

A major problem when using conventional AI service sires in organic dairy farms is the magnitude of G x E interaction between organic and conventional farming systems. The G x E interaction is a phenomenon that different genotypes express differently in different environment. To prove G x E via analysis of variance, the phenotypic variance is partitioned into a genetic component, an environmental component, and a genotype by environment interaction. In dairy cattle, genetic connectedness across production systems is better than in poultry or in swine because of a wide application of AI. Therefore, in dairy cattle, genetic correlation between traits measured in different environments is employed to quantify the magnitude of G x E interactions (Falconer and Mackay, 1996). In 1959, Robertson proposed that a genetic correlation lower than 0.8 indicates G x E interactions and re-ranking of sires in different environments. Moreover, significant G x E interactions or low correlations between the same trait in organic and conventional farming systems (i.e. milk yield in environment A and in environment B) suggest that genetic material coming from conventional dairy breeding programs would not perform well in organic farms.

It is imperative to investigate G x E interactions between the two farming systems, because a lot of organic farmers still use AI bulls of commercial breeds from breeding companies until now. Nauta et al. (2006) reported that genetic correlations between organic and conventional production for milk, fat and protein yield in the Netherlands were 0.80, 0.88 and 0.71, respectively. Therefore, milk as well as protein yield were genetically different traits in the two environments. However, the correlations were close to unity for fat percentage, protein percentage and somatic cell score (SCS). Nauta et al. (2006) also found that a correlation of 0.80 for milk production results in a re-ranking of the top 10 breeding bulls. Berry et al. (2003a) found a low genetic correlation of 0.63 for milk yield between high and low concentrate feeding level groups in Ireland as well. Wallenbeck et al. (2009) reported Spearman rank correlations between organic and conventional EBV of values 0.48 and 0.42 for growth rate and carcass leanness, respectively, for Swedish pigs.

It is predicted that the G x E interaction will increase with increasing differences between conventional and organic farming systems. The differences might extend via two aspects. First, standards and managements of organic farming will be more severe in the future. For example, only concentrates with at least 95% organic ingredients can be used in European organic farms since 2005. To reduce the cost for feeding organic dairy, more farmers would choose roughage to replace the concentrates (Nauta et al. 2006). It will probably widen the gap between the two production systems. Second, number of crossbreeds or local breeds adapted to naturalness of organic farms will have a further increase, which will result in a decline of genetic correlations of traits expressing in the two environments.

Inbreeding

The coefficient of inbreeding gives the probability that two alleles at any locus in an individual are identical by descent (Falconer and Mackay, 1996). Inbreeding is accumulating rapidly in most commercial livestock species due to efficient genetic selection programs (Weigel, 2001). Farmers from both organic and conventional production systems are concerned about inbreeding depression that results from the high inbreeding rate. Inbreeding depression is a phenomenon that reduces the mean phenotypic value of traits related to reproduction capacity or physiological efficiency (Falconer and Mackay, 1996). However, the improvement of functionality including reproduction capacity and physiology efficiency and the conservation of genetic diversity are the most important aspects in overall breeding goal in

organic farming systems. Therefore, it is necessary to take inbreeding coefficients seriously into account in the management of organic production systems.

Inbreeding may increase more rapidly in organic systems than in conventional dairy farming for two reasons. Firstly, the traits of interest in organic farming often have low heritabilities. Selection of traits with low heritabilities could increase inbreeding rapidly due to higher weight on family versus individual information (Strandén et al., 1991). Secondly, NS is preferred in organic farms. Selection of NS sires based on families is expected to increase inbreeding despite the fact that more than one sire may be kept as NS sire in each of the organic farms. In addition, the herd size in organic farms is usually very small in comparison with conventional dairy farms, which should also increase the accumulation of inbreeding. In organic breeding schemes, it is important to find a satisfactory balance between the degree of inbreeding, improvement of desirable traits and mating designs.

With the availability of high-density arrays of SNP markers, inbreeding coefficient can be calculated based on pedigree information and genome-wide SNP data (Li et al., 2011; VanRaden et al., 2011). It has been found that inbreeding was lower in breeding schemes with genomic information (Buch et al., 2012a). The reason is probably that the EBV is predicted based on information of relatives, and close relatives may have higher chance of getting the same allele coming from the common ancestor. Pedersen et al. (2009) reported that marker-assisted selection can reduce probabilities of identity by descent as well as pedigree-estimated inbreeding. Nevertheless, when selection is based on breeding values predicted from genomic data, control of inbreeding should also be done at the genomic level, i.e., taking genomic inbreeding into account (Sonesson et al. 2012). However, the aim of selection is to improve performance of traits of interest, so frequency of favorite alleles of QTL controlling these traits will increase in the long term.

Functional traits and new traits

The term functional traits represent all the traits which increase efficiency by reducing costs of input. Traits like health, fertility, calving ease, efficiency of feed utilization, and milkability belong to the class of functional traits (Groen et al., 1997). Some functional traits have already been included in the selection index in many breeding programs, e.g. fertility and SCS. Due to the development of new phenotyping technologies, some new traits such as efficiency

of feed utilization and more health traits are also expected to be added into selection indices. However, genetic gains for functional traits can hardly be detected in conventional dairy farming systems. The most important reasons for that are the negative genetic correlations between milk production and functional traits (Berry et al., 2003b; Pimentel et al., 2010), and the higher economic weights were put on production traits. Furthermore, low heritabilities of some functional traits, which lead to a lower selection accuracy, also contribute no or negative genetic gain for the functional traits.

In order to meet naturalness in organic farming systems, higher emphasis is put on functional traits rather than milk production traits (Nauta et al., 2009; Rozzi et al., 2007). The effects of negative genetic correlations between functional and milk production traits decline because generally functional traits have higher economic weight in organic farms. However, although some special sires have an ‘ecological index’ (cited from Nauta et al., 2005), almost all AI bulls used in organic farms are chosen with no or only little concern on functional traits. Due to the small size of organic herds, EBVs of organic bulls usually have low accuracy. Moreover, real occurrence of diseases in organic farms may be higher than the recorded treatments because of limited usage of medicine. This will probably introduce some bias on the accuracy of selection and EBV. Actually, systematic breeding strategies for organic farming are not established because no clear breeding goal has been agreed upon and the number of prerequisite parameters is limited.

Introduction of genomic selection into organic farming might solve the problem of the low accuracy for functional traits caused by low heritability. Buch et al. (2012a) reported that breeding schemes with genomic selection resulted in higher annual genetic gain in functional traits than breeding schemes without genomic selection. Buch et al. (2012b) also showed that the accuracy of direct genomic values was higher for a reference population of cows with phenotypic records than for a reference population of proven bulls with daughter yield deviations if a functional trait with small-scale recording was examined. Therefore, introduction of genomic selection into organic farming systems may be a beneficial approach.

Objectives of the thesis

This thesis aims to estimate genetic parameters of traits of interest using data recorded in low input Brown Swiss farms in mountainous region in Switzerland and meanwhile to compare

differences of genetic gain and inbreeding coefficient between applying own organic breeding programs and using AI bulls from conventional breeding schemes.

In chapter 2, heritabilities of production traits and genetic correlations between milk yield and other production traits were estimated with a multivariate animal random regression model using days in milk as a time-dependent covariate. Eight reproduction traits were also analyzed: age at first parity, interval from calving to first service, days open, gestation length, calving interval, calving ease, number of inseminations and stillbirth. Reproduction traits were analyzed with linear or threshold sire random regression models using parity as a time covariate. In addition, genetic correlations between conception rate and production traits were estimated in the first two thirds of the lactation.

Chapter 3 gives an insight into the genetic background underlying five health traits: mastitis, metritis, retained placenta, ovarian cysts and acetonemia. Animal/sire, repeatability and random regression models were used to estimate genetic parameters. Heritabilities of the health traits varied from different models and traits, but they were lower than 0.1 in most cases.

Chapters 4 and 5 compare a variety of breeding scenarios with the consideration of genomic selection. The evaluation criteria employed in the two simulation studies performed in these chapters were the average of true breeding values and inbreeding coefficients of selected sires. Chapter 4 focuses on modifying and re-building breeding programs to use accurate information from genomic selection efficiently in conventional dairy populations. Chapter 5 investigates possibilities of applying own organic dairy cattle schemes.

A general discussion of the thesis is presented in Chapter 6. Implications of breeding schemes in organic farming systems are discussed based on genetic parameters of routinely recorded traits estimated in Chapters 2 and 3 and genetic gain in conventional and organic dairy populations simulated in Chapters 4 and 5.

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2nd CHAPTER**Genetic Parameters for Gaussian and Categorical Traits in Organic and Low Input Dairy Cattle Herds based on Random Regression Methodology**

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ABSTRACT

Organic and low input farming differ substantially from conventional farming, suggesting the need for separate breeding programs. This requires knowledge of (co)variance components of important traits in low input or organic production systems. Test-day data for production and data for reproduction traits from 1,283 Brown Swiss cows kept in 54 small, low input farms across Switzerland were available. Production traits milk yield (MY), fat percentage (Fat%), protein percentage (Pro%), lactose percentage (Lac%), somatic cell score (SCS), and milk urea nitrogen (MUN), were analyzed with a multi-trait random regression animal model with days in milk (DIM) as a time covariate. Female fertility traits number of inseminations (NI), stillbirth (SB), calving ease (CE), calving to first service (CTFS), days open (DO), and gestation length (GL) were analyzed with parity as a time covariate, with threshold methodology was applied for the first three traits. A threshold-linear sire model was applied to estimate daily correlations between MY, Fat%, Pro%, SCS, MUN and the binary distributed fertility trait conception rate (CR). In general, daily heritabilities for production traits followed the pattern as found for high input production systems. Expected genetic antagonisms were found between MY and Pro%, and between MY and Fat% for all DIM. An antagonistic relationship between MY and SCS was only found directly after calving in parity 1. In parities 2 to 7, heritabilities for an interval trait describing the cows' ability to recover after calving, e.g. CTFS, were lower than estimates for traits associated with a successful insemination, e.g. NI and DO. Pronounced antagonistic relationships between MY and CR were in the range of -0.40 to -0.80 from DIM 20 to DIM 200. In this study, we showed the variety and flexibility of random regression methodology which can be applied to data from small herds, and for a limited number of repeated measurements of a categorical trait per cow. Estimated genetic parameters for reproduction traits were partly different from those estimated in high input production systems. In particular, these differences underline the necessity to implement an own organic breeding program using estimates from the current study which are based on data obtained only from cows in organic or low input herds.

Key words: Organic and low input farms, random regression models, genetic parameters

INTRODUCTION

Traditionally, conventional dairy cattle farming have focused on improving productivity of cows while functional traits were neglected. Based on arguments from the genetic point of view, e.g. antagonistic relationships between productivity and functionality (e.g. Pimentel et al., 2010), and based on results from studies that derived economic weights (e.g. Schierenbeck et al., 2009), functional traits have been included gradually and increasingly in total net merit indices (Miglior et al., 2005). Unidirectional selection on productivity in the past decades resulted in a negative energy balance with detrimental impact on fertility and health (Rauw et al., 1998). Conventional farmers can compensate such energy deficiencies in early lactation by feeding concentrates or specific energy components (e.g. glycerin), but organic farmers have to follow strict rules and limitations that may not permit the use of such supplements. Furthermore, an increased amount of consumers are concerned about product quality, animal welfare and environmental impact. Traditionally, functional traits play an important role in organic or low input dairy cattle farming (Rozzi et al., 2007). The concept of organic farming focuses on the sustainability of agro-ecological systems. There are strict limitations on the use of pharmaceuticals and chemicals in organic farming, and diversity, animal welfare and the ability to adapt to the local environment are highly appreciated (Boelling et al., 2003).

With the increased demand for organic dairy products, the number of organic farms is rapidly growing in some European countries (Haskell et al., 2009; Nauta et al., 2006). Also, in the United States, organic sales have been steadily increasing and reached an economic value of \$24.6 billion in 2008 (Organic Trade Association's, 2009). During the process of conversion from conventional to organic farming, management practices (e.g. husbandry and feeding) are changed while mostly maintaining the general breeding strategies. In particular, this means that sires from conventional progeny testing schemes are used breeding objectives in organic production systems. However, because of substantial differences in production systems, and including further restrictions on feeding, husbandry and management in organic and low input environments (Roesch et al., 2005), genotype by environment interactions between conventional and organic production systems may exist (Nauta et al., 2006). This phenomenon may result in re-ranking of bulls in organic environments having been progeny tested in conventional herds. Re-ranking of bulls suggests the implementation of an own genetic evaluation for the organic and low input population, and furthermore, the initialization of an own organic breeding program.

Mulder et al. (2006) identified the genetic correlation between two production systems as a crucial parameter for the need of two different or of one common breeding program. The threshold value of the genetic correlation in their simulation study was $r_g = 0.61$. Yin et al. (2011) evaluated the potential of independent organic breeding programs in the era of genomic selection. Again, crucial factors were genetic correlations of the same traits recorded in conventional and organic production systems, and accuracies of genomic breeding values for natural service sires. According to Schmidtko (2007), further arguments for implementing own organic breeding programs address general aspects of breeding program designs, especially the utilization of reproduction biotechnologies such as artificial insemination, embryo transfer, and sexed semen. Substantial differences in feeding, breeding, and husbandry strategies may cause substantial differences in phenotypic performances. Comprehensive comparative studies pointing at differences for a broad variety of traits was done by Sundberg et al. (2009) and by Reksen et al. (1999).

Traits in organic breeding goals comprise all conventional traits, but place a higher emphasis on functionality (Schmidtko, 2007). Furthermore, organic farmers in Switzerland request that new health traits should be included in overall breeding goals. A variety of such traits currently recorded in organic farms within the framework of the 'low input breed' project is mostly in line with a list of new functional traits as described by Mark (2004). An essential prerequisite for the implementation of genetic evaluations in organic breeding programs for both categories of traits, i.e. the 'conventional' and the 'new functional' traits, are estimates of genetic parameters based on phenotypes from organic herds. Genetic parameters may change during an animals' lifetime based on changes in the physiological background. Such changes in genetic parameters can be modeled using random regression methodology (Swalve, 2000; Schaeffer, 2004).

Consequently, the aim of the present study was the estimation of (co)variance components of both production and female reproduction traits for Brown Swiss cows kept in organic and low input farms in different regions in Switzerland. Different statistical models with a focus on random regression methodology combined with threshold methodology for different types of longitudinal data were applied to this particular dataset comprising organic or low input farms with small herd sizes.

MATERIALS AND METHODS

Data

The original production trait dataset comprised 36,877 test-day records from 1,283 Brown Swiss cows kept in 54 (organic and low input) farms from different regions of Switzerland. Both organic and low input farming strategies are characterized by limitations on the use of feeding concentrates, using antibiotics and hormones, and putting strong emphasis on animal welfare in alternative production systems. In contrast to low input farming, 'organic' is an official farming status which implies that organic farms have to follow official guidelines mainly related to restrictions in feeding and dairy cattle husbandry, whereas 'low input' is less stringent and on a voluntary base. Average herd size was extremely small, i.e. only 24 cows per herd with in average 9.79 observations per herd-test-date. Average number of records per cow per lactation was 8.10, 8.41, and 8.07 and number of cows per lactation was 1,283, 920, and 694 for parity 1, 2, and 3, respectively. Restrictions for data editing were adopted from the official genetic evaluation for Brown Swiss cattle in Switzerland as summarized in Table 1. Descriptive statistics for all test-day production traits (MY = milk yield, Fat% = fat percentage, Pro% = protein percentage, Lac% = lactose percentage, SCS = somatic cell score, MUN = milk urea nitrogen measured in mg/dl) by parity after editing are given in Table 2.

Test-day production data from calving years 1996 to 2010 have been merged with female fertility traits data. Data editing for female reproduction traits (AFC = age at first calving, CTFS = calving to first service, DO = days open, GL = gestation length, CI = calving interval, NI = no. of insemination, CE = calving ease, SB = still birth, and CR = conception rate) were also based on restrictions that are used for official genetic evaluations (Table 1). The minimum CI in our data was 296 days, and 240 days as defined as official minimal criterion did not apply. In addition to those limits, gestation length was required to range between 240 d to 300 d (Jamrozik et al., 2005). Descriptive statistics for female reproduction traits are shown in Table 3. Number of records in higher parities were relatively small, e.g. for CTFS, no. of records were 1,273, 1,008, 749, 520, 399, 269, 164, and 104 for parities 1 to 8, respectively. For both trait complexes, production and female fertility, pedigrees were used from the official genetic evaluation which traced back four generations.

Table 1. Restrictions as used for data editing

Criterion	Minimum	Maximum
Days-in-milk	5	365
Milk yield (in kg)	1.5	90.0
Fat %	1.50	9.00
Protein %	1.00	7.00
Somatic Cell Count (in thousand)	1	9999
Calving Interval (in d)	240	Open ¹
Calving Age for n-th lactation (in month)	17+11*(n-1)	50+18*(n-1)
Calving Date for 1 st lactation	01.01.1989	Open ¹
Calving Date for 2 nd lactation (missing 1 st .lactation)	01.01.1994	Open ¹
Calving Date for 3 rd lactation (missing 2 nd .lactation)	01.01.1995	Open ¹

¹ No restriction for maximal value

Statistical Models

Model 1: Time dependent covariate (DIM) for production traits

For production test-day records (MY, Fat%, Pro%, Lac%, SCS, MUN), a multiple-trait random regression model (RRM) was used simultaneously for parities 1, 2, and 3. Following the method of Bohmanova et al. (2008), test-day data were from 5 to 365 days in milk (= time dependent covariate DIM). In matrix notation, model 1 can be described as:

$$y = Xb + Z_1u + Z_2p + Z_3h + e, \quad [1]$$

where y = vector of observations for test-day records; b = vectors of fixed effects of herd-year, and regressions on DIM using third-order Legendre polynomials for all traits; u and p = vectors of additive genetic, and permanent environmental effects, respectively, for random regression coefficients of order three using Legendre polynomials; h = vector of random herd-test-date effects, and e = vector of random residual effects (residuals were equal for all DIM but not for parities); and X , Z_1 , Z_2 , and Z_3 = incidence matrices for b , u , p , and h , respectively. The variance-covariance structure of the random effects was assumed as

$$\text{var} = \begin{bmatrix} u \\ p \\ h \\ e \end{bmatrix} = \begin{bmatrix} G \otimes A & 0 & 0 & 0 \\ 0 & P \otimes I_p & 0 & 0 \\ 0 & 0 & H \otimes I_h & 0 \\ 0 & 0 & 0 & R \otimes I_n \end{bmatrix}$$

where G and P = (co)variance matrices of random regression coefficients for the genetic and permanent environmental effects, respectively; A = additive genetic relationship matrix; I_p = identity matrix for p cows; H = matrix for herd effects, I_h = identity matrix for h herds; I_n = identity matrix for n observations, R = (co)variance matrix for residual effects of dimension 3×3 with random residual variances for parity 1, 2, and 3, and \otimes = direct matrix product.

Following Tsuruta et al. (2009), independent proper priors based on a uniform distribution and no degrees of freedom were assigned to elements in vector b . For elements in vectors h , u , and p , multivariate normal prior distributions were assumed. Independent scaled inverse Wishart distributions were used as priors for the (co)variance matrices for H , U , P , and R .

Model 2: Time dependent covariate (parity) for female reproduction traits

Model 2 was similar to the multiple animal RRM for production traits, and applied for the female reproduction traits dataset (CTFS, DO, GL, CI, NI, CE and SB). However, without repeated measurements within lactation, parity was used instead of DIM as a time dependent covariate. In this RRM, vector b included fixed effects of the herd, calving age, calving year, and calving season (1 = December-February, 2 = March-May, 3 = June-August, and 4 = September-November). Additionally, the effect of the service sire (for DO and CI), and accordingly of the sire of the calf (for CE, and SB), was included as a further random effect in the statistical model. Hence, for these traits, the (co)variance structure of the random effects was extended as follows:

$$\text{var} = \begin{bmatrix} \mathbf{u} \\ \mathbf{p} \\ \mathbf{s} \\ \mathbf{e} \end{bmatrix} = \begin{pmatrix} \mathbf{G} \otimes \mathbf{A} & 0 & 0 & 0 \\ 0 & \mathbf{P} \otimes \mathbf{I}_p & 0 & 0 \\ 0 & 0 & \mathbf{S} \otimes \mathbf{I}_s & 0 \\ 0 & 0 & 0 & \mathbf{R} \otimes \mathbf{I}_r \end{pmatrix}$$

where S is a sire (co)variance matrix of service sire (for CE) or sire of the calf (for SB), and I_s is the belonging identity matrix. For categorical traits with only one (SB: 1 = stillbirth, 0 = calf alive), or several thresholds (CE: 1 = no assistance, 2 = some assistance, 3 = mechanical assistance, and 4 = caesarean section), threshold methodology was applied.

Model 3: Time dependent covariate DIM for one female reproduction trait

Because in general, and also cows in this study have a limited number of observations for CR (0 = cow was not pregnant after insemination, 1 = cow was pregnant after insemination) in one particular time interval in first parity. The average no. of inseminations per cow in the time interval was 3.07 ± 1.56 . The RRM can extract genetic parameters for each day through the connections created by sires. Hence, a series of bivariate two-trait threshold-linear random regression sire models were applied to estimate (co)variance components over DIM for one categorical fertility trait (CR) and for the five Gaussian test-day production traits (MY, Fat%, Pro%, SCS, MUN) in parity 1. The date of the insemination was assigned to the nearest herd-test-date, and consequently, we selected test-days with a corresponding insemination date for statistical analyses. The statistical model 3 in analogy to Tsuruta et al. (2009) was:

$$\begin{bmatrix} \mathbf{l} \\ \mathbf{y} \end{bmatrix} = \begin{bmatrix} \mathbf{Xb} + \mathbf{Ws} + \mathbf{Z}_1\mathbf{u} + \mathbf{Z}_2\mathbf{p} + \mathbf{Z}_3\mathbf{h} + \mathbf{e} \\ \mathbf{Xb} + \mathbf{Z}_1\mathbf{u} + \mathbf{Z}_2\mathbf{p} + \mathbf{Z}_3\mathbf{h} + \mathbf{e} \end{bmatrix} \quad [3]$$

where \mathbf{l} = vectors of unobserved liabilities for service records to a binary outcome (no conception or conception); \mathbf{y} = vectors of observations for test-day production records; \mathbf{b} = vector of fixed effects of herd year, and regressions on DIM using third-order Legendre polynomials; \mathbf{s} = vector of random effects for the service sire only for CR; \mathbf{u} = vector of random sire of cow effects using third-order Legendre polynomials for DIM; \mathbf{p} = vector of random permanent environmental effects for cows using Legendre polynomials of order three for DIM; \mathbf{h} = vector of random herd-test-date effects, and \mathbf{e} = vector of random residual effects; and \mathbf{X} , \mathbf{W} , \mathbf{Z}_1 , and \mathbf{Z}_2 are incidence matrices for \mathbf{b} , \mathbf{s} , \mathbf{u} and \mathbf{p} , respectively. The (co)variance structure was as follows: e

$$\text{var} = \begin{bmatrix} \mathbf{s} \\ \mathbf{u} \\ \mathbf{p} \\ \mathbf{h} \\ \mathbf{e} \end{bmatrix} = \begin{pmatrix} \mathbf{S} \otimes \mathbf{I}_s & 0 & 0 & 0 & 0 \\ 0 & \mathbf{G} \otimes \mathbf{A}_u & 0 & 0 & 0 \\ 0 & 0 & \mathbf{P} \otimes \mathbf{I}_p & 0 & 0 \\ 0 & 0 & 0 & \mathbf{H} \otimes \mathbf{I}_h & 0 \\ 0 & 0 & 0 & 0 & \mathbf{R} \otimes \mathbf{I}_r \end{pmatrix}$$

where \mathbf{S} is a 2×2 sire (co)variance matrix of service sire for both traits (because of no service sire effect for test-day observations, the variance for test-day observations and the covariance between test-day observations and CR were set to zero); \mathbf{I}_s is an identity matrix for the effect of the service sire; \mathbf{G} is a 8×8 additive genetic (co)variance matrix for sire of cow effects for CR and one test-day production trait; \mathbf{A}_u is an additive genetic (co)variance matrix for sires of cows; and matrices \mathbf{P} , \mathbf{I}_p , \mathbf{H} , \mathbf{I}_h , \mathbf{R} , and \mathbf{I}_r are explained above (see model 1). For this specific model 3, residual variances for the binary trait (CR) were set equal to 1. Assignment of prior

distributions for fixed and random effects are identical to model 1, and also for the matrix S , independent inverse Wishart distributions were used as priors.

For models 1, 2, and 3, Gibbs sampling was used to infer genetic parameters by applying the program THRGIBBS1F90 (Misztal et al., 2002). Convergence of the Gibbs sampling chains (residuals and (co)variances among random regression coefficients) were monitored by visual examination. In total, 100,000 samples were generated for each analysis, and 40,000 of them were discarded as in the burn-in process. From the remaining 60,000 samples, every 5th sample was used to calculate posterior means and posterior standard deviations. The effective sample size for the random effects of HTD, service sire, and residual was larger than 2,000. For additive genetic and permanent environmental effects, the effective sample size approximated 50.

RESULTS AND DISCUSSION

Descriptive statistics

Generally, descriptive statistics for production traits (Table 2) and female reproduction traits (Table 3) from organic and low input data were within the well-known range which is relevant for dairy cattle farming in Switzerland (Swiss Brown Cattle Breeders' Federation, 2011). As our study used data from low input farms only, the overall mean of MUN (25.11 mg/dl) was relatively high. Most of the previous studies reported values of MUN ranging between 12 to 15 mg/dl. For example, Wood et al. (2003) found a mean value of 12.61 mg/dl of for the first three lactations. Mitchell et al. (2005) reported that the average value for infrared MUN and for wet chemistry MUN were 12.92 mg/dl and 14.30 mg/dl, respectively. Two studies conducted in conventional dairy cattle farms reported levels of MUN in the range from 20 to 23 mg/dl (Butler et al., 1996; Stoop et al., 2007). König et al. (2008) found an average MUN value of 26.71 mg/dl in conventional farms in a pasture based production system in the maritime region of Lower Saxony, and they reported antagonistic relationships between MUN and female fertility traits. The comparably high value for MUN also for cows in organic and low input farms in Switzerland reflects that diets are high in degradable protein and deficient in fermentable carbohydrates. Amaral-Phillips (2005) gave two reasons for high levels of MUN, especially being relevant for low input farming: First, diets may contain a very high percentage of alfalfa haylage, or secondly, cows are fed on lush vegetative pasture.

Table 2. Descriptive statistics for test-day production traits by parity

Parity	Trait	#records	Mean	SD	Min	Max
1	Milk yield (in kg)	10,338	19.04	4.57	2.0	35.5
	Fat%	10,303	4.04	0.56	1.50	9.65
	Protein%	10,306	3.40	0.33	2.48	5.82
	Lactose%	10,306	4.94	0.17	2.13	5.52
	Somatic cell score	10,304	1.98	1.43	-3.64	9.64
	Milk urea nitrogen (in mg/dl)	10,302	25.70	8.40	5	90
2	Milk yield (in kg)	7,736	21.87	6.02	2.7	47.0
	Fat%	7,716	4.07	0.60	1.84	9.61
	Protein%	7,719	3.48	0.36	2.48	5.68
	Lactose%	7,719	4.85	0.18	2.21	5.55
	Somatic cell score	7,719	2.45	1.45	-3.64	9.01
	Milk urea nitrogen (in mg/dl)	7,719	25.03	8.74	5	67
3	Milk yield (in kg)	5,604	23.61	6.62	4.2	50.4
	Fat%	5,589	4.06	0.64	1.61	8.44
	Protein%	5,589	3.45	0.36	2.23	4.98
	Lactose%	5,589	4.81	0.19	3.38	5.42
	Somatic cell score	5,589	2.78	1.48	-2.06	9.64
	Milk urea nitrogen (in mg/dl)	5,588	24.59	8.58	5	68

Values for SCS from cows in organic and low input farms of the present study were marginally lower compared to those values from cows kept in conventional dairy cattle farms in Switzerland. Neuenschwander et al. (2005) reported a mean SCS of 2.13, 2.49 and 2.81 for the first three lactations. In the present study, the average SCS in the low input population for parities 1, 2, and 3 was 1.98, 2.45 and 2.78, respectively. Nauta et al. (2006) compared SCS of Holstein cows in first parity in four environmental groups in The Netherlands, i.e. an organic, a pre-organic, a converting-to-organic, and a conventional group. In their study, SCS was highest in the organic group. Also Rozzi et al. (2007) reported relatively high values for SCS of cows kept in organic farms in Canada, maybe due to restrictions regarding the use of antibiotics. In The Netherlands (Nauta, 2001), Great Britain (Pryce et al., 2001) and Canada (Rozzi, 2007), large differences between organic and conventional dairy cattle farming exists. In contrast, in Switzerland and in Denmark (Kristensen and Pedersen, 2001), herd characteristics such as herd size and feeding strategies of organic farms are almost identical to

conventional dairy cattle farms in the same country. This could be a further explanation for the comparatively high status in udder health for dairy cows in organic farms in Switzerland.

Table 3. Descriptive statistics for female reproduction traits

Trait	#records	Mean	SD	Min	Max
Age at first calving (in d) ¹	1388	939.49	100.68	700	1351
Calving to first service (in d)	4486	69.95	28.30	6	320
Days open (in d)	4486	98.58	59.71	12	500
Gestation length (in d)	3466	290.30	5.93	242	300
Calving interval (in d)	3496	388.62	58.55	296	791
No. of insemination	4484	1.68	1.09	1	11
Calving ease (scale 1-4)	4443	1.31	0.54	1	4
Still-birth (0 or 1)	4828	0.05	0.22	0	1

¹ only first parity

Heritabilities and variances for production traits by DIM

In most cases, heritabilities in parities 1, 2, and 3 were lowest at the beginning of lactation (Fig. 1). This is not a particularity for organic farms, and in line with several studies based on 'conventional data' (e.g. Odegard et al., 2003; Strabel and Jamrozik, 2006; Strabel et al., 2005). Strabel et al. (2005) based their studies on a large dataset of test-day records, and they showed different pattern of curves for daily heritabilities when changing statistical modelling. Hence, they clearly indicate the impact of the statistical model on estimates of genetic parameters irrespective of the size of the dataset.

In our study, with regard to the middle and to the end of lactation in all parities, heritability was highest for MY and Pro% with the highest value of 0.55 that was found at the end of lactation 2 and in the middle of lactation 3. Heritabilities for MY higher than $h^2 = 0.50$ are in the upper range of values reported in the literature. Nauta et al. (2006) stratified their data into four groups of herds: conventional, pre-organic, converting, and organic. Heritability for MY ($h^2 = 0.70$) was highest in the organic group. Same trends, i.e. an increase of heritabilities going along with a decrease of intensity of the production system from conventional towards organic was observed for fat yield and protein yield. Nauta et al. (2006) considered the findings of higher heritabilities in organic data 'surprising', an assumption maybe based on the theory of pronounced genetic differentiation of production traits in better environments as

explained by Schierenbeck et al. (2011). König et al. (2005) reviewed the literature for estimates of genetic parameters with a focus on low input production systems, especially low input grazing production systems in New Zealand, Australia, and Ireland: Relatively low values of genetic parameters from international comparisons were in line with estimates from own studies conducted in a pasture-based production system in the north-western part of Germany. Hence, additional factors may exist which are typical for organic farming systems in The Netherlands and in Switzerland, and which are different from so-called low input pasture based systems.

In the present study, apart from 2nd parity, heritability of MY increased from the beginning to the middle of lactation, and substantially decreased at the end of lactation. However, MY in parity 2 revealed the highest heritability at the very end of this lactation, and the lowest heritability was found at DIM 275. A continuous upward trend could be observed for the heritability of Pro% and Fat% in parity 1 and 2 throughout lactation. Heritabilities for Fat% at the beginning of lactation were generally lower as expected. A reason might be the possibility to mobilize body fat reserves at the beginning of lactation to overcome restrictions in feeding concentrates. Heritabilities for Lac% increased in parity 1 and 2 by DIM, but this trend was opposite in parity 3. Literature focussing on the estimation of genetic parameters for lactose is rare, but values as found in our study in parity 1 are in line with estimates based on data from conventional herds in Canada (Miglior et al., 2007). Among all production traits, heritabilities were lowest for MUN, with a value close to 0.13 from the beginning to the end of lactation. These estimates at the beginning of lactation correspond to results by König et al. (2008), who focussed on single test-day observations from the onset of lactation. For MUN, the effect of the HTD explained 68.89%, 72.83%, and 71.20% of the total variance in parities 1, 2, and 3, respectively, which was substantially higher compared to other traits. For completeness, posterior estimates for variance ratios (in %) of the herd-test-day effect and the residual effect expressed in relation to the phenotypic variance in parity 1, 2, and 3 are given in Table 4.

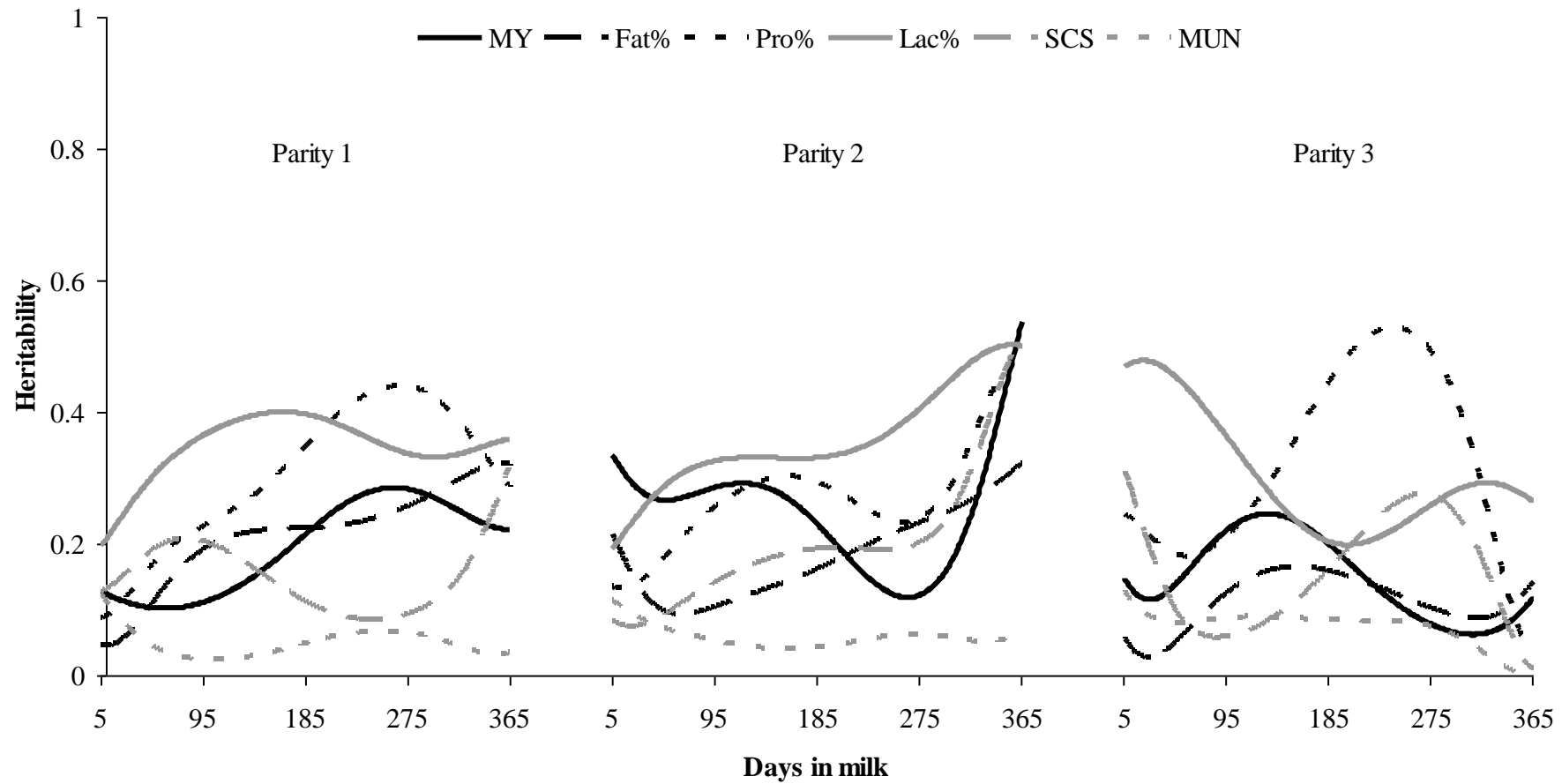
Table 4. Posterior estimates for variance ratios (in %) of the herd-test-day effect (HTD) and the residual effect expressed in relation to the phenotypic variance in parity 1, 2, and 3 (MY = milk yield, Fat% = fat percentage, Pro% = protein percentage, Lac% = lactose percentage, SCS = somatic cell score, MUN= milk urea nitrogen). SD are given in brackets.

Trait	Parity 1		Parity 2		Parity 3	
	HTD	Residual	HTD	Residual	HTD	Residual
MY	15.05 (1.63)	32.20 (3.49)	14.23 (2.11)	29.34 (4.36)	13.57 (2.20)	37.43 (6.08)
Fat%	17.89 (1.49)	52.50 (4.36)	21.72 (2.44)	52.33 (5.89)	19.29 (1.37)	59.78 (4.24)
Pro%	22.23 (4.16)	28.79 (5.38)	22.60 (4.26)	27.50 (5.18)	17.42 (3.40)	28.49 (5.56)
Lac%	11.27 (1.57)	40.09 (5.60)	12.04 (3.24)	33.22 (8.94)	6.81 (1.62)	33.14 (7.89)
SCS	4.27 (0.28)	43.72 (2.82)	7.75 (1.02)	40.55 (5.33)	3.22 (0.50)	47.13 (7.30)
MUN	68.89 (2.31)	19.92 (0.67)	72.83 (2.51)	16.41 (0.57)	71.20 (2.14)	17.87 (0.54)

Heritabilities for SCS revealed remarkable changes by DIM and parity. For example in parity 1, the highest heritability with a value of 0.31 was found at the end of lactation. In contrast in parity 3, heritability for SCS was highest at the beginning ($h^2 = 0.31$) and at DIM 270 ($h^2 = 0.27$), but substantially dropped to a low value of $h^2 = 0.01$ at DIM 365. Relatively high heritabilities for SCS of value 0.29 were also used by Biscarini et al. (2011) when deriving genomic breeding values for the conventional Brown Swiss population in Switzerland. Heritabilities for SCS in organic and conventional farms in The Netherlands were identical for the two production systems, with a value of 0.10 (Nauta et al., 2006).

In our data from organic herds, we observed some remarkable differences within same traits across and within lactations. Minor changes in pattern of curves are expected when increasing complexity of statistical modelling, e.g. allowing heterogeneous residual variances within and across lactations.

Figure 1. Posterior estimates of daily heritabilities in parity 1, 2, and 3 for six test-day production traits by DIM (MY = milk yield, Fat% =fat percentage, Pro% = protein percentage, Lac% = lactose percentage, SCS = somatic cell score, MUN= milk urea nitrogen). Posterior SD of daily heritabilities ranged from 0.022 - 0.087 for MY, 0.008 - 0.053 for Fat%, 0.026 to 0.068 for Pro%, 0.024 to 0.097 for Lac%, 0.008 to 0.081 for SCS, and 0.001 to 0.029 for MUN.



Genetic correlations among production traits by DIM

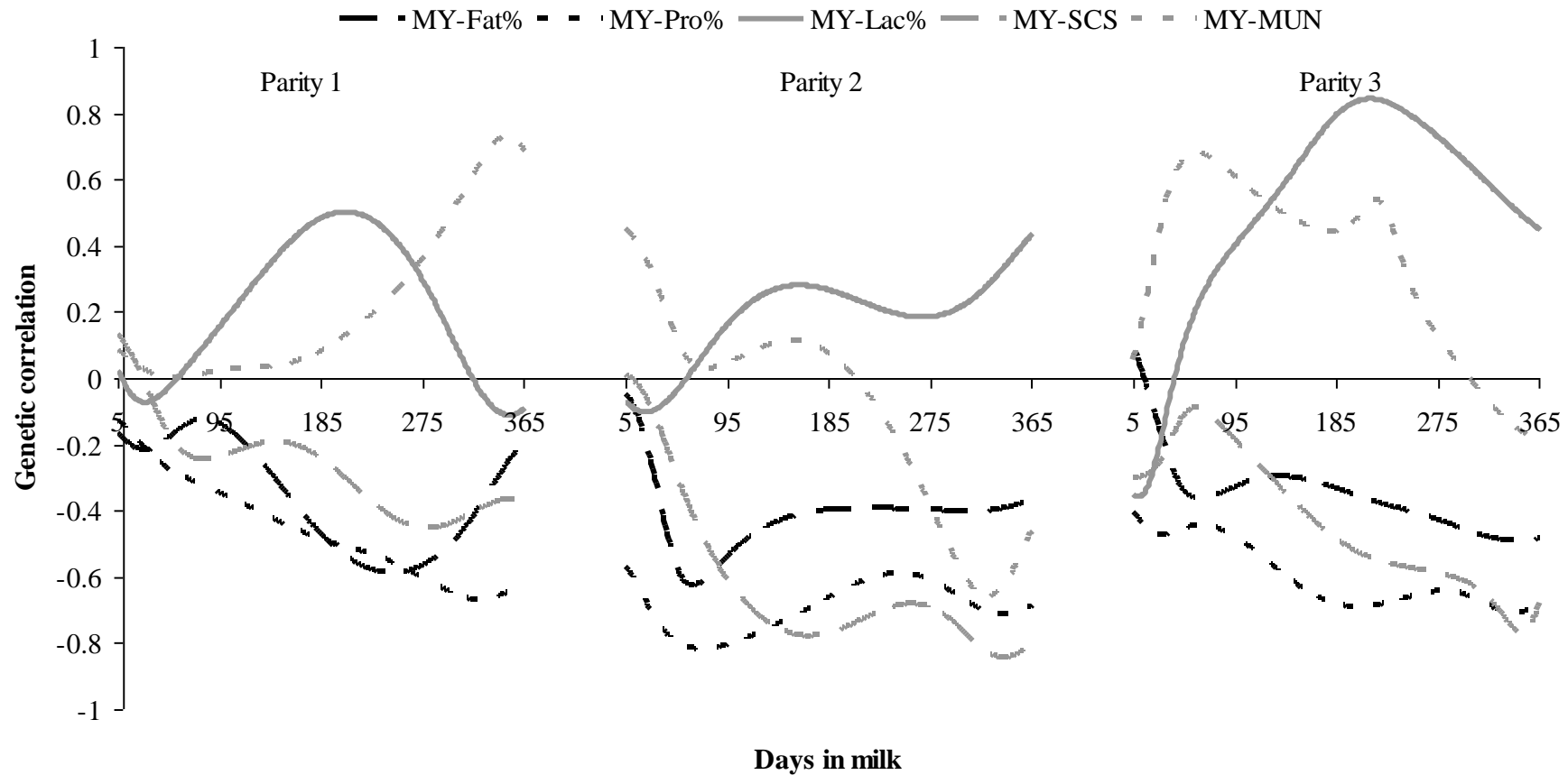
Generally, genetic correlations were negative between MY and Fat%, MY and Pro%, and MY and SCS, but positive between MY and Lac%, and MY and MUN (Fig. 2). Apart from MUN, the pattern of curves or trends of associations were relatively similar when comparing estimates from parity 1, 2, and 3. However, the genetic correlation between MY and Fat% was slightly negative and positive directly after calving in parity 2 and 3. This finding might be explained by physiological mechanisms, i.e. by the mobilization of body fat reserves early in lactation (Collard et al., 2000). Daily genetic correlations between MY and Lac% showed the opposite trend, i.e. being negative in the first third of lactation from 1 to 50 DIM, but increasing to $r_g = 0.84$ at DIM 270 in parity 3. A comprehensive, multi-trait study based on random regression model likewise revealed this change in genetic parameters for Lac%, i.e. daily heritabilities and daily genetic correlations (Miglior et al., 2007). Hence, based on the pronounced genetic background for Lac% (Fig. 1 and Fig. 2), a general possibility is given to include Lac% in an official genetic evaluation for the Brown Swiss low input population, and furthermore into an overall breeding goal. However, the pre-requisite when including a new trait into an overall breeding goal implies economic importance, and the availability of an economic weight or value.

Daily genetic correlations between MY and Pro% were consistently negative over DIM ranging from $r_g = -0.14$ at DIM 5 in parity 1 to $r_g = -0.81$ at DIM 70 in parity 2. This antagonistic relationship between MY and Pro% across DIM and parities and across breeds and production systems is well known in dairy cattle breeding. Genetic correlations between MY and MUN were mostly positive over DIM in parity 1 and 3, and also in the first half of lactation in parity 2. A positive correlation between MY and MUN implies that more energy is diverted to milk and less to protein production, resulting in an energy shortage for protein production and increased levels of MUN.

Interestingly, a genetic antagonism between MY and SCS was only found in the beginning of lactation in parity 1. In parity 2 and 3, genetic correlations between MY and SCS were throughout negative, which indicates improved udder health for high yielding cows. However, the non-linear relationship between SCS and mastitis should be kept in mind, meaning that a higher SCS below the threshold indicating mastitis is not indicating a bad udder health. Samore et al. (2008) found positive genetic correlation between MY and SCS only in the

beginning of lactation in first parity, but the correlation was negative both at later stages of first lactation and throughout subsequent lactations. This is quite comparable to results in our study (Fig. 2). Jamrozik et al. (2010) found antagonistic relationships between MY and SCS from DIM 25 to DIM 295 in first parity, but in second parity, the antagonism could only be observed from DIM 25 to DIM 135. In third parity, the genetic correlation between MY and SCS was negative throughout the entire lactation. Hence, no clear agreement for longitudinal associations between MY and SCS can be reported. This is mainly due to a variety of factors and their interactions influencing SCS. On the phenotypic level, the relationship between MY and SCS can be affected by three major factors: the effect of infection, the effect of stress, and the effect of dilution (Jamrozik et al., 2010). Additionally, possible feedback situations or recursive biological systems between MY and SCS complicate the interpretation of results. For animal breeding objectives, first applications of recursive models have been discussed by de los Campos et al. (2006a, 2006b). On one pathway, they found an increased risk of an infection in the udder with increasing milk yield. The feedback situation is described via a second path, such that an infection in terms of increasing somatic cell scores decreases milk yield in the ongoing lactation. Such biological systems, in which one phenotype is directly involved in the phenotypic expression of other traits, cannot be modeled adequately when applying standard linear mixed model theory. Furthermore, the effect of high milk yield is bidirectional: On the one hand there is an increasing risk of a mastitis with increasing milk yield, but on the other hand there is the effect of dilution for somatic cells (Jamrozik et al., 2010).

Figure 2. Posterior estimates of daily genetic correlations in parity 1, 2, and 3 between test-day milk yield (MY) and other test-day production traits by DIM (MY = milk yield, Fat% = fat percentage, Pro% = protein percentage, Lac% = lactose percentage, SCS = somatic cell score, MUN= milk urea nitrogen). Posterior SD of daily genetic correlations between MY and other traits ranged from 0.068 to 0.152 for Fat%, 0.037 to 0.177 for Pro%, 0.063 to 0.199 for Lac%, 0.044 to 0.193 for SCS, and 0.078 to 0.200 for MUN.



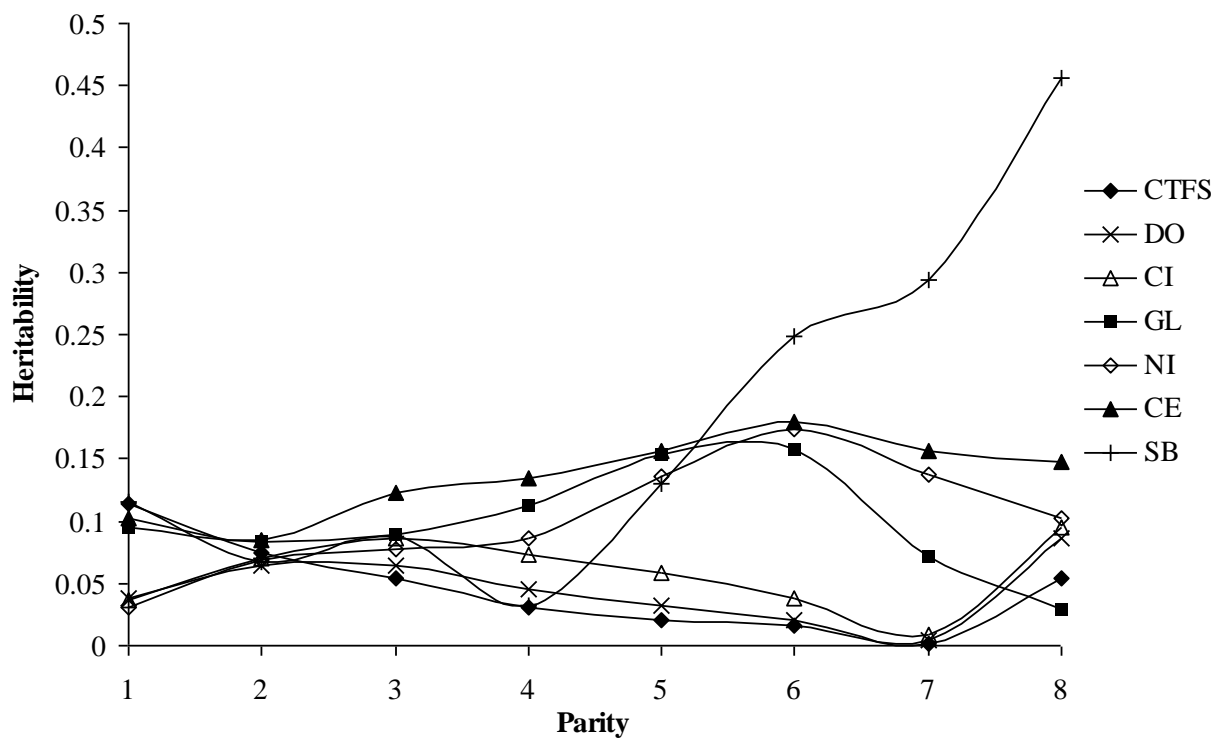
Genetic parameters for female reproduction traits by parity

In parities 1 to 4, posterior heritabilities were lower than 0.15 for all female fertility traits (Fig 3). Due to the limited observations in parity four and later, those estimates should be interpreted with caution. Based on this approach using random regression methodology, an interval trait describing the cow's ability for recovering after calving, i.e. CTFS, heritabilities in parities 2 to 8 were lower compared to fertility traits that include the component of a successful conception after an insemination (NI and DO; Fig. 3). Only in the first parity, heritabilities for the 'interval trait' CTFS were slightly higher than for the 'conception traits' NI and DO. Posterior SD of heritabilities were relatively high, but this finding agrees with König et al. (2008), who estimated genetic parameters for NR56, NR90, and CTFS in first parity for Holstein cows kept in a pasture-based production system in Germany. Heritability was 0.029 for NR56, 0.029 for NR90, and was higher for CTFS with a value of 0.073. This is also in line with the estimates of NR and CTFS in a subset of the Brown Swiss population in Switzerland, which were 0.04 and 0.08, respectively (Schnyder and Stricker, 2002). The fertility trait CI considers both aspects of a successful insemination and of an early start of the first cycle after calving. That is the reason why Pasma et al. (2006) suggested CI as an overall fertility trait for genetic evaluation.

Heritabilities for GL in parities 4 to 7 ranged between 0.07 and 0.16 and were higher than for CTFS, DO, CI or NI (Fig. 3), but lower than reported in the literature. The direct heritability estimate for GL in a comprehensive study by Jamrozik et al. (2005) was also highest among all analyzed fertility traits, i.e. 0.31 in parity one, and 0.27 in later parities. Also in the studies by Cervantes et al. (2010) and by Hansen et al. (2004), heritabilities for GL were higher than 0.30. As parameter estimates in the present study are based on data from organic farms only, they are relatively unbiased and free from disturbing effects of preferential treatment. In a survey by König (2004) including a subset of high input farms in Germany, the use of hormones was identified as a quite common practice to induce the birth of a calf, especially for high index cows in first parity. Santos et al. (2004) analyzed the effect of bovine somatotropin application in dairy cattle, which improved conception rates in cyclic cows. The impact of preferential treatment on genetic evaluation in general has been discussed for production traits (Kuhn et al., 1994). Statistical models cannot account for such unknown effects that apply only to a small fraction of cows within a herd. This problem was the main reason for implementing tests on station for potential bull dams (König et al., 2007). Such

biases may also be relevant for female reproduction, but will be less relevant when analyzing data from organic and low input dairy cattle farms due to the general prohibition of hormone use in organic farming. Further preferential treatment for female reproduction is possible when applying hormones for heat synchronization. This is a common treatment to synchronize heifers or cows that are used as recipients for embryo transfer in conventional farms. Heat synchronization affects female reproduction traits such as CTFS and AFC. Consequently, the estimates from our present study for CTFS and AFC ($h^2 = 0.09$) are assumed to be unbiased and may reflect the true genetic background. Also Goodling et al. (2005) found different heritabilities when analyzing different subsets of data stratified according to synchronization or heat detection treatments.

Figure 3. Posterior estimates of heritabilities for female reproduction traits by parity of the cow (CTFS = interval from calving to first service, DO = days open, CI = calving interval, GL = gestation length, NI = number of insemination, CE = calving ease, SB = stillbirth). Posterior SD of heritabilities in different parities ranged between 0.008 to 0.078 for CTFS, 0.006 to 0.054 for DO, 0.008 to 0.101 for GL, 0.013 to 0.085 for CI, 0.010 to 0.056 for NI, 0.016 to 0.094 for CE, and 0.039 to 0.130 for SB.



Heritabilities for CE were lower than for SB in parity 6, 7 and 8. Estimates for CE are based on subjective appraisals recorded by farmers on a scale from 1 to 4. Additionally, as found in

several previous studies (e.g. König et al., 2008) the variance of the service sire (not shown) for CE was close to zero. An alternative for improving selection on CE is the implementation and the utilization of objective measurements such as the birth weight of calves instead of using subjective scores. Recording the moderately heritable trait birth weight of calves was a wish long time ago for improvements in animal breeding (e.g. Plum et al., 1965), but has been hampered due to the difficulties of data collection in the whole population. Within the framework of the low input breed project in Switzerland, a variety of functional traits will be recorded and analyzed with the objective of improving dairy cattle programs in organic production systems via direct selection strategies instead of using indicator traits. In our present study, heritabilities for the binary trait SB were higher compared to heritabilities for CE (Fig. 3). Stillbirth is an objective measurement, because the calf could be either alive or dead within 24 h after birth. In contrast for CE, four subjective scores were assigned to describe the variation of this trait resulting in three thresholds when applying threshold methodology (model 2). Generally, traits related to calving difficulties (SB and CE) had higher heritabilities than remaining fertility traits associated with pregnancy after insemination.

Estimates for genetic correlations among fertility traits were in the expected range (not shown) previously identified for conventional dairy cattle farming. From the point of animal breeding, an important result is the genetic correlation between an interval trait (i.e. CTFS), and a trait describing the success of an insemination (i.e. NI). In accordance with König et al. (2008), this correlation was close to zero reflecting that breeding on short intervals or on early estrous after calving does not necessarily impair non-return rates.

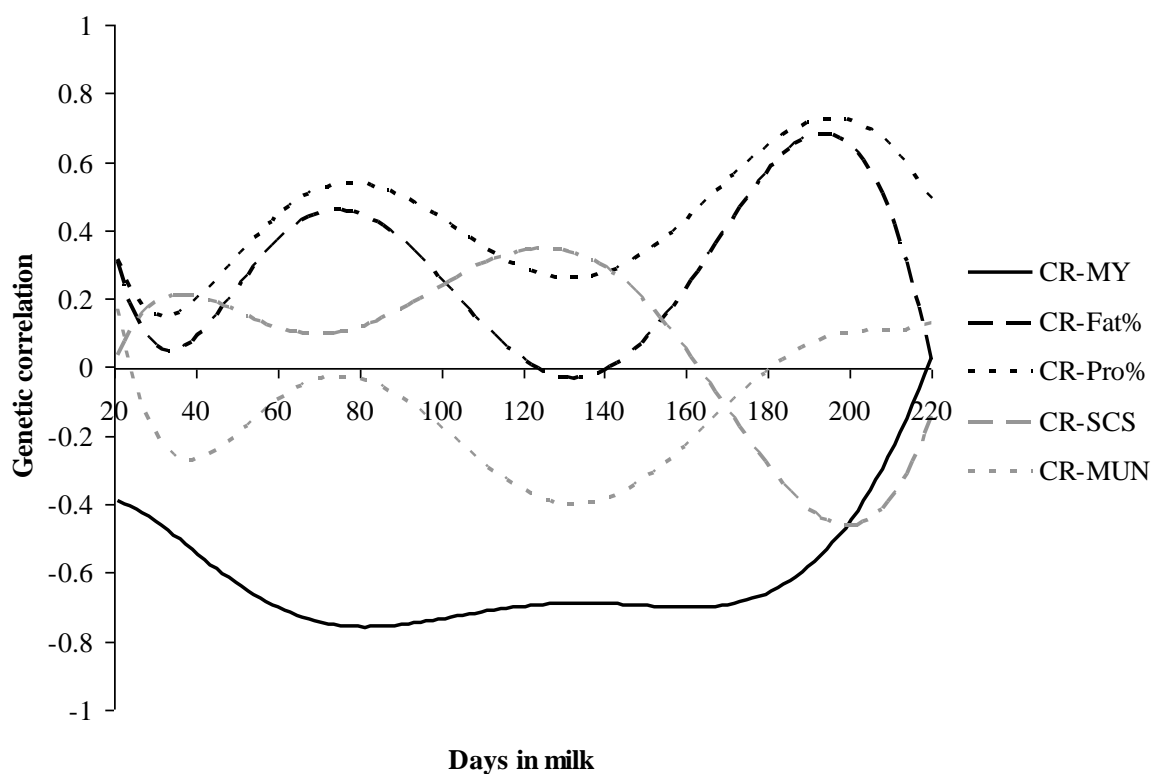
To our knowledge, so far there is a lack of scientific literature focusing on estimates of genetic parameters for female reproduction traits based on data from organic cows. Ahlman et al. (2010) defined the binary trait 'fertility determined survival'. Estimates of heritabilities ranged between 0.03 and 0.06 for Swedish Red and Swedish Holstein in both organic and conventional environment.

Daily relationships between production traits and conception rate

Genetic correlations between CR and Fat%, CR and Pro%, and CR and SCS were positive, but negative between CR and MY, and between CR and MUN (Fig. 4). Correlations with MY

were relatively constant from DIM 30 to DIM 210, i.e. indicating a pronounced antagonistic relationships with values in the range from $r_g = -0.80$ to $r_g = -0.40$. Posterior SD for genetic correlations were relatively high, especially at DIM characterized by a limited no. of observations. Posterior SD for genetic correlations between one production trait and CR were relatively constant and moderate in the middle and at the end of lactation (e.g. 0.22 when correlating Fat% and CR at day 178), but substantially higher up to factor 2 in the early period of lactation.

Figure 5. Posterior estimates of daily genetic correlations between conception rate (CR) and milk yield (MY), fat percentage (Fat%), protein percentage (Pro%), somatic cell score (SCS), and milk urea nitrogen (MUN) by DIM in parity 1. Posterior SD of daily genetic correlations between CR and production traits ranged from 0.162 to 0.314 for MY, 0.226 to 0.322 for Fat%, 0.207 to 0.328 for Pro%, 0.252 to 0.312 for SCS, and 0.236 to 0.337 for MUN.



Interestingly, results show a clear genetic antagonism between MUN and CR in the period from 25 d to 180 d after calving. Genetic correlations ranged from 0 to -0.40. Studies addressing the genetic relationship between MUN and female fertility traits are relatively rare. Fertility traits investigated were non-return rates and CTFS (e.g. Mitchel et al., 2005; König et al., 2008). König et al. (2008) only analyzed the early period of lactation, and they found that

a higher level of MUN was genetically associated with a longer CTFS and slightly lower non-return rates after 56 d and after 90 d. Based on the low to moderate genetic correlations, these authors suggest focusing on direct selection strategies for reproduction traits instead of using MUN as an indicator trait. Due to the higher heritabilities for MUN than for CR, and moderate to strong genetic correlations between MUN and CR, selection strategies or breeding goals including MUN can be an alternative to currently used systems for the improvement of female fertility in organic and low input production systems in Switzerland.

CONCLUSIONS

Daily heritabilities for production traits from Brown Swiss cows located in organic production systems in Switzerland were similar to estimates as reported in the literature for high input production systems. Genetic variation by DIM was also found for Lac%, but only traits having an economic value should be included in an overall breeding goal. Expected genetic antagonisms were found between MY and Pro%, and also between MY and Fat% for all DIM. Genetic relationships between MY and SCS showed some fluctuations in the course of lactation. Genetic correlations between MY and MUN were mostly positive over DIM in parity 1 and 3, and also in the first half of lactation in parity 2. For female reproduction traits and modelling parity as a time covariate, posterior heritabilities were generally lower than 0.15 in parities 1 to 4. In first lactation, heritabilities were slightly higher for 'interval traits' describing luteal activity after calving (e.g. CTFS) than traits associated with success of an insemination (e.g. NI and DO). Results obtained from random regression sire threshold models including one binary trait (CR) and Gaussian distributed test-day observations clearly showed the genetic antagonism between CR and MY, and between CR and MUN over DIM in first lactation. Especially MUN was identified as a valuable indicator trait to improve female fertility which can be realized by including MUN in an overall breeding goal and utilizing correlated selection response. The present study demonstrates the feasibility of applying different versions of random regression models to infer genetic parameters for organic and low input farms in different regions in Switzerland characterized by small herd sizes. One limitation of statistical modeling, i.e. assuming equal residuals in different lactations, should be kept in mind. Subsequent analyses will focus on random regression methodology for mostly binary distributed new functional health traits, and on the development of an overall organic breeding goal in Switzerland.

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3rd CHAPTER**Genetic analyses of binary longitudinal health data in small low input dairy cattle herds
using generalized linear mixed models**

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ABSTRACT

Records for mastitis, metritis, retained placenta, ovarian cysts and acetonemia from 1,247 Brown Swiss cows in first parity kept in 53 organic and low input farms in Switzerland were used to infer genetic parameters. Animal and sire models, repeatability models, and random regression models (RRM) in combination with generalized linear mixed model were applied to analyze the health disorder data. Five health traits were defined as binary data, count data between days in milk (DIM) -1 and 120, and longitudinal binary data during test-day. Firstly, the five health traits defined as binary data between DIM -1 and 120 were analyzed by linear animal and sire models as well as threshold animal and sire models with probit as a link function. Secondly, data of total number of diseases cases during the same period were analyzed by linear models and Poisson mixed models on animal and sires respectively. Thirdly, linear repeatability models, linear RRM, threshold repeatability models and RRM with probit link function were used to analyze test-day records for health diseases. Disease incidences of the five health disorders occurs in organic farms were lower than corresponding incidences in conventional farms. Apart from heritabilities of 0.32 and 0.39 for mastitis and retained placenta respectively, heritabilities for binary traits and categorical traits were low. Repeatabilities and heritabilities for longitudinal data from repeatability models were relatively low as well. Substantial increase between heritability of 0.01 to repeatability of 0.14 was only found for longitudinal recorded ovarian cysts, suggesting a substantial permanent environmental effect. Daily heritabilities for all health traits from linear and threshold RRMs were the highest at the beginning of lactation and at the end of the defined interval. Bayesian information criterion (BIC) favored threshold animal and sire models, threshold repeatability models, but did not favor threshold RRM. Similar BIC values were found between animal models and sire models, indicating little difference existed by applying animal and sire models on the health data.

Key words: organic and low input farms, health diseases, genetic parameters

INTRODUCTION

Especially in the early period directly after calving up to and including the ‘peak phase’ of lactation, dairy cows are particularly susceptible for infections of udder quarters (e.g. Schwarz et al., 2011). Furthermore within the first 100 days in milk (DIM), metabolic diseases occur

frequently, and fertility disorders related to the puerperium are only relevant in the early stage of lactation. An overview of incidences for a variety of health disorders is given by Gernand et al. (2012). For all categories of health traits, i.e. fertility, metabolism, claw disorders, and mastitis, they found a substantial decrease of disease incidences with increasing DIM. König et al. (2005), and König et al. (2008) used a variety of statistical modeling approaches to analyze the genetic background of claw disorders, but data always focused on the first third of lactation. The above-mentioned studies used data from Holstein cows kept in large-scale contract herds located in East Germany, which are characterized by a high production level, especially at the first test-days directly after calving. Consequently, energy intake does not match energy requirement, and the negative energy balance is associated with an increasing risk of occurrence of health disorders in the ongoing lactation (Collard et al., 2000).

Test-day milk yield in the early period of lactation of Brown Swiss cows kept in organic or low input dairy cattle farms in Switzerland is substantially lower compared to the production level of Holstein cows from East German contract herds (Yin et al., 2012a). Nevertheless, also health disorders including fertility and metabolism, play an import role in organic production systems in Switzerland, but claw disorders are less relevant (Yin et al., 2012b). The economical loss per cow and year or per herd and year due to clinical mastitis in low input or high input production systems was calculated in several studies (Scheepers and Dijkhuizen, 1991). Of economic relevance are also health disorders including female fertility and metabolism. Both categories contribute to the increase of involuntary dairy cow cullings (Dubuc et al., 2011; Kesler and Garverick, 1982; Østergaard and Grohn, 1999). Functional health traits have a high priority especially in organic dairy cattle farming systems, which underlines their relevance in an independent overall organic breeding goal (Rozzi et al., 2007).

Prerequisites for traits to be included in an overall breeding goal are their economic importance, the availability of a suitable recording system (data quality), the value of additive genetic variance or of heritability, and genetic correlations to other traits of interest. The latter three arguments address statistical methodology for data preparation and genetic analyses. For test-day production data, official and identical recording systems across country borders exist, but for functional health traits, the variety of possible data definitions and completeness of data may cause differences in estimated genetic parameters. Using large datasets, such problems can be compensated, e.g. Shook et al., 2012 who used 4,531,536 fertility records for different data quality definitions, but organic and low input populations are characterized by a

comparatively small population size and small herd sizes as well. The small number of contemporary groups in organic herds was a substantial problem for genetic evaluation of production traits when applying over-parameterized statistical models (Yin et al., 2012a). Basically, health data preparation in the early period of lactation includes three definitions. The easiest way is to focus on a specific interval, and to assign a score of 1 for diseased cows, irrespective the number of disease cases (e.g. König et al., 2005). Secondly, using the code = 1 for diseased cows, and considering all disease cases in the interval, generates a longitudinal data structure (e.g. Carlen et al., 2009; Gernand et al., 2012). A third option is to count the total number of disease cases occurring within a given interval, resulting in broader range of scores compared to the binary scores, as done by König et al. (2007) for female fertility traits. The latter two definitions make it difficult to distinguish between a new case of a disease, or an ongoing treatment. Usually, a 5 d interval was used to separate a new from a pre-existing disease (Hinrichs et al., 2005).

Regarding statistical modeling for genetic evaluation of binary data, main questions addressed comparisons of sire versus animal models, and applications of the threshold concept instead of assuming a Gaussian data distribution. In the early 1980s, threshold models reported by Gianola and Foulley (1983) or by Harville and Mee (1984) were developed based on Wright's threshold concept for analyses of categorical data in animal breeding. Later, this concept was applied in a multitude of studies or in official genetic evaluations (e.g. Koeck et al., 2010b). Theoretically, threshold models studying the trait of interest on an underlying liability scale are more appropriate for depicting the physiological background than linear models. However, problems may occur for data with extreme incidences, such that some sub-cells of effects are underrepresented for certain scores (Hoeschele and Tier, 1995). In most of the genetic analyses, threshold methodology for binary traits was applied within a Bayesian framework using a large number from Gibbs sampling to calculate posterior means and SD of estimates (e.g. Gernand et al., 2012; Sorensen et al., 2009). An alternative to Bayesian procedures is to apply REML and generalized linear mixed models (GLMM). Using GLMM, different link functions can be invoked to analyze data with different distributions, e.g. an identity link function for Gaussian traits, a probit or logit link function for binary data, or a log link function for Poisson distributed 'count data' (McCullagh and Nelder, 1989). An overview of methodologies in the context of GLMM applications to analyze categorical traits is given in Table 1. As a further methodological innovation for time series or longitudinal binary data, GLMM can be extended to random regression methodology (RRM). RRM allows inferring

genetic effects in dependency of a time dependent covariate, and effects may change due to changes of the physiological background, e.g. aging of an animal. Traditionally, RRM have been developed for longitudinal production test-day records (e.g. Schaeffer and Dekkers, 1994), but can be extended to type traits, fertility, health, and longevity (Schaeffer, 2004). So far for health data, linear and threshold RRM were used by Carlen et al. (2009) and Chang et al. (2004) for relatively large mastitis datasets.

The objective of the present study was to apply GLMM for genetic analyses of health traits using appropriate link functions according to data distributions. Applications of GLMM start with relatively simple univariate linear and threshold models for a single observation in distinct intervals, then address GLMM with log link functions for ‘count data’, and continue with longitudinal data analyses in the early period of lactation using repeatability and random regression models. A main focus was to evaluate the possibility of GLMM applications in low input farms characterized by relatively low disease incidences and comparably small herd sizes. Comparison of sire versus animal models was also addressed at the same time.

Table 1. Overview of applications of generalized linear mixed models for analyses of categorical data in animal breeding

Author (Breed)	Type of data	Traits	Link function
Kadarmideen et al., 2004 (SLW)	Binary	OL ² in head of numerus	Probit
	Binary	OL in head of numerus	Logit
	Category	OL in distal epiphyseal cartilage of ulna	Log
König et al., 2005 (HOL)	Binary	Digital dermatitis	Logit
	Binary	Sole ulceration	Logit
	Binary	Wall disorder	Logit
	Binary	Interdigital hyperplasia	Logit
Guerra et al., 2006 (COR)	Binary	Calving rate	Probit
	Binary	Calving rate	Logit
	Binary	Calving survival	Probit
	Binary	Calving survival	Logit
König et al., 2007 (HOL)	Count	Transferable embryos	Log
	Count	Unfertilized oocytes	Log
Vazquez, 2009a (NOR)	Binary	Clinical mastitis	Linear
	Binary	Clinical mastitis	Logit
	Count	Clinical mastitis	Log
Vazquez, 2009b (HOL)	Binary	Clinical mastitis	Probit
	Count	Clinical mastitis	Log
Fuerst-Waltl et al., 2010 (HOL)	Binary	Heifer mortality	Logit
Koeck et al., 2010a (FLE)	Binary	Metritis	Logit
	Binary	Retained placenta	Logit
	Binary	Ovarian cysts	Logit
Koeck et al., 2010b (FLE)	Binary	Clinical mastitis	Probit
	Binary	Clinical mastitis	Logit

¹⁾ SLW = Swiss Large White, HOL = Holstein, COR = Crossbreed between Angus, Brahman, Charolais, and Hereford breeds, NOR = Norwegian red cows, FLE = Fleckvieh dual-purpose cows

²⁾ Osteochondral lesions

MATERIALS AND METHODS

Data and health trait definitions

The five health traits with highest incidences in first parity were mastitis, metritis, retained placenta, ovarian cysts and acetonemia. Consequently these traits were used for genetic analyses. After editing, data comprised health disorders from 1,247 Brown Swiss cows in first parity kept at 53 organic and low input farms from calving years 2000 to 2009, and resulting in 353 herd-calving-year levels. Average herd size was 3.53 cows per herd-calving year, with a maximum value of 17 cows. Age at first calving ranged from 18 to 45 months. Due to the fact that the five health traits are only relevant in the first third of lactation, records were from -1 d to 120 d after calving. The 1,247 Brown Swiss cows were daughters of 362 different sires, which implies an average of 3.44 daughters per sire. The maximum number of daughters per sire was 51, five sires had 31 to 50 daughters, five sires had 21 to 30 daughters, 13 sires had 11 to 20 daughters, 24 sires had 6 to 10 daughters, 125 sires had 2 to 5 daughters, and 189 sires had only 1 daughter. For sire models, the pedigree file included 2,426 animals, and for animal models, 5,834 animals were considered. Generally, the pedigree was traced back to four generations. Regarding data preparation, three different definitions for the five health traits were used. Firstly, only the early period directly after calving was considered. Within this period from -1 d to 120 d after calving, health disorders were defined as a classical all-or-none binary trait. Trait definition implies that a score = 1 was assigned for cows with at least one entry of the health disorders within in this period, irrespective the number of entries of the same disease. For healthy cows, a score = 0 was assigned. The five health disorders were analyzed separately, and labeling of mastitis, metritis, retained placenta, ovarian cysts, and acetonemia was Mast_I, Met_I, RP_I, OC_I, and Acet_I, respectively. Incidences of health disorders for this first strategy of health trait definition are given in Table 2. Secondly, records of mastitis (Mast_II), metritis (Met_II), retained placenta (RP_II), ovarian cysts (OC_II), and acetonemia (Acet_II) from -1d to 120 d after calving were defined as ‘count data’, i.e. the total number of unique episodes. Within the defined time period for each trait, at least 5 d were requested to count a treatment as a new disease case (Gernand et al., 2012). The total numbers of unique episodes of the five health traits are shown in Table 3. Thirdly, to create time-dependent data, a period starting from 1 d before calving was partitioned into four intervals of 30 days length. Following Carlen et al. (2009), only the first case of the same health disorder within an interval was used. For creating the time dependent covariate DIM, the day within the interval at which the disease first occurred was used. For healthy cows, the midpoint of the interval was assigned. Disease incidences of the five health traits for the third

trait definition are listed in Table 4. Abbreviations of the five health traits edited by the third definition were Mast_III, Met_III, RP_III, OC_III, and Acet_III.

Statistical Models

Estimates of (co)variance components were obtained by using the AI-REML algorithm as implemented in the DMU package (Madsen and Jensen, 2010). Generalized linear mixed models were applied for "Gaussian" traits (identity link function = linear mixed model), for binary traits (probit link function = threshold methodology), and for count variables (log link function for Poisson distributed traits). All health disorders were analyzed separately in consecutive runs. The residual variance for threshold and Poisson models was fixed to 1.

Model 1: Univariate sire and animal models

Univariate linear sire and animal models, and univariate threshold sire and animal models were applied for all health disorders as specified in Table 2. In matrix notation, the linear model 1a for a Gaussian trait was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{u} + \mathbf{Z}_2\mathbf{h} + \mathbf{e} \quad [1a]$$

For a binary trait, the generalized linear model 1b using the probit link function was:

$$\mathbf{l} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{u} + \mathbf{Z}_2\mathbf{h} + \mathbf{e} \quad [1b]$$

where \mathbf{l} = vectors of unobserved liabilities for a health trait from a binary outcome; \mathbf{y} = vectors of observations for a health trait regarded as a Gaussian trait; \mathbf{b} = vector of fixed effects of age of first calving (in month) and calving month; \mathbf{u} = vector of random sire of cow or animal additive genetic effects; \mathbf{h} = vector of random herd- calving year effects, and \mathbf{e} = vector of random residual effects; and \mathbf{X} , \mathbf{Z}_1 , and \mathbf{Z}_2 are incidence matrices for \mathbf{b} , \mathbf{u} and \mathbf{p} , respectively. The (co)variance structure of the random effects was assumed as

$$\text{var} \begin{bmatrix} \mathbf{u} \\ \mathbf{h} \\ \mathbf{e} \end{bmatrix} = \begin{pmatrix} \sigma_a^2 \mathbf{A}_u & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \sigma_h^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \sigma_e^2 \end{pmatrix}$$

where σ_a^2 , σ_h^2 , and σ_e^2 are the variances of additive genetic, herd-year, and residual effects, respectively; \mathbf{A}_u is an additive genetic (co)variance matrix for sires (sire model), or for cows (animal model).

Model 1c was a generalized linear model including fixed and random effects as specified for models 1a and model 1b, but using a log link function for Poisson distributed ‘count data’ as specified in Table 3.

Model 2: Repeatability sire and animal models

For longitudinal health data (Table 4), univariate repeatability models with pedigree relationships based on sires (sire model) or on cows (animal model) were fitted. The health disorders were analyzed both as Gaussian traits using a linear model, and as binary traits applying threshold methodology (probit link function). In matrix notation, the statistical model 2a for a Gaussian trait was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{u} + \mathbf{Z}_2\mathbf{h} + \mathbf{Z}_3\mathbf{p} + \mathbf{e} \quad [2a]$$

Consequently, the statistical model 2b for a binary trait was:

$$\mathbf{l} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{u} + \mathbf{Z}_2\mathbf{h} + \mathbf{Z}_3\mathbf{p} + \mathbf{e} \quad [2b]$$

where \mathbf{p} = vector of random permanent environmental effects for cows and \mathbf{Z}_3 = incidence matrices for \mathbf{p} . Fixed effect, additive genetic effect and herd-year effect were identical as defined in models 1. The (co)variance structure of random effects was extended as follows:

$$\text{var} \begin{bmatrix} \mathbf{u} \\ \mathbf{h} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{pmatrix} \sigma_a^2 \mathbf{A}_u & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \sigma_h^2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \sigma_p^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \sigma_e^2 \end{pmatrix}$$

where σ_p^2 is the variance of permanent environmental effect.

Model 3: Random regression sires models

The “extreme category problem” may occur when applying animal models to analyze categorical traits (Hoeschele and Tier, 1995; Luo et al., 2001). Therefore, this problem may have major relevance for random regression animal models. Consequently in the present study, only random regression sire models were applied. Model 3 is an extension of model 2, because in addition, a change of genetic parameters by intervals for DIM via random regression methodology was allowed. The additive genetic relationship matrix was built up from relationships among sires. Hence, similar to models 2, the linear random regression sire model 3a was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{u} + \mathbf{Z}_2\mathbf{h} + \mathbf{Z}_3\mathbf{p} + \mathbf{e} \quad [3a]$$

and for a binary trait, the threshold sire model 3b was:

$$\mathbf{l} = \mathbf{X}\mathbf{b} + \mathbf{Z}_1\mathbf{u} + \mathbf{Z}_2\mathbf{h} + \mathbf{Z}_3\mathbf{p} + \mathbf{e} \quad [3b]$$

where \mathbf{l} and y are the same as used in model 1; \mathbf{b} = vector of fixed effects of age at first calving (in month), calving month and regressions on lactation stages (intervals) using third-order Legendre polynomials; \mathbf{u} = vector of random effects using third-order (for Mast_III) and second-order (for Met_III, RP_III, OC_III and Acet_III) Legendre polynomials for recorded time intervals; \mathbf{p} = vector of random permanent environmental effects for cows using Legendre polynomials of order three for Mast_III and order two (for Met_III, RP_III, OC_III and Acet_III) for recorded time intervals; \mathbf{h} = vector of random herd-year effects at calving, and \mathbf{e} = vector of equal random residual effects; and \mathbf{X} , \mathbf{W} , \mathbf{Z}_1 , \mathbf{Z}_2 , and \mathbf{Z}_3 are incidence matrices for \mathbf{b} , \mathbf{s} , \mathbf{u} , \mathbf{p} and \mathbf{h} , respectively. The (co)variance structure of random effects was as follows:

$$\text{var} \begin{bmatrix} \mathbf{u} \\ \mathbf{h} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{pmatrix} \mathbf{G} \otimes \mathbf{A}_u & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \sigma_h^2 \mathbf{I}_h & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{P} \otimes \mathbf{I}_p & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \sigma_e^2 \mathbf{I}_n \end{pmatrix}$$

where \mathbf{G} is a 4 x 4 (for Mast_III) and 3 x 3 (for Met_III, RP_III, OC_III and Acet_III) variance-covariance matrix of random regression coefficients for the sire effects; \mathbf{P} is a (co)variance matrix of random regression coefficients for permanent environmental effects, respectively; σ_h^2 and σ_e^2 are the variance of herd-year and residual effects, respectively. \mathbf{A}_u is an additive genetic relationship matrix; \mathbf{I}_h is an identity matrix for h herds; \mathbf{I}_p is an identity matrix for p cows; \mathbf{I}_n is an identity matrix for n observations, and \otimes is the direct matrix product.

Standard errors of heritabilities were calculated by the methodology reported by Fisher et al. (2004). A Taylor series expansion was used to estimate the variance of heritability at time i , and the equation was:

$$\text{var} \left(\frac{g_{i,i}}{y_{i,i}} \right) = \text{var}(h_i^2) \approx \frac{y_{i,i}^2 \text{var}(g_{i,i}) + g_{i,i}^2 \text{var}(y_{i,i}) - 2g_{i,i}y_{i,i} \text{cov}(g_{i,i}, y_{i,i})}{y_{i,i}^4} \quad [4]$$

where $g_{i,i}$ and $y_{i,i}$ are diagonal elements of genetic and total phenotypic (co)variance matrix, and $\text{var}(g_{i,i})$, $\text{var}(y_{i,i})$ and $\text{cov}(g_{i,i}, y_{i,i})$ are variance and covariance of genetic and phenotypic variance at time i .

RESULTS AND DISCUSSION

Descriptive statistics

Disease incidences of Mast_I, Met_I, RP_I, OC_I, and Acet_I recorded between -1 and 120 days were 5.78%, 2.97%, 4.01%, 0.64% and 1.36%, respectively (Table 2). The incidence of 5.78% for Mast_I was in line with results from 20 organic farms in Ontario (Rozzi et al., 2007). Appuhamy et al. (2009) also found a low disease incidence of 2.7% for mastitis in 398 commercial dairy herds in the first 100 days of first lactation. However, incidences were substantially lower than a mean incidence of 34.6% for clinical mastitis (CM) which was found in Holstein populations in large-scale contract herds of the eastern part of Germany (Gernand et al., 2012). Generally, incidences of mastitis are lower in organic herds compared to conventional herds. Hardeng and Edge (2001) showed that the percentage of treated cows for mastitis within 305 days of lactation was 29% in 93 conventional, and 14% in 31 organic Norwegian dairy cattle herds. Pol and Ruegg (2007) also found a higher incidence of mastitis in conventional herds located in Wisconsin, i.e. 40.9%, which was significantly higher than the incidence in organic dairy farms (20.5%) from the same region. Low mastitis incidences of 2.6%, 4.2% and 5.0% for parity 1, 2, and 3+, respectively, were also observed in organic Danish dairy cows (Bennedsgaard et al., 2003). The main reason for lower mastitis incidences in organic herds may be that organic production systems put more emphasis on disease prevention via selection strategies in the past decades (Kijlstra and Eijck, 2006). The incidence with a value of 2.97% for Met_I was lower than the metritis incidence of 9.3% in organic and 15.3% in conventional populations in Wisconsin (Pol and Ruegg, 2007). In organic farms in Ontario, Rozzi et al. (2007) analyzed metritis and retained placenta together, however, even for the combined trait, disease incidence was extremely low (0.5%). Disease frequencies for mastitis, ketosis, retained placenta, metritis, and cystic ovaries in our current study were also lower than the corresponding incidences reported for Canadian Holsteins (Koeck et al., 2012). In our study, only health disorders in first parity were analyzed. However, disease incidences increase with increasing age of cows (Lin et al., 1989).

Table 2. The number of diseased cows and incidences of mastitis (Mast_I), metritis (Met_I), retained placenta (RP_I), ovarian cysts (OC_I), and acetonemia (Acet_I) based on the first health trait definition¹.

Health trait	Days from calving	# of cows	# of diseased cows	Incidence %
Mast_I	-1 to 120	1,247	72	5.78
Met_I	- 1 to 120	1,247	37	2.97
RP_I	- 1 to 120	1,247	50	4.01
OC_I	- 1 to 120	1,247	8	0.64
Acet_I	- 1 to 120	1,247	17	1.36

¹) Presence (= 1) or absence (= 0) of health disorders during -1 to 120 d after calving

With regard to Mast_II, Met_II, RP_II, and OC_II, for a large proportion of diseased cows, only a single disease case during the first lactation was observed (Table 3). For instance, 33 cows had one disease case of metritis, 2 cows had two cases of metritis, and another 2 cows had three cases of metritis. There was just one threshold for Acet_II, because no cow had more than one case of acetonemia. Consequently, acetonemia is only relevant directly after calving, and Acet_I and Acet_II were identical traits. Disease incidences for the longitudinal health data structure are given Table 4. Incidence of Mast_III from DIM -1 to 30 d was identical with results by Vallimont et al. (2009), but incidences in later intervals from our study were substantially lower. The highest incidences in the first interval for Mast_III, Met_III, RP_III and Acet_III are associated with physiological stress directly after calving, or even calving difficulties.

Table 3. The total number of unique episodes of mastitis (Mast_II), metritis (Met_II), retained placenta (RP_II), ovarian cysts (OC_II), and acetonemia (Acet_II) defined based on the second health trait definition¹.

Health trait	Days from calving	# of cows	# unique episodes				
			0	1	2	3	4
Mast_II	-1 to 120	1,247	1,175	63	8	1	-
Met_II	- 1 to 120	1,247	1,210	33	2	2	-
RP_II	- 1 to 120	1,247	1,197	47	3	-	-
OC_II	- 1 to 120	1,247	1,239	6	-	1	1
Acet_II	- 1 to 120	1,247	1,230	17	-	-	-

¹) Total number of disease cases during -1 to 120 d after calving = 'count data'

Table 4. The disease incidence of mastitis (Mast_III), metritis (Met_III), retained placenta (RP_III), ovarian cysts (OC_III), and acetonemia (Acet_III) based on the third health trait definition¹.

Interval	Days from calving	Incidence %				
		Mast_III	Met_III	RP_III	OC_III	Acet_III
1	-1 to 30	4.09	2.25	3.69	0.08	0.96
2	31 to 60	0.72	0.48	0.16	0.16	0.16
3	61 to 90	0.80	0.24	0.08	0.40	0.16
4	91 to 120	0.64	0.24	0.16	0.16	0.08

¹) Presence (1) or absence (0) of health disorders during test-day intervals

Genetic parameters

Apart from OC_I and Acet_I, heritabilities of binary health traits on the underlying liability scale were higher when using threshold models compared to heritabilities on the observed scale from linear models (Table 5). This finding was confirmed in several previous studies using large datasets (e.g. Vallimont et al., 2009). Furthermore, heritabilities from sire model were generally higher than heritabilities from animal models (Table 5). Average heritability of Mast_I from the different models was 0.19, in a range from 0.06 to 0.32. The highest heritability for Mast_I was from the threshold sire model, while the lowest value was found when a linear animal model was applied. Heritability of $h^2 = 0.32$ was significantly higher than values reported in other studies, e.g. $h^2 = 0.14$ for mastitis in Danish Holsteins (Sørensen

et al., 2009). However, the heritability for mastitis from the remaining three models was in a reasonable range. Heritabilities of Met_I ranged from 0.02 to 0.13. The averaged heritability from all models for Met_I was 0.05, and in agreement with results reported by Appuhamy et al. (2009), and only slightly lower than estimates by Zwald et al. (2004) in US Holstein cows. Heritability of OC_I was the lowest among all traits and models ($h^2 = 0.002$). For OC_I, only the linear animal model converged. Heritability with a value of $h^2 = 0.02$ for Acet_I from the linear sire model was higher than $h^2 = 0.006$ from a linear animal model (Zwald et al., 2004). Threshold models analyzed Acet_I did not converge. For RP_I, all models converged, and as expected, the highest heritability with $h^2 = 0.18$ was estimated when applying the threshold sire model. The heritability of $h^2 = 0.08$ from the threshold animal model was comparable to results obtained from identical statistical models, e.g. Gernand et al. (2012).

Table 5. Heritability and standard error (SE) of heritability (h^2) for mastitis (Mast_I), metritis (Met_I), retained placenta (RP_I), ovarian cysts (OC_I), and acetonemia (Acet_I) from animal model and sire model based on the first trait definition².

Health trait	Model	Link function / assumed data distribution			
		Identity / Gaussian		Probit / Binary	
		h^2 (x 100)	SE (h^2)	h^2 (x 100)	SE (h^2)
Mast_I	Animal	6.14	0.0753	13.92	0.1709
Mast_I	Sire	21.21	0.0264	31.68	0.1150
Met_I	Animal	1.63	0.0343	2.84	0.4091
Met_I	Sire	1.65	0.0104	12.90	0.1711
RP_I	Animal	2.29	0.0374	8.34	0.3070
RP_I	Sire	0.91	0.0108	18.25	0.1525
OC_I	Animal	0.22	0.0344	x	x
OC_I	Sire	x	x	x	x
Acet_I	Animal	0.55	0.0288	x	x
Acet_I	Sire	2.38	0.0104	x	x

¹) Presence (1) or absence (0) of health disorders during -1 to 120 d after calving

²) Not converged

Heritabilities for retained placenta and ovarian cysts were generally higher when using the second trait definition for ‘count data’ (Table 6) instead of analyzing only one observed case in a defined time interval (Table 5). Especially for RP_II, the heritability was extremely high,

i.e. $h^2 = 0.39$, when a sire model with a log link function for Poisson data was applied. Comparing results from linear animal models, heritabilities were higher when count data instead of binary data was used. For example for OC_II, heritability of 0.08 was substantially higher than estimates from animal linear model for OC_I. In 2009, Valimont et al. applied GLMM with a log link function for mastitis, but in their study, heritability was about 6% smaller compared to estimates for Mast_II from our study. For Met_II and RP_II, heritabilities from linear sire and linear animal models were almost identical, but for Mast_II and for OC_II, heritabilities were higher when using the linear sire model, i.e. $h^2 = 0.10$ versus $h^2 = 0.07$ for Mast_II, and $h^2 = 0.13$ versus $h^2 = 0.08$ for OC_II. For count data, the lowest heritabilities among all traits were estimated for Met_II with values close to zero for both linear models. GLMMs for Met_II with a log link function for the Poisson distribution did not converge.

Table 6. Heritability and standard error (SE) of heritability (h^2) for mastitis (Mast_II), metritis (Met_II), retained placenta (RP_II), ovarian cysts (OC_II), and acetonemia (Acet_II) from animal model and sire model based on the second trait definition².

Health trait	Model	Link function / assumed data distribution			
		Identity / Gaussian		Log / Poisson	
		h^2 (x 100)	SE (h^2)	h^2 (x 100)	SE (h^2)
Mast_II	Animal	6.77	0.0477	27.52	0.1629
Mast_II	Sire	10.31	0.0190	17.58	0.1219
Met_II	Animal	0.09	0.0304	x	x
Met_II	Sire	0.09	0.0089	x	x
RP_II	Animal	4.16	0.0391	14.44	0.1219
RP_II	Sire	3.62	0.0119	38.70	0.1243
OC_II	Animal	7.95	0.0494	x	x
OC_II	Sire	12.63	0.0212	14.01	0.0880

¹⁾Total number of disease cases during -1 to 120 d after calving

^{x)}Not converged

Heritabilities and repeatabilities from repeatability models 2a and 2b are shown in Table 7. Substantial differences between heritabilities and repeatabilities were found for OC_III, suggesting a substantial permanent environmental effect. Repeatability for OC_III was 0.14, but heritability for OC_III was only 0.01 underlying that repeated non-genetic effects have

major impact on occurrence of ovarian cysts during lactation. Variance ratios for permanent environmental effects for Mast_III and Met_III, averaged from both the linear animal and sire model, were 1.93% and 2.19%, respectively. However, several other studies (Vallimont et al., 2009; Wolf et al., 2010) have found a substantial larger variance of permanent environment effects for mastitis compared to results from our study. As shown by Gernand et al. (2012), the permanent environmental effect was extremely small for retained placenta. But this finding is due to the 'biological nature' of this trait.

Daily heritabilities by DIM from RMM are depicted in Fig. 1a when using linear sire model, and in Fig. 1b when using threshold methodology and the probit link function. In contrast to the theoretical expectation heritabilities on the observed scale from the linear model were generally higher than on the underlying liability scale from the threshold model. From the threshold model over the whole trajectory for DIM, heritabilities were close to zero. Only for retained placenta, slightly higher heritabilities were found on the underlying liability scale. For both models and all analyzed health traits, heritabilities were highest at the beginning of lactation, and only increased for Mast_III at the end of the defined interval. A similar shape of curves for the heritability of mastitis was found for CM in first parity Swedish Holstein cows (Carlén et al., 2009). Mastitis was recorded during the entire lactation, whereas health disorders of the categories 'female fertility' and 'metabolism' were only relevant directly after calving which may explain the low genetic variation after DIM 50. In the study by Carlén et al. (2009), they applied a linear sire RRM, but not a threshold sire RRM. Also Döhne et al. (2012) concluded high data quantity and data quality is imperative for the application of a threshold RRM for binary claw disorders. Estimates of heritabilities for Mast_III from the linear sire RRM were in the range reported in the literature for comparable DIM (e.g. Chang et al. 2004).

Genetic correlations between DIM 5 and remaining days in the interval from calving to DIM 125 showed the same pattern for the linear RRM (Fig. 2a) and the threshold RRM (Fig. 2b). Genetic correlations between neighboring days were close to 1, but substantially dropped when correlating day 5 with days in the interval from DIM 50 to DIM 100. In the linear model, genetic correlations of $r_g = -1$ suggest a complete re-ranking of sires for different days in milk. Low genetic correlations in the same health disorder for test-days being far apart were also found in other studies applying RRM for binary health data (Carlén et al., 2009; Döhne et al., 2012), but curves were smoother, and negative correlations did only exist for

large intervals between days of interest. For production traits, in small organic (Yin et al., 2012a) as well as in large-scale conventional dairy cattle herds (Gernand et al., 2007), minimum of genetic correlations in the same trait between different DIM was $r_g = 0.50$. Low genetic correlations in same health traits between different days also indicate that mastitis, metritis, and ovarian cysts are completely different traits before and after DIM 50. Hence, ongoing research should focus e.g. on specific major pathogens as done by Schafberg et al. (2006) which have different relevance at different stages of lactation. Such a deeper analysis might contribute to a deeper understanding of the physiological and genetic background of clinical mastitis. Also metritis is defined as a multi-factorial disease, which can be caused by a variety of major pathogens including bacteria, viruses, and fungi (Foldi et al., 2006). For interpretation of results of genetic correlations, extremely large Bayesian information criterion (BIC) and SEs for sire threshold RRM should be kept in mind.

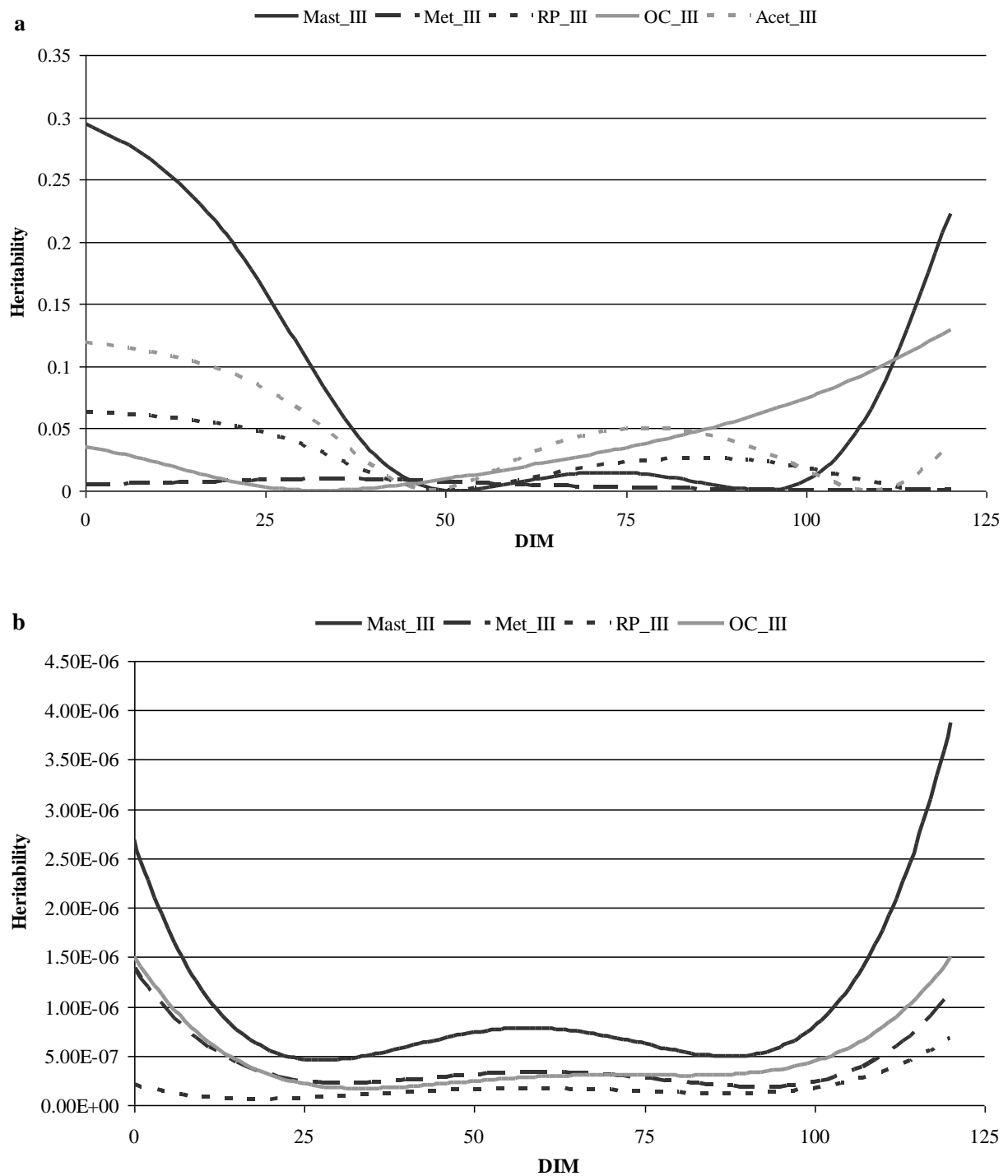
Table 7. Heritability, standard error (SE) of heritability (h^2), repeatability (r) and SE of repeatability for mastitis (Mast_III), metritis (Met_III), retained placenta (RP_III), ovarian cysts (OC_III), and acetonemia (Acet_III) from animal and sire repeatability model based on the third trait definition².

Health trait	Model	Link function / assumed data distribution							
		Identity / Gaussian				Probit / Binary			
		h^2 (x100)	SE (h^2)	r (x100)	SE(re)	h^2 (x100)	SE (h^2)	r (x100)	SE(re)
Mast_III	Animal	2.62	0.0148	3.76	0.0134	7.62	0.0976	7.62	0.0892
Mast_III	Sire	4.57	0.0065	7.29	0.0136	22.22	0.0468	22.22	0.0904
Met_III	Animal	0.67	0.0101	2.61	0.0133	9.60	0.1708	10.07	0.1407
Met_III	Sire	0.62	0.0030	3.06	0.0132	8.00	0.0502	8.00	0.1453
RP_III	Animal	0.52	0.0089	0.52	0.0126	x	x	x	x
RP_III	Sire	0.53	0.0029	0.53	0.0125	6.83	0.0483	6.83	0.1474
OC_III	Animal	1.76	0.0155	13.56	0.0152	x	x	x	x
OC_III	Sire	1.19	0.0045	14.33	0.1510	x	x	x	x
Acet_III	Animal	x	x	x	x	x	x	x	x
Acet_III	Sire	0.37	0.0026	0.38	0.0128	0.29	0.0287	0.29	0.0457

¹⁾ Presence (1) or absence (0) of health disorders during test-day intervals

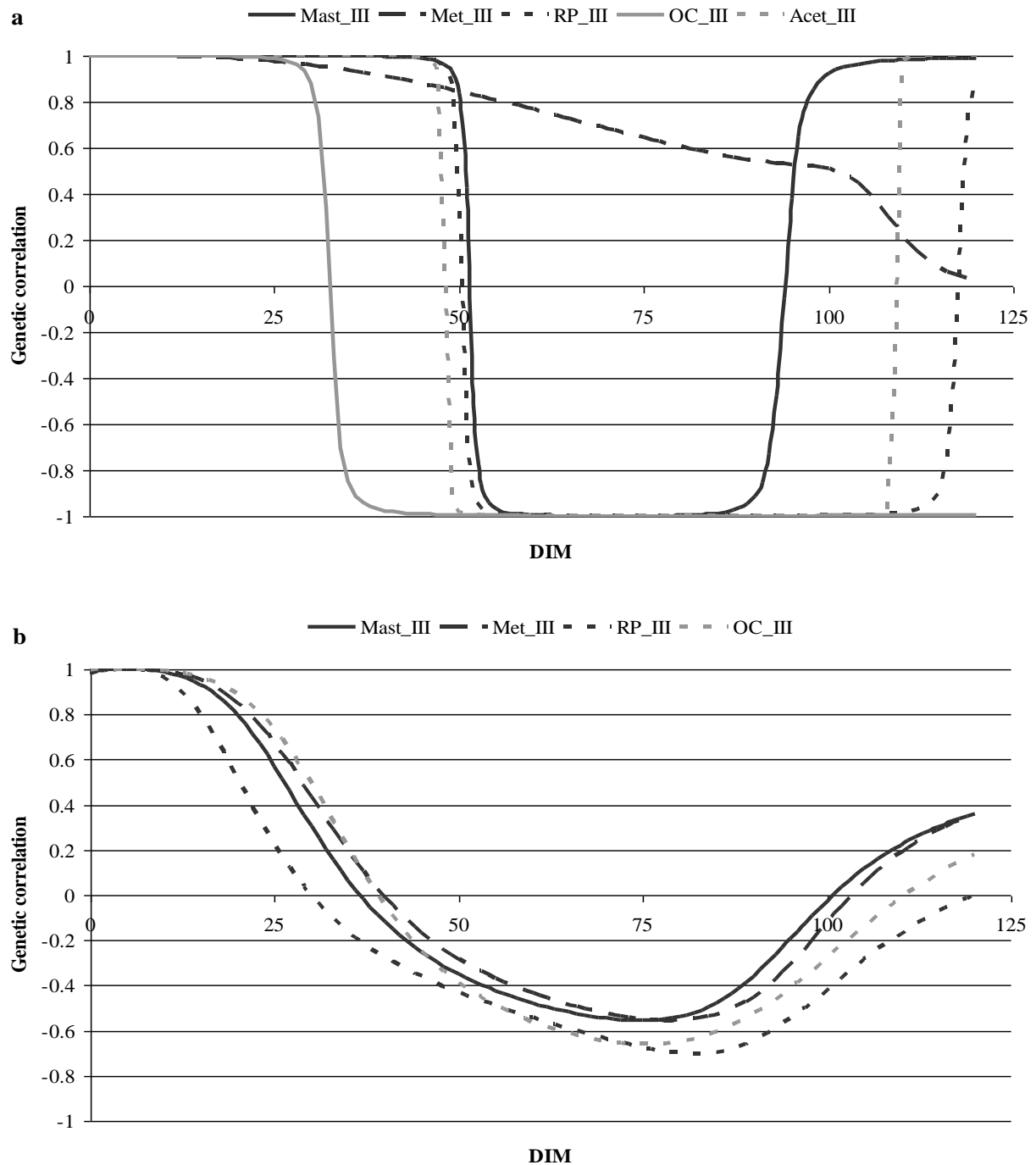
^{x)} Not converged

Figure 1. Heritability of mastitis (Mast_III), metritis (Met_III), retained placenta (RP_III), ovarian cysts (OC_III), and acetonemia (Acet_III) from linear (a) and threshold (b) sire random regression model with link function of identity and probit based on the third trait definition¹.



¹) Presence (1) or absence (0) of health disorders during test-day intervals

Figure 2. Genetic correlation between 5 days after calving and other days for mastitis (Mast_III), metritis (Met_III), retained placenta (RP_III), ovarian cysts (OC_III), and acetonemia (Acet_III) from linear (a) and threshold (b) random regression sire model with link function of identity and probit based on the third trait definition¹.



¹) Presence (1) or absence (0) of health disorders during test-day intervals

Comparison of models

Convergence problems were more likely to occur when threshold methodology was used compared to linear model applications (Table 8). This finding is especially valid for ovarian cysts and acetonemia, which characterized by extremely low disease incidences. Convergence problems were less relevant for sire compared to animal models, maybe due to the above mentioned properties of threshold methodology. When applying sire instead of animal models, the number of animals in the pedigree decreased from 5,834 to 2,426 which reduces substantially the number of solutions that have to be estimated.

Average SE of heritabilities when using threshold models (model 1b and 2b) was 0.13, and decreased to 0.0235 when linear models (Model 1a and 2a) were applied. Koeck et al. (2010a) found that SEs for heritabilities from logit threshold sire models were around 5 times as large as SEs from linear models. Also Pérez-Cabal et al. (2009) reported larger SEs for heritabilities from threshold and Poisson models compared to linear model applications. For models 1 and 2, average SE from sire models with a value of 0.054 was significantly different from animal models (SE = 0.083). The maximum SE for heritability (0.41) was found when using an animal model, although the corresponding SE from the sire model was also quite high (0.17). In a study by Ghavi Hossein-Zadeh et al. (2009), slightly higher SEs for estimated heritabilities were found from animal models as well. SEs of heritabilities estimated by threshold and linear RRM followed the same pattern. Relatively high SEs were found at the very beginning of lactation as well as in the last interval. However, in general SEs for RRM were relatively large, which might be attributed to the small number of records in the low input population and the extremely small herd sizes.

The main evaluation criterion was BIC. BIC is a criterion for model selection and it depends on log likelihood function and number of parameters to be estimated. Apart from Mast_I and model 3, BIC from animal and sire models were almost identical, while health traits analyzed with probit or log link functions always revealed a lower BIC than the application of linear models. The fundamental reason is that health disorders are categorical traits which are not following Gaussian distributions. Hence, our study favored the general threshold concept over linear models for the analysis of categorical traits. Tempelman and Gianola (1999) clearly demonstrated that negative binomial mixed models were more appropriate for the analysis of binary female fertility traits than linear mixed models. However, evaluation of RRM does not

fit in this theoretical context. BIC from threshold sire RRM was larger than BIC from linear sire RRM and sire and animal repeatability models, which is in line with the extremely large SEs for heritabilities estimated from the threshold sire RRM.

Using Poisson mixed models for genetic analyses of count data are not only applied in our study but also in other studies (Vallimont et al., 2009; Vazquez et al., 2009a; Vazquez et al., 2009b) and higher variance components for additive genetic effects were found in the studies. However, cows without diseases are significantly higher than cows with one or more cases of diseases, e.g. frequencies of cows without health disorders were higher than 94% in this study. Due to the high percentage of healthy cows, Poisson distribution can not characterize count data for health disorders accurately. Alternatively, Rodrigues-Motta et al. (2007) compared zero-inflated Poisson models with a standard Poisson model to analyze total number of cases for CM in Norwegian Red cattle. Only small differences were found between the two models as the rank correlation of sires was 0.98. Nevertheless, the high percentage of cows without mastitis in this and other studies suggested that zero-inflated models may warrant further development (Vallimont et al., 2009).

Table 8. Bayesian information criterion¹ (BIC) for mastitis, metritis, retained placenta, ovarian cysts and acetonemia from animal and sire model (Model 1), animal and sire repeatability model (Model 2) and sire random regression model (Model 3) based on the three definitions.

Model	Link function	Pedigree	Mast_I	Mast_II	Met_I	Met_II	RP_I	RP_II	OC_I	OC_II	Acet_I
Model 1	Identity	Animal	-1017	-1748	-2989	-2410	-2623	-2420	-4770	-3121	-3877
		sire	-2222	-1747	-2989	-2410	-2623	-2419	x	-11338	-3878
Model 1	Probit	Animal	-1071	-3551	-5298	x	-4567	-4238	x	x	x
		sire	-2179	-3511	-5313	x	-4550	-4182	x	-19890	x
			Mast_III		Met_III		RP_III		OC_III		Acet_III
Model 2	Identity	Animal	-15610		-18857		-17711		-25708		x
		sire	-15610		-18852		-17706		-25702		-22987
Model 2	Log	Animal	-44430		-18123		x		x		x
		sire	-44754		-21572		-48762		x		-59539
Model 3	Identity	sire	-17368		-21120		-24614		-26275		-24550
Model 3	Probit	sire	186596		10340		31223468		671		x

¹⁾ The lower the BIC value is, the better the model fit.

^{x)} Not converged

CONCLUSIONS

Disease incidences of mastitis, metritis, retained placenta, ovarian cysts and acetonemia recorded in the early stage of lactation were relatively low in organic dairy farms in Switzerland. Generally, genetic parameters of the five health traits were in a reasonable range. Marginally lower heritabilities might be due to the low disease incidences, which can result in low additive genetic variances. For routine genetic evaluation, the optimal statistical model should be identified. Based on the BIC information criterion, Poisson and Binomial mixed models were favored compared to linear models. Only when applying RRM, the linear sire model gave a better fit to the data than the threshold sire model. When applying RRM, SEs of estimated genetic parameters were relatively high and genetic correlations for the same disease between different DIM dropped to negative values. Number of parameters to be estimated and complexity of calculations increase dramatically by using longitudinal data and applying RRM. Hence, for small datasets and small contemporary groups combined with low disease incidences in organic farms, we suggest a robust application. Instead of using a longitudinal data structure or only a single observation within a given time interval, the total number of unique episodes of a disease (count variable) might be a promising alternative for practical applications.

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4th CHAPTER**Optimal Strategies for the Use of Genomic Selection in Dairy Cattle Breeding Programs**

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ABSTRACT

The objective of the present study was to conduct a stochastic simulation study on the possible benefits of an application of genomic selection in dairy cattle breeding programs according to a variety of selection schemes. In addition, the heritability of the trait in question, the accuracy of genomic breeding values, and the number of animals to be genotyped were varied. Specifically, the question of genotyping males and / or females was addressed. Selection schemes were compared with a young bull breeding program. The main criterion for comparison was the average of true breeding values of selected young males to be used as replacements for A.I. bulls. Stochastic simulations were run with 50 repetitions each to generate individuals with phenotypes, breeding values estimated by BLUP, and true breeding values. Genomic breeding values were generated from true breeding values with defined accuracy. Examined scenarios included a group of selection schemes that featured genotyping of parents of future bulls only. Such schemes can be viewed as improvements of young bull programs and were found to be competitive or superior with a classical young bull program. However, usually, a genomic breeding program will consist of at least genotyping young male candidates. A second group of selection schemes reflected this requirement. Scenarios in this group were found to be superior over the young bull program by 1.0 SD to 1.2 SD of the average true breeding value of young male candidates. Within this group of scenarios, one scheme referred to an ideal situation under which genotypes for male calves are available without limitation. Using the average of true breeding values as the criterion for comparison, this idealistic scenario is only competitive with other scenarios, if the reliability of genomic breeding values is larger than 0.50. Conventionally, not all males available will have genotypes, and the two most promising scenarios included a pre-selection step for dams of future bulls. This pre-selection step can be based on conventional BLUP EBV for bull dams, because differences with a scheme under which both parents and the resulting male offspring are genotyped were marginal. Genotyping of young male candidates should be the main focus of activities of a today's breeding organization.

Key words: Genomic selection, breeding program, pre-selection

INTRODUCTION

Basing selection decisions on the results of genotyping animals for high-density arrays of single nucleotide polymorphisms (SNP) denotes what is now called genomic selection. It consists of estimating breeding values applying previous knowledge from so-called calibration or reference samples. This new tool in dairy cattle breeding has the potential of overcoming the up to now existing obstacle of a costly and time-consuming progeny test for future bulls to be used in artificial insemination. Meuwissen et al. (2001) have shown the enormous potential of such a strategy, and Schaeffer (2006) using simple deterministic calculations outlined the use of genomic selection comparing traditional and new strategies with respect to genetic gain and costs. Since then, numerous authors have studied the benefits of genomic selection in dairy cattle breeding programs.

It is quite obvious that the accuracy of a genomic evaluation, i.e. the correlation between a breeding value estimated from genomic data, and incorporating the results from calibration samples, with the true breeding value, often referred to as r_{mg} , plays a critical role in the success of implementing genomic selection into a breeding program. The current knowledge on what can be achieved considering this parameter points to accuracies that will be high enough to resemble accuracies obtained from costly and time consuming progeny testing. Amongst others, Goddard and Hayes (2009) have emphasized that the size of the calibration sample which is composed of bulls with high accuracies of their progeny test genetic evaluations is the most critical parameter determining r_{mg} . However, other factors, like the extent of linkage disequilibrium in the specific population will also play a role. VanRaden et al. (2009) showed that reliabilities (r_{mg}^2) of genomic breeding values were as high as 69 % for a calibration sample of 3,576 bulls but depended on the trait analysed. For traits with lower heritability, lower values will be found. Hayes et al. (2009) also showed the dependencies between the size of the calibration sample and the reliability obtained. Latest results from various countries were presented at the World Congress on Genetics Applied to Livestock Production. Wiggans et al. (2010) reported a value for r_{mg}^2 of 71 % for milk yield and 76 % for fat yield, based on a calibration sample of 7,113 Holstein animals consisting mostly of bulls but also incorporating cows. For the German calibration sample of 5,025 bulls, Liu et al. (2010) presented values for r_{mg}^2 of 68 % for milk yield and 72 % for fat yield. Lund et al. (2010) showed results from the up to now largest reference population consisting of bulls that has been assembled for the Holstein breed by a team effort of the countries France, The Netherlands, Denmark, Sweden, Finland, and Germany. This reference population includes 15,966 bulls and has contributed to further increase the reliabilities obtained in the respective

individual countries by substantial margins. For the German calibration sample, reliabilities based on the combined reference population and compared to the national reference were increased by 11 %, averaged over traits (Lund et al., 2010). On the other hand, also countries with smaller breeds will adopt genomic selection and will have to cope with lower accuracies. Thus, concluding from the wide range of results for reliabilities or accuracies of genomic breeding values that have been reported so far, it will be necessary to reflect this wide range in model calculations studying the benefits of genomic selection.

In quite a few countries or even through collaborative efforts across countries, procedures for genomic selection have already been implemented so far. Interbull (Interbull, 2010) lists eight Holstein populations from 11 countries that provided information for the validation of their genomic evaluation system. However, within population or country, breeding organizations at present are facing the question on how to make use of the genomic evaluation provided and especially have to answer the question which animals should be genotyped as candidates for selection. In conventional progeny testing programs, the most crucial step of selection is the selection of bull dams since potential selection candidates are spread across herds, regions, and even countries and are subject to preferential treatment. The male paths of selection are less problematic as long as a progeny test with sufficient numbers of progeny is conducted in an unbiased way. Therefore, a topic of intense discussion is whether to genotype males, or females, or both sexes as candidates for selection.

The overall objective of the present study was to conduct a stochastic simulation study on the possible benefits of an application of genomic selection in dairy cattle breeding programs. A stochastic simulation was preferred over a deterministic calculation since means and variances of individuals can be studied and also due to the fact that a stochastic simulation allows for greater flexibility when analysing the simulated data. Within the general objective, the present study aims at varying the most critical parameters and scenarios. This specifically pertains to genotyping a wide range of animals, females and males, and also varying the reproductive rate of females, thus resulting in a categorization of general strategies and varying selection intensities within strategies. The overall approach is to take the view of a breeding organization. This is not only reflected by varying selection intensities but also by defining the main criterion for comparison as the average of true breeding values of the selected bulls that are the ultimate product of an A.I. organization. Additionally, the genetic structure and inbreeding coefficients of the bull calves selected to be future replacements for bulls used in widespread artificial insemination will be examined.

MATERIAL AND METHODS

Simulation was based on the application of the QMSIM program (Sargolzaei and Schenkel, 2009). QMSIM is a very powerful simulation program to be used for the stochastic simulation of animal populations covering a population genetic level as well as the genomic level and featuring the simulation of historical populations to create linkage disequilibrium. The genomic level includes the capability of defining several chromosomes with QTL and marker maps. In the present study, however, QMSIM was used to simulate populations consisting of individual animals under a defined genetic structure of the entire population along with their true breeding values and phenotypes. Features simulating high-density marker maps were not used since the objective of this study was not to simulate the entire process of genomic selection including calibration samples, estimation of genomic breeding values, validation, and finally the use of formulae to predict breeding values for young selection candidates without phenotypes. Rather, genomic breeding values, i.e. breeding values estimated from genomic data without the use of phenotypes, were simulated with defined accuracies based on the true breeding values.

Simulation of populations using QMSIM

A founder population was generated over 1000 generations with a constant population size of 50,500 animals, the last generation containing 50,000 females and 500 males. Based on this founder population, 20 generations of a population under selection were simulated. Animals of the last historic generation were parents of generation 1 for the population under selection. For females, a replacement rate of 25 % was set. For males, 50 % of the individuals were replaced by males from the following generation. Selection of males and females under these replacement strategies was based on BLUP EBV for a single trait. Within the selected fractions of males and females, mating was at random. The assumption of random mating appears to hold as breeders have many individual reasons for choosing a bull from those selected and offered by breeding organizations. In contrast, a strictly assortative mating scheme would be way off to what happens in the real world of dairy cattle breeders. From generation 1 to generation 5 the number of females in the population was increased by 25 % of the original population size to reflect the growth of a superior breed. Thus, the number of

females for generations 1 to 5 was 50,000, 62,500, 75,000, 87,500, and 100,000. The number of sires was kept at 500. After generation 5, the size of the population was constant.

Within the simulation of generations 1 to 19, the reproductive rate of females was set such that one offspring, with a probability of 50 % for being male or female, was produced by every cow. However, for potential bull dams, this may not be applicable. Modern dairy cattle breeding programs almost regularly use embryo transfer to increase the reproductive rate of females. In the simulation studies by Sorensen and Sorensen (2010), Buch et al. (2010), and Pedersen et al. (2010), the success rate of embryo transfer was set to 5 offspring per cow. Although such a value may be achievable, in this study we used a much lower success rate such that in the last generation 20, all cows produced one male offspring. In a second set of simulation scenarios, the rate of male offspring per bull dam in generation 20 was set to 0.5.

In total, two single traits with mean zero and phenotypic SD of 1.00 were independently simulated in different simulation runs for a heritability of 0.10 and 0.30. Simulations using QMSIM were repeated 50 times. Within each repetition means for true breeding values for desired numbers of selected bull calves were computed. Then, means for repetitions were averaged and SDs were calculated across repetitions and within scenario and number of selected bull calves.

Selection was based on BLUP EBV as supplied by QMSIM. In summary, the variables simulated for every individual applying QMSIM and used for further processing were phenotypes, conventional BLUP EBV, true breeding values (TBV), and the inbreeding coefficients. In all further steps, only animals from generation 20 were considered as young candidates for selection to mimic the actual situation of breeding organizations.

Simulation of genomic EBV

Based on the output of the QMSIM program, all further computational steps were undertaken by own programming using SAS and C as programming languages. Given the objective to analyze various scenarios differing by the correlation between breeding values estimated from genomic data with the TBV, direct genomic breeding values were simulated based on the TBV as supplied by QMSIM according to the following formula

$$gbv_i = ((1-r_{mg}^2)^{1/2} z_{g_i} + r_{mg} \cdot TBV_i / sd(TBV_i)) sd(TBV_i)$$

where gbv_i is the genomic breeding value of animal i , r_{mg} is the accuracy of the genomic breeding value, TBV_i is the true breeding value of animal i , $sd(TBV_t)$ is the standard deviation of TBV in generation t , and z_g is a random variable sampled from $N(0,1)$.

For some scenarios, the population was divided into groups to imitate large herds to be used as a nucleus for selection activities. Herd sizes were from 200 to 800 cows, i.e. with a mean of 500 cows and an SD of herd size of 100. Selection of such herds by breeding organizations most likely will be according to phenotypic level. This was mimicked by deriving herd effects which were correlated with the average genetic level of the herd according to

$$hm_j = ((1-r_{hm,EBV}^2)^{1/2} z_{g_j} + r_{hm,EBV} \cdot EBV_{Herdj} / sd(EBV_{Herd})) sd_{hm}$$

Where hm_j denotes the herd effect of herd j , $r_{hm,EBV}$ is the correlation between the vector of herds effects (hm) and the vector of herds EBV averages (EBV_{Herd}), and $sd(EBV_{Herd})$ is its standard deviation. EBV_{Herdj} is the average EBV of all cows in herd j . A fixed value of 0.3 was used for $r_{hm,EBV}$.

Scenarios for comparison

All scenarios centered on comparing the genetic merit of selected young bull calves as potential replacements for A.I. bulls. Figure 1 gives an overview of the scenarios simulated for comparisons. In Figure 1, scenarios are grouped by three main strategies. Scenario REF is the reference scenario referring to the initial step of a conventional progeny testing program, i.e. the selection of young bulls for progeny testing. In this scenario, bull calves are selected through selection of parents with outstanding EBV, i.e. by a pedigree index defined as the mean of parents' BLUP EBV. Selection simply consisted of selecting the best n bull calves according to their pedigree index in a single step. Thus, scenario REF denotes a young bull program. In conventional programs, these young bulls would then be subject to progeny testing and their genetic merit with accuracy typical for progeny testing would only be known five years later. Given that the conventional estimation of breeding values would be unbiased, a selection among these calves according to pedigree index would result in average values for TBV corresponding to average EBV that would be available five years later. However, REF differs from a conventional progeny testing program as only the pre-selection step of a conventional program was applied for this scenario.

GPROG – Bull calves are genotyped					
ALL All bull calves are genotyped	RANDOM n bull calves are genotyped at random	BD_BLUP n bull dams are pre-selected based on BLUP-EBV, their bull calves are genotyped	BD_PHEN n bull dams are pre-selected based on phenotype, their bull calves are genotyped	BD_HERD n bull dams are pre-selected from specific herds, their bull calves are genotyped	BD_GENO n bull calves are pre-selected on PI-GBV and genotyped
GPAR – Parents are genotyped, bull calves are not					
ALL All parents are genotyped; No shortage of bull dams with genotypes		BD_BLUP Pre-selection of n bull dams based on BLUP-EBV		BD_PHEN Pre-selection of n bull dams based on phenotype	
REF – Bull calves are selected on pedigree index					

Figure 1. Characteristics of the simulated scenarios.

Scenario GPAR consists of a group of scenarios describing a situation in which a breeding organization is reluctant to use the technology of genomic selection or wishes to minimize any costs associated with it. In such a situation, a breeding organization could rely on the availability of GBV for bulls and especially sires of bulls already genotyped by other breeding organizations worldwide. Additionally, many potential bull dams will already have been genotyped, financed by the individual owner rather than the breeding organization. Such a scenario can also be viewed as a scenario describing the situation of a breeding organization not having access to genomic selection technology and hence relying on publicly available data or on data supplied by individual breeders. This could also denote the case of individual traders of genetic material that select bull calves based on genomic evaluations of parents which will or may be publicly available and market these young bulls for A.I. or as natural service bulls under the term “genomically selected”. In all GPAR scenarios, GBV are available for parents, i.e. potential bull sires and bull dams. Scenario GPAR_ALL denotes a situation in which all females that could possibly be used as bull dams, i.e. all females, will have a GBV and the GBV of potential sires of bulls will be publicly available. In GPAR_BD_BLUP, a pre-selection step is introduced such that bull dams with a high conventional EBV will be genotyped. Scenario GPAR_BD_PHEN is similar to scenario GPAR_BD_BLUP, however, bull dams are pre-selected according to phenotype rather than

EBV. For GPAR_BD_BLUP and GPAR_BD_PHEN, the number of pre-selected females was varied to build selection pools of 50, 100, or 500 females. These numbers were chosen to reflect the current situation in which the number of potential bull dams is still limited and can be viewed as a contrast to an unlimited access to genotyped bull dams simulated in GPAR_BD_ALL.

In all GPROG scenarios, bull calves as potential candidates for selection are always genotyped and thus have a GBV. Disregarding costs and all other expenses within a breeding program, such scenarios will always have the clear advantage of having a GBV associated with each bull, the final product of all efforts of the breeding organization. In GPROG_ALL, the “bull calf program” as suggested by König and Swalve (2009) is represented. All male calves will have a GBV thus assuming an ideal situation in which costs of genotyping would be negligible. Scenario GPROG_RANDOM is a variation of GPROG_ALL but now defining limits to a number of randomly genotyped bull calves. For scenario GPROG_BD_BLUP, a pre-selection step is introduced. Bull dams are pre-selected according to their conventional BLUP EBV and only their male offspring has to be genotyped. Scenario GPROG_BD_PHEN is similar to scenario GPROG_BD_BLUP, but the pre-selection step is based on phenotypes of cows. In scenario GPROG_BD_HERD, selection of bull dams is restricted to specific herds that could be called “supplier herds” (Weigel, 2008) since they are the source to supply new genetic material. Scenario GPROG_BD_HERD can also be viewed as the initiation of a nucleus scheme where herds are selected to form the nucleus and from then on selection, at least of females as future bull dams, is practiced within these herds. As explained above, large herds of size 500 were formed to simulate this situation. In order to avoid a further pre-selection step which would again create a need for variation, all females in these herds were considered as potential bull dams and hence selection took place within their male calves. Finally, in scenario GPROG_BD_GENO all animals involved in the selection process will have a GBV, bull sires, bull dams, and their male offspring. Pre-selection steps in GPROG_BD_GENO hence are based on the GBV of parents. For all scenarios GPROG_RANDOM to GPROG_BD_GENO, the number of bull calves or bull dams with either 0.5 or one male offspring, was varied by increments of 1000 from 1000 to 5000 bull calves with genotypes and hence with GBV available for selection. Not for all scenarios a variation of the reproductive rate for bull dams is reasonable. This pertains to GPROG_ALL and GPROG_RANDOM and hence was not simulated.

In summary, all scenarios, REF, GPAR and GPROG can also be viewed as young bull programs in which young bulls directly enter service as A.I. bulls. The question of acceptance of this genetic material by breeders and commercial dairy producers is not addressed but has been discussed elsewhere (e.g. König et al., 2009). Neglecting the specific topic of the reproductive rate of bull dams, a total of 10 main scenarios were compared. Accounting for the variations of pre-selected animals in all scenarios except REF, GPAR_ALL, and GPROG_ALL, a total of 34 scenarios were evaluated for six levels of r_{mg} and the entire set was repeated for heritabilities of 0.10 and 0.30.

Criteria for comparison

Breeding organizations most likely will seek to compare alternative selection strategies based on the average of breeding values of the bulls finally selected for A.I. since this parameter will determine their share in a competitive market. Scenarios that will be optimal under this criterion will also be the scenarios resulting in maximization of genetic gain. Averages and SD of TBV for varying numbers of selected animals were used. This is also in line with studies by de Roos et al. (2010) and Winkelman and Spelman (2010). Given that genetic evaluations performed will be unbiased, animals selected based on TBV as available in simulation studies will be identical to animals selected based on EBV with high accuracy.

An evaluation of alternate breeding strategy would not be complete without examining inbreeding coefficients of the selected animals as only strategies with acceptable inbreeding coefficients will be sustainable. This is acknowledged by most authors conducting similar simulation studies (e.g. Pryce et al., 2010). Inbreeding coefficients were analyzed as supplied for all individual animals by the QMSIM program.

RESULTS and DISCUSSION

Results for a comparison of all ten main scenarios including all sub-scenarios for pre-selection steps are given in Figure 2 for a heritability of 0.10 and an accuracy r_{mg} of 0.70 and in Figure 3 for a heritability of 0.30 and an accuracy r_{mg} of 0.90. These two sets of parameters were chosen since they reflect the German situation for genomic selection in Holsteins based on the Eurogenomics calibration sample. For functional traits with a low heritability, accuracies of around $r_{mg} = 0.70$ are achieved and for traits with a moderate heritability of around 0.30,

accuracies close to $r_{mg} = 0.90$ have been obtained. All values on the y-axis of the two graphs refer to the average of the TBV. Under the parameters used to simulate the population, the SD of TBV is 0.32 for $h^2 = 0.10$ and 0.55 for $h^2 = 0.30$. Scenario REF denotes the reference scheme under which bull calves are selected according to their pedigree index. It is well known that a wide-spread use of young bulls would be advantageous as recently shown again by Buch et al. (2010). For all scenarios, the averages of the TBV of the best five bulls are given.

In scenarios GPAR, the bull calves itself are not genotyped. This leads to a substantial disadvantage compared to scenarios GPROG and reflects the fact that an additional meiosis is involved from parents to sons. Generalizing, this disadvantage will amount to one SD of TBV between the best GPAR and GPROG scenarios. In scenario GPAR_ALL, there is no shortage in potential bull dams as all females are genotyped and sires of bulls are always genotyped. Selection of bull calves under GPAR_ALL is based on genomic pedigree index. Especially for a low $r_{mg} = 0.70$, improvements can be obtained when a pre-selection step involving 50, 100 and especially 500 bull dams are pre-selected based on their conventional BLUP EBV is implemented. This finding may be surprising but is readily explained by the fact that for low r_{mg} , the access to a large population of genotyped females is not very helpful when the goal is to find superior animals according to their TBV. As expected a pre-selection of bull dams according to phenotype results in lowest average values of TBV of bull calves. This is especially evident for a low heritability (Figure 2). Thus, breeding organizations or individual marketers of genetic material without access to the technology of genomic selection will not be competitive when attempting to market young bulls or their semen based on GBV of their parents only. For a moderate heritability (Figure 3), however, this low cost strategy would be competitive to the reference scenario. This strategy then could also be called an improved juvenile scheme.

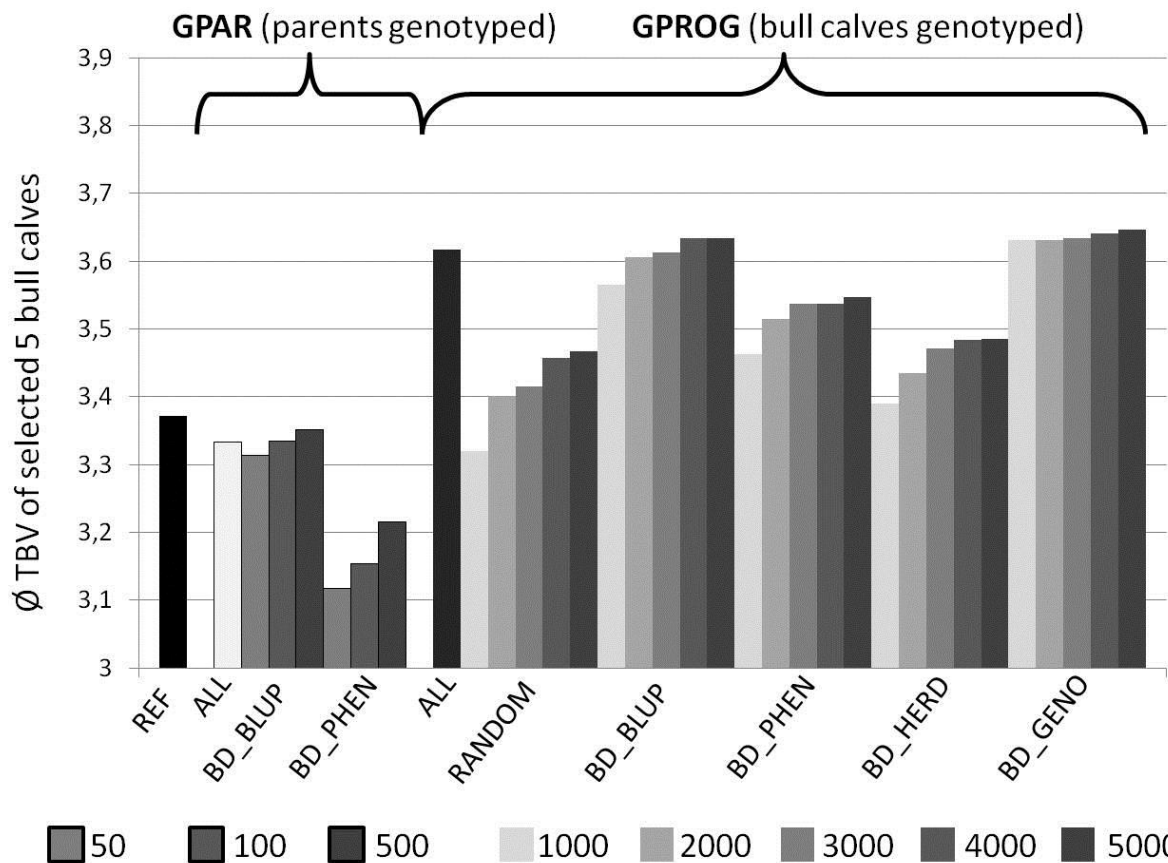


Figure 2. Average of true breeding values (TBV) of five selected bull calves for the scenarios examined under parameters $h^2=0.1$ and $r_{mg}=0.7$.

All GPROG scenarios obtain impressive results of an advantage of around 1.0 SD (Figure 2) or 1.2 SD (Figure 3) over the reference scenario. Scenario GPROG_ALL refers to the very idealistic scenario under which all male calves would be genotyped. However, as can be seen when comparing Figures 2 and 3, this would only be a distinct advantage for a higher r_{mg} . When comparing all scenarios, it should be kept in mind, that Figures 2 and 3 display the average TBV of the five young bulls selected by their GBV. This explains why even an ideal situation of a completely genotyped male population will not be of great help when r_{mg} is low and hence selection according to GBV is not accurate. As expected, a restriction of the pool of genotyped males available leads to lower values of TBV (scenario GPROG_RANDOM). However, the drop is not as marked as could be envisaged and underlines that a “bull calf program” according to König and Swalve (2009) would indeed produce young bulls with superior breeding values as compared to scenarios REF and GPAR. Even under a restriction of selecting from a pool of a few thousands of genotyped bull calves only and completely neglecting any pre-selection GPROG_RANDOM would be competitive with any scenario REF or GPAR. The comparison between scenarios GPAR_ALL and GPROG_ALL also can

be interpreted as what is gained from genotyping male calves, i.e. directly focussing on the product of a breeding organization, as opposed to concentrate on identifying superior females. In both scenarios, there is no shortage of genotyping, however, the superiority of GPROG_ALL in terms of the accuracy of selection is very clear.

A highly competitive scenario will be to include a pre-selection step for the bull dams and genotype their male offspring. Under low r_{mg} (Figure 2), this strategy even would be superior over the idealistic scenario GPROG_ALL. For higher r_{mg} (Figure 3), the advantage of GPROG_ALL over the GPROG_BD_BLUP scenarios would only be small. GPROG_BD_BLUP would also be cost-effective, as bull dams are not required to have genotype information. Thus, investments could be concentrated on genotyping an increasing number of bull calves from bull dams that are pre-selected according to their conventional BLUP EBV. Increasing the number of bull calves to be genotyped will be very beneficial for low r_{mg} and an increase from 1000 to 2000 bull calves (Figure 2) but benefits will be small or negligible thereafter. For higher r_{mg} and heritability (Figure 3), a pre-selection step will still yield improvements.

Analogous to the comparison of GPAR scenarios, also for GPROG scenarios a pre-selection step for bull dams based on phenotypes is not advisable. Again and as expected, the differences between scenarios GPROG_BD_BLUP and GPROG_BD_PHEN are larger for a low heritability (Figure 2) as compared to a moderate heritability (Figure 3). An even stronger reduction in the average TBV of the five selected bull calves is obtained when selection is practised in a few herds that have been pre-selected based on herd effects (scenario GPROG_BD_HERD). This result would underline that when selection is going to be conducted in selected herds only, these herds should be pre-selected according to genetic merit.

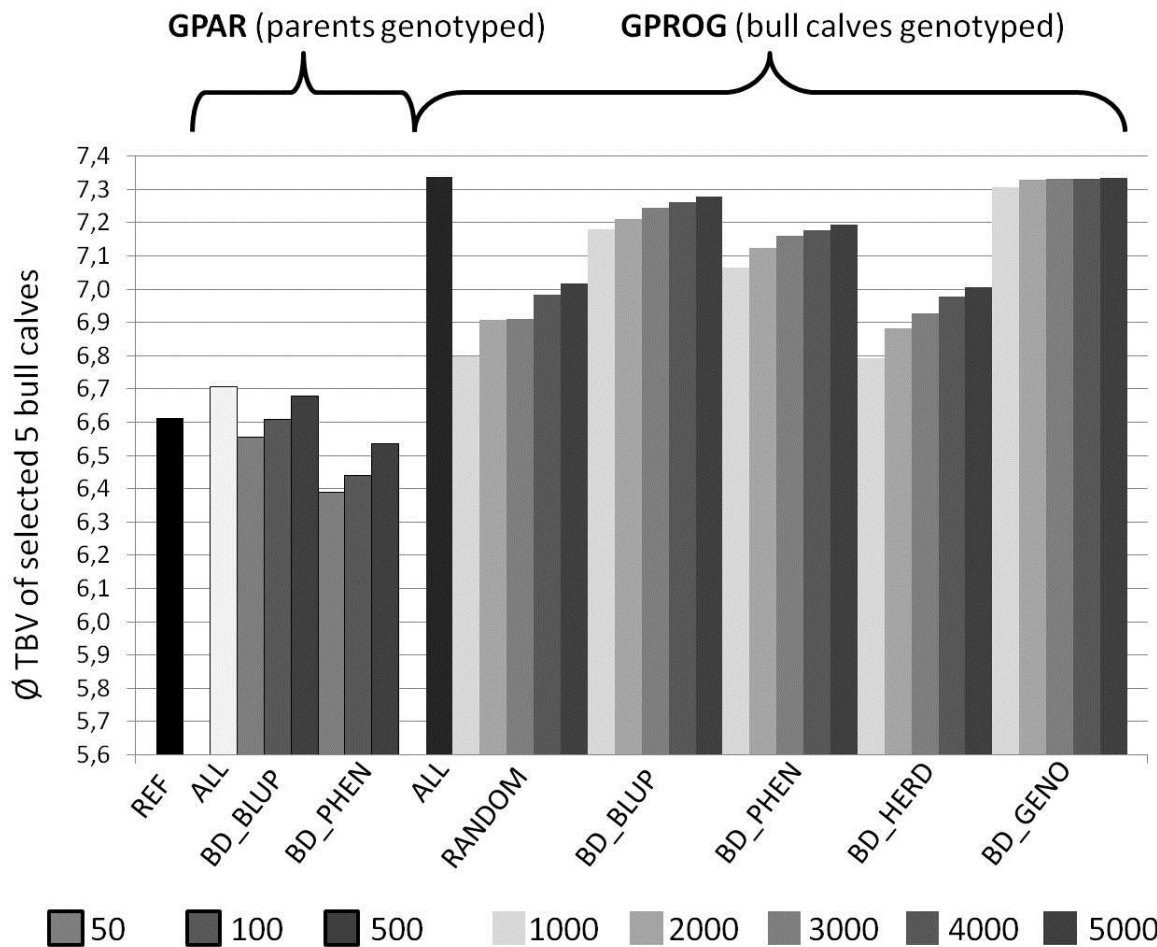


Figure 3. Average of true breeding values (TBV) of five selected bull calves for the scenarios examined under parameters $h^2=0.3$ and $r_{mg}=0.9$.

Highest averages of TBV of selected bull calves can be achieved when bull dams in addition to bull sires are pre-selected based on their GBV and additionally also bull calves will have GBV (scenario GPROG_BD_GENO). However, as evident when comparing GPROG_BD_BLUP and GPROG_BD_GENO, the advantage of the latter over the former would not be large. The slight increase has to be paid for through the costs of genotyping all potential bull dams. In practice, some scheme in between GPROG_BD_BLUP and GPROG_BD_GENO should be sought for as many bull dams will be genotyped on the expense of the breeders and thus the breeding organization could stick to a strategy of not genotyping bull dams on their own expense. This result is in line with Sorensen and Sorensen (2010) who stated that it would not be advisable to genotype females unless operating under a MOET situation with five offspring per female. As explained above, in the present study, a 'limited MOET condition' was assumed with one male offspring per selected female.

The question on whether to genotype females as potential bull dams also relates to the question of the extent and impact of preferential treatment of potential bull dams in dairy cattle breeding programs. A distinct advantage of genotyping females and basing any selection on genomic breeding values instead of conventional ones is that genomic selection nullifies the problem of preferential treatment (König and Swalve, 2009). Therefore, the ultimate decision of a breeding organization on whether to genotype females and pay for the genotyping should be based on the extent to which identifying superior females by conventional means is disturbed by preferential treatment. If a substantial extent of preferential treatment has to be assumed, scenario GPROG_BD_GENO would be the scheme of choice.

Figure 4 and 5 contain details on the mean value of TBV for all GPROG scenarios as these scenarios clearly are superior over REF and GPAR as seen from Figures 2 and 3. Figures 4 and 5 allow for a comparison of different r_{mg} (0.5 to 0.9) for both values of h^2 , $h^2 = 0.10$ and $h^2 = 0.30$. In scenario GPROG_ALL all bull calves in the population are assumed to be genotyped. In scenario GPROG_BD_GENO GBV are available for bull sires, bull dams and bull calves. Both scenarios perform equally with increases in average TBV from $r_{mg} = 0.5$ to $r_{mg} = 0.9$ amounting to 1.5 SD for $h^2 = 0.1$ and to 1.4 SD for $h^2 = 0.30$. These are substantial increases and explain the high variation of literature results based on different assumptions for r_{mg} . Results for a different value for the number of selected bull calves are not shown since no changes of relative differences between scenarios result from different values. Averages of TBV for higher numbers of selected bull calves simply decrease due to decreasing selection intensity. For a range of 5 to 20 selected bull calves, differences in average TBV are marginal.

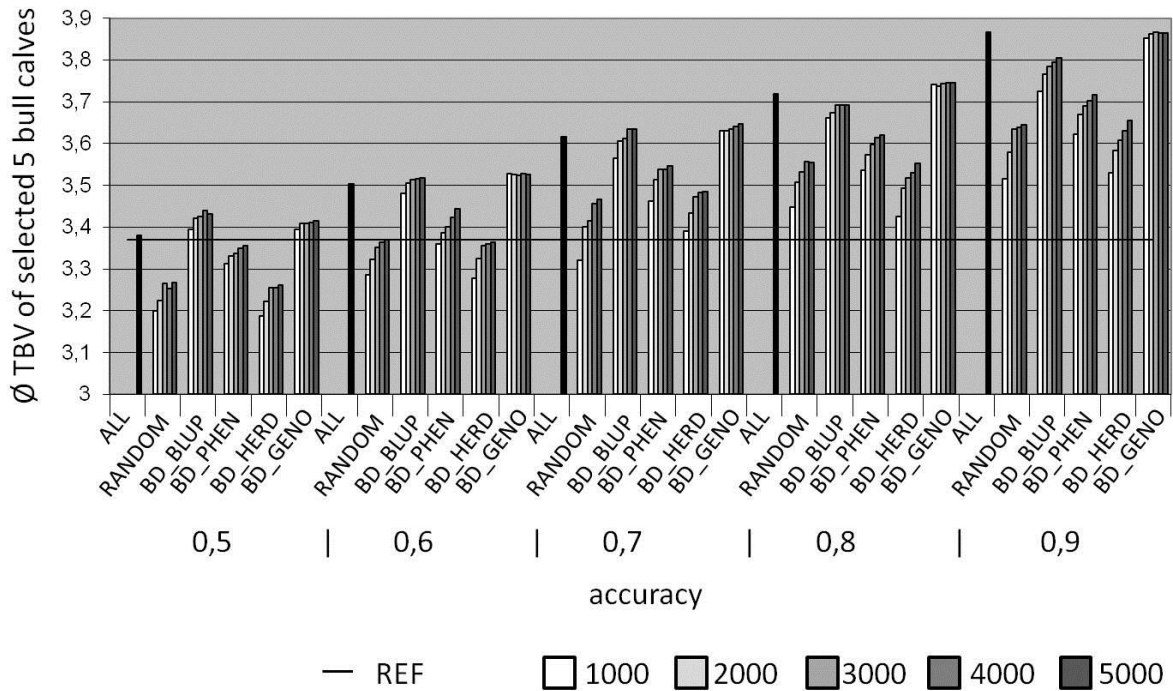


Figure 4. Average of true breeding values (TBV) of five selected bull calves for GPROG-scenarios and the REF-scenario under parameters $h^2=0.1$ and varying r_{mg} (0.5 to 0.9).

Standard deviations of TBV (not shown in Figures) were examined. As could be expected, SD increase with increasing heritability and increasing average TBV. Also, SD for small numbers of selected bull calves were higher than for larger numbers. This finding is due to the stochastic nature of the simulation and reflects random fluctuations which are more visible when considering only very few selected animals.

Average inbreeding coefficients of selected bull calves for the GPROG scenarios, varying r_{mg} and varying the number of selected bull calves, 5 or 20, were examined. Differences for inbreeding coefficients between the two values of the number of selected bull calves were very small. For $h^2 = 0.10$, average inbreeding coefficients were in the range of 6.86 % to 8.40 % and substantially higher than those for $h^2 = 0.30$ (range: 4.80 % to 5.90 %). A reason for this might be that the information from relatives becomes less important with increasing heritability. Within each set of results for $h^2 = 0.10$ or $h^2 = 0.30$, clearly scenario GPROG_BD_BLUP resulted in higher levels of inbreeding since this scenario relies on pre-selection of bull dams according to conventional BLUP EBV. Average inbreeding coefficients for GPROG_BD_BLUP were in the range of 7.72 % to 8.40 % for $h^2 = 0.10$ and in the range of 5.26 % to 5.90 % for $h^2 = 0.30$.

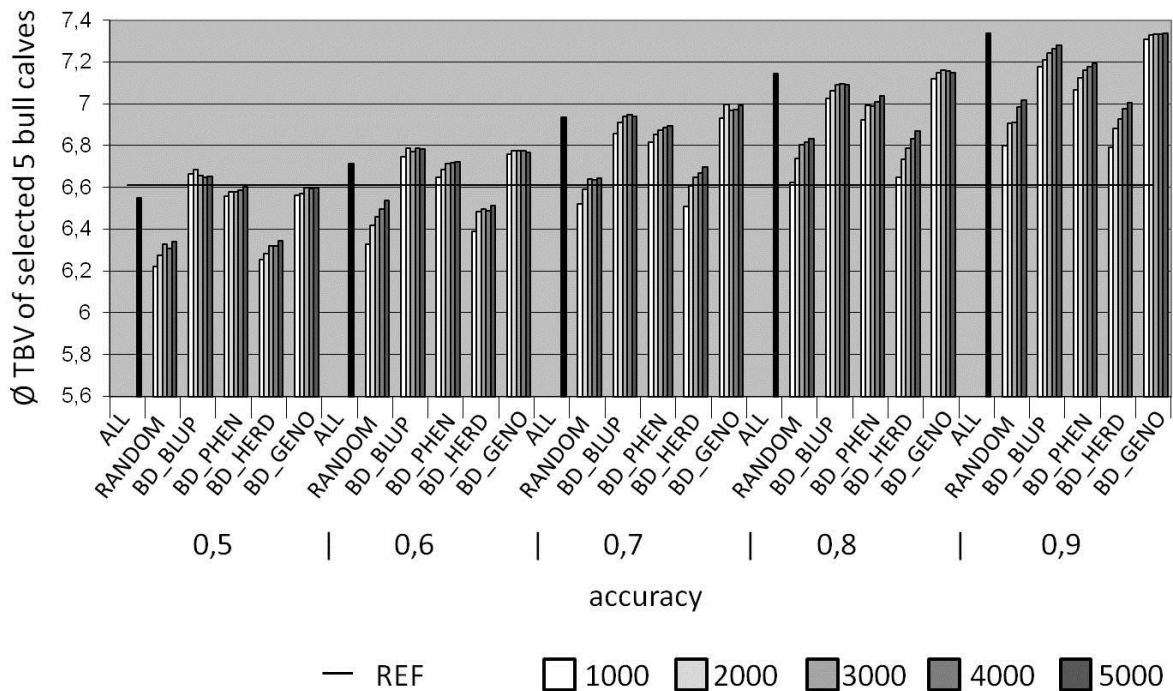


Figure 5. Average of true breeding values (TBV) of five selected bull calves for GPROG-scenarios and the REF-scenario under parameters $h^2=0.3$ and varying r_{mg} (0.5 to 0.9).

Inbreeding coefficients of selected animals in one generation can be seen as helpful information but may not be fully informative for an assessment of future inbreeding. As the entire simulation and selection of animals in the present study focuses on the very last generation, an additional hint on future inbreeding may be taken from the relationship of the selected animals. The number of sons per sire of sons was taken as an indicator value. This value was calculated based on determining the size of the half-sib group from which each selected calf would come and then averaged over the number of selected bull calves, 5 and 20, respectively. As the simulation scheme used is not optimized for a multi-paths selection model, many sire of sons may be sires of selected bull calves. Hence values close to unity indicate that all selected bull calves came from different sire families. In general, differences between all GPROG scenarios were marginal and in the range of 1.000 to 1.284 for $h^2 = 0.1$ and 1.000 to 1.277 for $h^2 = 0.30$. However, scenario GPROG_BD_GENO under which sires of sons, bull dams and the young bull calves are genotyped tends to favour fewer sire of sons and thus is an indication for higher future inbreeding as compared to all other scenarios. However, under scenario REF the average size of the half-sib group for selected bull calves for $h^2 = 0.10$ was 1.707 ($n = 5$ selected bull calves) and 2.881 ($n = 20$ selected bull calves) and for $h^2 = 0.30$ the average size of the half-sib group was 1.695 ($n = 5$ selected bull calves) and

2.579 ($n = 20$ selected bull calves). Given that scenario REF can be viewed as the initial step of a conventional progeny testing scheme, this is a very strong indication that breeding programs based on genomic breeding values lead to lower inbreeding as compared to conventional programs which was also underlined by de Roos et al. (2010).

In their deterministic model calculation, König et al. (2009) examined the competitiveness of genomic selection relative to a conventional progeny testing program and found both approaches on an equal level with respect to discounted profit when r_{mg} was 0.40. With increasing values of r_{mg} , the application of genomic selection was advantageous. Most studies trying to assess the benefits of genomic selection so far have worked with fixed values for accuracies of genomic breeding values. Schaeffer (2006) used $r_{mg} = 0.75$ and a very similar value of 0.71 was assumed in the studies of Buch et al. (2010), Sorensen and Sorensen (2010), and Pedersen et al. (2010). Relatively similar values for r_{mg}^2 of 0.44 and 0.52 in a two-stage selection procedure were used in the deterministic calculation of Winkelman and Spelman (2010). These values may appear somewhat low compared to values from large calibration samples as cited above but reflect the specific situation of the implementation of genomic selection in New Zealand. Apart from König et al. (2009), only the studies of de Roos et al. (2010) and especially Lillehammer et al. (2010) looked at varying levels for r_{mg}^2 . The latter study up to now is also the only simulation study examining the benefits of genomic selection in a breeding program that analysed a population across several generations accounting for the need of new calibration and considering the respective accuracies. Lillehammer et al. (2010) found a superiority of 46 % of genomic selection with respect to genetic gain over a conventional progeny testing breeding program. Lower values for the superiority of genomic selection over conventional programs were only found by Winkelman and Spelman (2010). This is in sharp contrast to other studies that have found an increase of genetic gain by 100 % or even larger (e.g. Schaeffer, 2006; König et al., 2009; Buch et al. 2010). In the present study, for a heritability of $h^2 = 0.10$, all GPROG scenarios are on a level for the average TBV of selected bull calves which is very similar to scenario REF when r_{mg} is as low as 0.50, i.e. the reliability of genomic breeding value is 25 %. Increases in r_{mg} then lead to distinct numeric advantages up to around 12 %. For a higher heritability of $h^2 = 0.30$, again all GPROG scenarios are on an equal level with scenario REF for $r_{mg} = 0.50$. Furthermore, the combination of $r_{mg} = 0.50$ for $h^2 = 0.30$ appears to be quite a way off from what would be expected even for small calibration samples. Increasing r_{mg} to values of 0.70 or even higher results in advantages of GPROG scenarios of around 10.5 %. Hence, genomic breeding

programs have the capacity of increasing the average of the TBV of selected bull calves by around 10 to 12 % in comparison with a young bull program. The reason for the varying degree of superiority of genomic selection when compared to other programs in the literature presumably is a result of the different assumptions on which different studies were based on. This not only applies to the accuracy of genomic selection but to a large extent will also be due to the selection intensities on the paths of selection that were studied. Unfortunately, virtually all studies mentioned so far have failed in analysing a wide range of selection intensities for various paths of selection. Most often, only fixed values were assumed. Examples are Schaeffer (2006) with a fixed value of 1000 pre-selected bull dams and a fixed selection of 20 bull calves out of 500 bull dams, Buch et al. (2010) who examined fixed values of 1000 pre-selected males and 2000 pre-selected females. Further examples include the work of Lillehammer et al. (2010) who used a fixed value of 750 genotyped males as a pool for selection and also Winkelman and Spelman (2010) when analysing only five different options of selection intensities and strategies. Pryce et al. (2010b) have examined the effect of varying the number of selection candidates to be genotyped for a range of 1000 to 10,000 for scenarios comparable to the GPROG scenarios of the present study. An important result from their study was that increases in response to selection are very small for values of candidates larger than 5000. This is very much in line with the present study as further increases of average TBV beyond 5000 candidates are not expected from the already marginal increases when comparing 4000 to 5000 candidates. It should be emphasized that scenario GPROG_ALL, denoting the unlimited availability of genotypes for young male candidates for selection only is advantageous for medium to high reliability of GBV. For low reliability, i.e. below 0.50, an unlimited availability of genotypes by itself is not helpful with respect to average TBV unless it is combined with a pre-selection of bull dams. In the case of a pre-selection of bull dams as simulated in scenarios GPROG_BD_BLUP and GPROG_BD_GENO then an “unlimited” availability can be reduced to values below 5000 candidates.

The examination of a wide range of selection intensities and selection strategies is of great interest to breeding organizations. The reason for this is the fact that the number of animals to be genotyped from the point of view of a breeding organization largely is a function of costs. The costs of genotyping with high-density SNP-arrays already has seen a substantial decrease when compared to the early days of genomic selection and also varies between the density of arrays. Low-density arrays with 3000 to 4000 SNP may have to be taken into account, at least

for pre-selection steps (Weigel et al. 2010), and ‘early’ high-density arrays like the Illumina 50K-Chip are now replaced or accompanied by arrays of much larger density.

Selection intensities, however, are not the only parameters that need variation in simulation studies. Intensity will be interwoven with strategy. A good example in this respect is the question whether it will be worthwhile to genotype females in addition to male animals. Hayes et al. (2009) stress this point and refer to Schaeffer (2006) who concluded that genotyping females could probably have a higher contribution to genetic gain than genotyping males. However, it may be argued that this statement is not independent of the assumption of fixed selection intensities when pre-selecting bull dams and selecting bull calves from these dams. Spelman et al. (2010) reported on the practical experience of implementing genomic selection in New Zealand. These authors concluded that genotyping females had been abolished completely by the breeding organization since it was not cost effective. König and Swalve (2009) argued that under the assumption of low costs for genotyping, a breeding program could be envisaged consisting of genotyping as many bull calves as possible and even ignoring any pre-selection. Such a breeding programme would narrow almost all selection decisions into one path of selection and would be competitive with a Schaeffer-type genomic selection program when assuming selection fractions of less than 0.1 %. Quite clearly, an application of such a program would only be possible for very low-cost genotyping and also could be improved upon by any reasonable pre-selection of dams of bulls. From our results, the main conclusion is that bull calves always should be genotyped. Scenario GPROG_BD_BLUP reaches response parameters on a level very comparable to GPROG_BD_GENO or GPROG_ALL without having to genotype females. For specific sets of parameters (h^2 , r_{mg}) it could be advantageous to promote genotyping of females in such a way that this would result in a GPROG_BD_GENO strategy, i.e. assuming that a large number of females would have been genotyped. A GPROG_BD_GENO strategy would take advantage of the fact that many breeders would genotype their best cows at their own expense.

The question of whether to genotype females is also not independent of the reproductive rate assumed for females. This was shown by Sorensen and Sorensen (2010) who assumed either one offspring per dam or five in a MOET situation. Under MOET, it was clearly beneficial to genotype females. Similar results were obtained by Pryce et al. (2010). In the present study, a more pessimistic approach towards the success rates possible under embryo transfer was taken. One male offspring per female was assumed and a decreased rate mimicking a situation

without embryo transfer was also examined. This latter scenario first of all affected the results for the REF scenario. Relative differences between the two sets of results for GPAR and GPROG scenarios, however, were too marginal to warrant presentation of results and did not result in a change of the relative superiority of scenarios.

CONCLUSION

Breeding programs for dairy cattle which partly or completely are based on breeding values estimated using genomic information and neglecting phenotypes for young selection candidates have the potential of at least doubling the selection response. In comparison with idealistic scenarios under which all available male calves are genotyped, a very similar selection response can be achieved with genotyping only a few thousands of selection candidates, i.e. bull calves, if bull dams are preselected based on either conventional EBV or on genomic breeding values and assuming that all sires of future sons are genotyped. A restriction of the selection of bull calves based on their GBV to herds selected by phenotypic herd average is not advisable. In general, phenotypic information should not be used for pre-selection of animals to be genotyped. Pre-selection steps based on conventional EBV always outperform the use of phenotypic information.

The need for a sufficient accuracy of genomic breeding values was again underlined by the results of the present study. Inbreeding can be reduced when using genomic breeding values and hence such breeding programs will lead to an increase of sustainability with respect to genetic diversity.

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5th CHAPTER**Assessing the Impact of Natural Service Sires and Genotype by Environment Interactions on Genetic Gain and Inbreeding in Genomic Breeding Programs****T. Yin^{*}, M. Wensch-Dorendorf[§], H. Simianer^{*}, H. H. Swalve[§], and S. König[#]**

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ABSTRACT

Organic breeding programs are characterized by a relatively small population size, alternative breeding goals with a strong focus on dairy cattle health, and an intensive use of natural service sires. Additionally, when selecting sires from conventional breeding programs, genotype by environment (G x E) interactions may exist. The objective of the present study was to compare genetic gain and inbreeding coefficients in organic breeding program designs by applying stochastic simulations. The main breeding strategies were: i) selecting sires from conventional breeding programs, but taking into account G x E interaction, ii) selecting genotyped sires from the organic environment for AI, and iii) selecting genotyped natural service sires in each of the organic herds. The simulated conventional population comprised 148,800 cows in 2,976 different herds with an average herd size of 50 cows per herd, and 1,200 organic cows were assigned to 60 herds. In a young bull program, selection criteria of young bulls in both production systems (conventional or organic) were either 'conventional' estimated breeding values (EBV) or genomic breeding values (GEBV) for two traits with low ($h^2 = 0.05$) and moderate heritability ($h^2 = 0.30$). GEBV were calculated for different accuracies (r_{mg}). When selecting sires in the conventional population, G x E interactions were depicted by modifying true breeding values (TBV) as simulated originally in the range from $r_g = 0.5$ to 1.0. Evaluation criteria were TBV and inbreeding coefficients of selected sires and their progeny in the next generation. For $h^2 = 0.05$ and $r_{mg} \geq 0.70$, an implementation of genomic selection and distributing selected sires via artificial insemination (AI) revealed higher genetic gain than selecting young sires in the larger conventional population based on EBV; even when neglecting G x E interactions ($r_g = 1.0$). Basing selection decisions in both environments on GEBV, $r_g \leq 0.80$ is the general threshold favouring selection in the organic population. Only for pronounced G x E interactions ($r_g = 0.5$) and highly accurate GEBV ($r_{mg} = 1.0$), TBV from genotyped organic natural service sires were competitive with TBV of conventional sires without genomic information. Inbreeding coefficients of selected sires and their offspring were generally lower in genomic breeding program designs. For new phenotypes or scarcely recorded traits, genomic selection is a breeding strategy enabling competitiveness for small organic dairy cattle populations.

Key words: Genomic breeding program, organic population, genotype x environment interaction

INTRODUCTION

Especially for organic or low input dairy cattle farming, new functional health traits play an important role (Rozzi et al., 2005). Mark (2004) gave an extended overview of these traits relevant for dairy cattle breeding in the near future. Examples are temperament and other behavior traits, feed intake, and a broad variety of health traits including the compound traits claw disorders, mastitis, and metabolism, which are generally not yet used for official national genetic evaluation. Due to the comparatively small population size in organic farming, implementation of an own organic breeding program design for new traits based on progeny testing should be associated with a loss in genetic gain and in associated economic evaluation criteria, e.g. fewer discounted return and fewer discounted profit (Hunt et al., 1974). Therefore organic dairy cattle farmers have continued to use semen of progeny tested sires or young bulls from conventional dairy cattle breeding programs. However, when allowing gene flow from high input to low input environments, the problem of genotype by environment (**G x E**) interactions may exist (König et al., 2005; Nauta et al., 2006). Furthermore, apart from attempts currently made in contract herds (Schierenbeck et al., 2011; Gernand et al., 2012), only a few, routinely recorded indicator traits are used to improve dairy cattle health by breeding. For example, SCC has been used in conventional breeding programs as an indicator trait for mastitis over decades, but the genetic correlations between SCS and clinical mastitis only range between 0.60 and 0.70 (e.g. Emanuelson et al., 1988; De Haas et al., 2002).

The concept of genomic selection (**GS**) offers new perspectives for the inclusion of new traits in organic dairy cattle breeding programs. Buch et al. (2011) stated that GS has focused on traits that have been recorded and used for official genetic evaluation for a long time, because for these traits, large calibration groups of progeny tested bulls with highly accurate, conventionally estimated breeding values (**EBV**) exist. The largest reference population for the Holstein breed including 15,966 bulls from France, The Netherlands, Denmark, Sweden, Finland, and Germany contributed to significant gain in accuracies of genomic estimated breeding values (**GEBV**) for the traditional list of traits (Lund et al., 2010) and this reference population has substantially increased in size in the past two years. Forming a joint reference population across countries implies a harmonization of traits and EBVs, as has been successfully implemented for international genetic evaluations for production traits, conformation, fertility, milkability, and longevity. For new health traits, large datasets are only available from Scandinavia (Heringstad et al., 2010) for Norwegian Red, and from

Austria (Koeck et al., 2010; Egger-Danner et al., 2012) for dual purpose Simmental cows, e.g. for directly recorded, clinical mastitis. For newly recorded traits, older proven bulls as used in 'conventional' reference populations have no reliable EBVs based on daughter records. As a solution, Buch et al. (2011) suggested to set up calibration groups of cows, and to use phenotypes instead of conventional sire EBVs as dependent variables to estimate effects of single nucleotide polymorphisms (**SNP**). With this strategy, for the same number of animals within the reference population, accuracies of GEBVs were higher than when using sires with lowly reliable EBVs. McHugh et al. (2011) showed via a simulation study that additional gain in terms of higher selection response and shorter generation intervals could be obtained when using genotyped females for optimization of genomic dairy cattle breeding programs. As a consequence, some breeding programs implemented reference groups of cows for new traits. One example, related to the current study, is the reference group including almost 1,200 Brown Swiss cows mostly from organic farms in Switzerland within the framework of the 'Low Input Breed' project. The objective of a study within the ROBUSTMILK- project (Berry et al., 2011) is to utilize genomic and phenotypic data on almost 4,000 Holstein-Friesian cows from experimental farms in Ireland, the UK, the Netherlands and Sweden to explore the complex of female fertility. Mixing of populations for the estimation of SNP effects has been suggested for beef cattle (Rolf et al., 2010), and offers new perspectives for collaborations in organic dairy cattle breeding.

In contrast to restrictions regarding the use of some reproduction biotechnologies such as embryo transfer (Nauta et al., 2005), the molecular tool of GS might be accepted in organic dairy cattle breeding. As a side effect, the implementation of GS will benefit natural service sires. Natural service sires are frequently used in organic dairy cattle farming, because artificial insemination (**AI**) conflicts with natural mating behaviour, and is as such considered by some organic organizations to have negative impact on animal welfare and integrity (Rutgers et al., 1996). When implementing GS, accuracies of GEBVs of natural service sires will be competitive with accuracies of GEBVs of sires offered for AI worldwide. The direct selection of genotyped male calves generates a new perspective for improving existing breeding programs in the era of genomic selection, and enables a modification of the 4-pathway model according to Rendel and Robertson (1950) when calculating annual genetic gain (König and Swalve, 2009).

In summary, improvement of new traits in small organic populations can be realized via i) selecting sires from conventional breeding programs, but taking into account G x E interaction, ii) implementing an own genomic breeding program and using genotyped sires for AI, or iii) implementing an own genomic breeding program, but only using genotyped natural service sires. In the present study, success of these breeding strategies was compared by applying stochastic simulations and evaluation of true breeding values (TBV) and inbreeding coefficients of selected sires and their offspring in the next generation.

MATERIALS AND METHODS

Stochastic simulation

Analogous to a previous study (Wensch-Dorendorf et al., 2011) assessing the effect of pre-selection in genomic breeding programs, the QMSIM program (Sargolzaei and Schenkel, 2009) was used to simulate a fictitious population including 150,000 cows. The input parameters for QMSIM were defined as follows: No. of replicates = 50, no. of generations for historical population = 1000, historical population size = 50,500 animals including 500 bulls, total heritability = 0.05 or 0.30, no. of generations for simulated population = 20, replacement ratio for sires per generation = 0.5, replacement ratio for dams per generation = 0.25, selection criterion over the 20 generations = high EBV, culling criterion = low EBV, mating design among selected males and females = random, population growth rate = 0.25 from generation 1 to 9, and 0 from generation 10 to 20. QMSIM also allows the simulation of parameters on the genomic level. Settings were: no. of chromosomes = 30, no. of markers per chromosome = 333, marker position = random, marker mutation rate = 2.5×10^{-6} with recurrent effects, quantitative trait loci (QTL) mutation rate = 2.5×10^{-6} , no. of QTL per chromosome = 5, additive genetic variances due to QTL = 20% of the total additive genetic variances. A considerable part of the simulation for studying varying scenarios of genomic breeding programs was conducted by firstly applying QMSIM, and secondly modifying the QMSIM output via own programming using the computer languages SAS and C. QMSIM output generated in this present study included phenotypes, TBV and EBV, but high throughput SNP data was neglected. For studying aspects of breeding program designs in various scenarios, GEBVs were 'imitated' using a strategy proposed by Wensch-Dorendorf et al. (2011) for saving computing time and reducing memory. In detail, TBVs and pre-defined correlations between

TBV and GEBV referred to as accuracy of GEBV (r_{mg}) were used to calculate GEBVs applying the following formula (1):

$$GEBV_i = ((1 - r_{mg}^2)^{1/2} RND + r_{mg} \cdot TBV_i / sd(TBV_t)) \cdot sd(TBV_t) \quad [1]$$

where $GEBV_i$ is the genomic breeding value of animal i , r_{mg} is the accuracy of the genomic breeding value altered in the range from 0.5 to 1.0, TBV_i is the true breeding value of animal i , $sd(TBV_t)$ is the SD of TBV in generation t , and RND is a random variable sampled from $N(0,1)$. Hence, GEBV for a wide range of r_{mg} can be depicted very easily without setting up specific designs for a calibration group.

Formula (1) was also used to depict the aspect of G x E interactions by altering genetic correlations (r_g) between different environments. For sires selected in the conventional population, and subsequently used in the organic population, TBV were modified (mTBV) by altering r_g in the range from 0.5 - 1.0. Altering TBV reflects the physiological background of G x E interactions, i.e. the change of an animals' true genetic value with altered gene expression in changing environments. Consequently, formula (2) for calculating mTBV was:

$$mTBV_i = ((1 - r_g^2)^{1/2} RND + r_g \cdot TBV_i / sd(TBV_t)) \cdot sd(TBV_t) \quad [2]$$

with parameters as defined above.

TBV for progeny of sires (pTBV) in the organic population were calculated according to formula (3):

$$pTBV_i = 0.5 (TBV_s + TBV_d) + \sqrt{0.5 - 0.25 (F_s + F_d)} \sigma_a \cdot RND \quad [3]$$

where $pTBV_i$ is the TBV of progeny i in the organic population; TBV_s is TBV of sire s (when directly selected in the organic population) or mTBV (when selected in the conventional population) of progeny i , TBV_d is the TBV of the dam d of progeny i ; F_s and F_d are inbreeding coefficients of sire and dam of progeny i , respectively; and σ_a^2 is the additive genetic variance of the trait of interest, and RND is a random variable sampled from $N(1,0)$. Simulation was performed for a low heritability trait ($h^2 = 0.05$), and for a moderate heritability trait ($h^2 = 0.30$).

Breeding program scenarios

With the aim of studying the impact of genotyped natural service sires in detail for both evaluation criteria, genetic gain and inbreeding, required assigning cows and bulls to individual herds with the restriction of matings to sires recruited from the same herd only.

Cows in the conventional population were distributed to 2,976 different herds with an average herd size of 50 cows per herd, and 1,200 organic cows were distributed to 60 different organic or 'low input herds' with an average herd size of 20 cows per herd depicting the current organic and low-input population structure for Brown Swiss in Switzerland (Yin et al., 2012). The essential steps of the simulation from the practical point of view along with analyzed breeding program scenarios and defined abbreviations for different scenarios are illustrated in Figure 1. In total, 5 different breeding strategies were defined to select service sires for the organic population. All strategies follow a young bull program as defined e.g. by Oltenacu and Young (1974) which implies a comparison of scenarios for identical generation intervals. Scenarios are labeled using the endings *_AI (selected young sires are used for artificial insemination in the organic population) or *_NS (matings of selected sires are restricted within herds).

In the first scenario (C_EBV_AI), based on their EBV, 5 young bulls were chosen for AI in the organic population from 2,976 conventional herds. Selected young bull were sons of influential proven bulls with an average of 500 daughters per proven bull. Without daughter information at this point of selection, the EBV of the young sire can be interpreted as a pedigree index. Such a scenario reflects the traditional situation that young sires without daughter records were used for approximately 30 % of inseminations in conventional progeny testing programs. G x E interaction between the conventional and the organic population was considered by altering sires' TBV. The second scenario (C_GEBV_AI) was realized by selecting 5 sires from conventional farms based on GEBV. Again, G x E interaction was mimicked by altering their TBV. The practical relevance can also be seen within the context of multiple across country evaluations enhanced with genomic information (**GMACE**). The last three breeding scenarios (O_GEBV_AI, O_GEBV_NS and O_EBV_NS) were carried out by selecting service sires directly in the small organic population, and by neglecting G x E interactions. In scenario O_GEBV_AI, 5 service sires for AI were selected in the whole organic population based on GEBV. In scenario O_GEBV_NS and scenario O_EBV_NS, selection criterion for natural service sires within herds was either GEBV or EBV, respectively. For AI, the 5 selected sires were used with equal frequencies in the organic production system, and selected natural service sires were mated only with cows from the same herd. To account for practical circumstances, matings between close relatives (sire - dam, sire - grand dam, sire - full-sib, sire - half-sib) were forbidden. This implies the availability of at least two selected natural service sires per herd. A further detailed

comparison was made between scenario O_GEBV_NS and an identical genomic scenario, but without mating restrictions (O_GEBV_NS_II).

Main evaluation criteria were the average TBV of selected sires (when the sire was directly selected in the organic environment) or mTBV (when the sire was selected in the conventional population), and the average pTBV of their progeny in the next generation. In addition to TBVs, inbreeding coefficients of sires and their progeny were monitored. For this objective, the software package 'Pedigreemm', (subroutine of the R 2.11.1-version by Bates and Vazquez, 2009), was used. The algorithm for computing inbreeding coefficients in this package is based on the approach by Sargolzaei and Iwaisaki (2005).

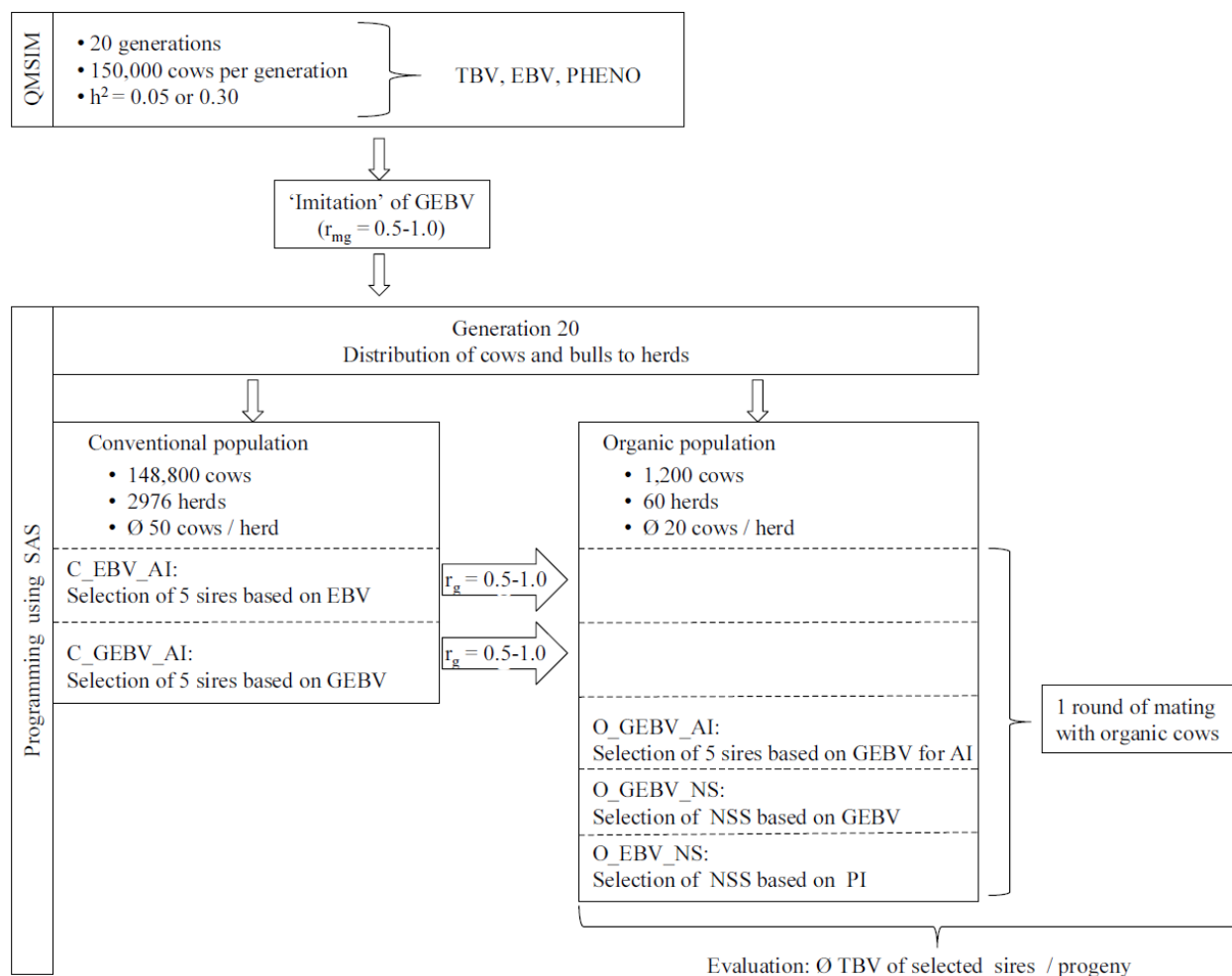


Figure 1. Explanation of the simulation for the evaluation of different scenarios of genomic breeding programs (TBV = true breeding value, EBV = conventional estimated breeding value, PHENO = phenotype, GEBV = genomic estimated breeding value, AI = artificial

insemination, NSS = natural service sires, r_{mg} = accuracy of GEBV, r_g = genetic correlation in the same trait between conventional and organic production system).

RESULTS AND DISCUSSION

True breeding value of selected sires and their progeny

A comparison of TBVs or mTBVs (hereafter generally named TBV) of selected sires and their progeny after one round of mating with organic cows for four different scenarios (C_EBV_AI, O_GEBV_AI, O_GEBV_NS, and O_EBV_NS, respectively) is given in Figure 2a for $h^2 = 0.05$, and in Figure 2b for $h^2 = 0.30$. Results from the more complex scenario C_GEBV_AI are shown in Figure 3a for $h^2 = 0.05$, and in Figure 3b for $h^2 = 0.30$. Same trends of increasing TBV with increasing r_{mg} or increasing r_g are depicted for the low and the moderate heritability trait for sires and for their progeny. As expected, genetic gain in terms of average TBV was higher for the trait with higher heritability. In order to ease interpretation of results, it should be noted that average SD of TBV from all male candidates in last generation was $SD = 0.20$ for $h^2 = 0.05$, and $SD = 0.49$ for $h^2 = 0.30$. For a low heritability trait ($h^2 = 0.05$; Figure 2a), and assuming r_{mg} of value 0.70 or higher, selection strategy O_GEBV_AI revealed highest TBV. Hence, from a more practical point of view, selecting 5 sires with moderately accurate GEBV directly in the organic population, and afterwards widespread used via AI, will ensure highest genetic gain. Average TBV from scenario O_GEBV_AI for $h^2 = 0.05$ and $r_{mg} = 0.70$ was even higher compared to a young bull program in the conventional population, i.e. when neglecting G x E interactions ($r_g = 1.0$). For the moderate heritability trait, superiority of scenario O_GEBV_AI over scenario C_EBV_AI was less pronounced (Figure 2b); here, r_{mg} of 0.80 or higher is required for achieving highest response in selection. For identical r_{mg} , and when directly selecting young sires in the organic population, the 'genomic AI scenario' (O_GEBV_AI) revealed higher genetic gain compared to the 'genomic natural service sire scenario' (O_GEBV_NS), e.g. TBV of values 2.27 versus 2.05 for $h^2 = 0.05$ and $r_{mg} = 0.70$ (Figure 2a). Scenario O_EBV_NS was not competitive at all.

For same heritabilities and same breeding scenarios, TBV of sires were throughout higher than pTBV of their progeny. This was especially the case when selecting sires for AI in the large conventional population in scenarios C_EBV_AI and C_GEBV_AI, but it was also valid for the smaller organic population in scenario O_GEBV_AI. Selecting a small no. of

only 5 sires from a total of 74,400 candidates in the conventional population, but also from 600 candidates in the organic population, imply very high selection intensities of $i = 4.05$ and $i = 2.73$, respectively. The impact of such an intensive selection of young sires for AI on the increase of their TBV was shown by König et al. (2011). Several theoretical investigations have supported the dominant role of the male pathways of selection in dairy cattle breeding programs (e.g. Van Tassel and Van Vleck, 1991). However, sires were selected based on EBVs or GEBVs for a single trait, whereas in practical breeding programs, realized selection intensities were lower than expected selection intensities due to a multitude of selection criteria not necessarily reflecting the genetic potential (König et al., 2007). Only a strong focus of selection on one target trait resulted in realized selection intensities on the cow-sire pathway close to theoretical expectations. One classical example is the rigorous selection on SCC when graduating cow sires in Sweden (Powell et al., 2003). Selection intensity of cows in the present study was comparatively low ($i = 0.55$). Hence, also cows with lower genetic merit were used for matings with young sires. Consequently, average pTBV of offspring were lower than TBV of their sires.

Natural service sire scenarios (O_GEBV_NS and O_EBV_NS) were generally not competitive with breeding strategies based on AI (C_EBV_AI and C_GEBV_AI). Only for pronounced G x E interactions between the organic and the conventional population ($r_g = 0.5$), and highly accurate GEBV ($r_{mg} = 1.0$), average TBV from scenario C_EBV_AI was lower than average TBV from scenario O_GEBV_NS. Both, the low genetic correlation in the same trait between production systems, and the extremely high accuracy of GEBV, are not consistent with practical results. König et al. (2005) gave an overview of r_g in same traits across country borders, or between different production systems within countries. Pronounced indications for G x E interactions for production traits with $r_g = 0.5$ or lower were only found for countries characterized by substantial, climatic differences, e.g. Kenya versus United Kingdom (Ojango and Pollot, 2002). When grouping herds into different subsets according to average production levels or intra-herd-variances within countries, lowest genetic correlations were in the range of 0.75 and 0.80 (e.g. Veerkamp and Goddard, 1998; Calus et al., 2002). Kearny et al. (2004a) analyzed G x E interactions based on data from two production systems (grazing versus conventional) within Ireland. Genetic correlations were 0.89, 0.88, and 0.91 for milk, fat, and protein yield, respectively. Also estimates of genetic correlations between the two environments for low heritability reproduction traits (days open, days to first service

and number of services per conception) were high and not significantly different from unity (Kearny et al., 2004b).

Accuracy of GEBV is moderate to high when GS is based on a large set of bulls in a calibration group, which is the case e.g. in the EuroGenomics project (Lund et al., 2010) or in the collaborative project in North America (VanRaden et al., 2009). For new traits especially in rare breeds or in small, low input populations, large calibration groups of sires with highly reliable conventional EBV do not exist. The only alternative would be to base GS on a calibration group of cow phenotypes, but first results revealed comparably low values for r_{mg} . Veerkamp et al. (2011) used 1,841 genotyped cows and 194 genotyped sires. Accuracies of direct genomic values ranged from 0.40 to 0.58 for milk, fat and protein yield. In the study by Verbyla et al. (2010), 527 genotyped Dutch Holstein-Friesian heifers with records for rare phenotypes were the base for estimating direct genomic values for energy balance. The small no. of phenotypes in the calibration group resulted in a low value of $r_{mg} = 0.29$. Those first results, and the general dependency of r_{mg} on the no. of phenotypes in the calibration group (e.g. Goddard, 2009), should be kept in mind when comparing TBV of selected sires from the 'genomic low input breeding strategies' O_GEBV_AI and O_GEBV_NS to the 'conventional selection strategy' C_EBV_AI in the conventional population (Figures 2a and 2b).

In addition to the size of the calibration group, heritability of the trait is a crucial parameter determining accuracy of genomic evaluations. Heritability also has strong impact on accuracy of conventional EBV. Correlations between EBV and TBV for proven sires in the conventional population with an average of 500 daughter records were 0.90 for $h^2 = 0.30$, and 0.75 and for $h^2 = 0.05$. For GEBV and for pre-defined values of r_{mg} , the no. of animals required in a calibration set decreases with increasing heritabilities (e.g. Goddard, 2009). The use of dense SNP chips (777K SNP chip) for high heritability traits offer the possibility to transfer estimates of SNP effects to other populations or even to other breeds. Rolf et al. (2010) outlined this concept for highly heritable meat quality traits in beef cattle, but this strategy might be difficult to realize for low heritability health traits in dairy cattle. Assuming high values of r_{mg} in combination with high genetic correlations between environments, highest average TBV were achieved in scenario C_GEBV_AI (Fig. 3a and 3b). Assuming an optimal sub-scenario with $r_{mg} = 1$ and $r_g = 1$, TBV of selected sires were 2.20 for $h^2 = 0.05$, and 7.63 for $h^2 = 0.30$. When comparing scenarios O_GEBV_AI (Figure 2a) and C_GEBV_AI (Figure 3a) for same values of r_{mg} , higher average TBV were realized when

selecting sires in the large conventional population for r_g in a range between 0.70 and 1.0. Additionally, results from the present study indicate the value of genotyped young bulls from foreign countries. VanRaden and Sullivan (2010) pointed out that more than 50,000 dairy cattle worldwide are genotyped with high-density SNP chips. Consequently, they developed statistical procedures for GMACE- applications. Hence, international genetic evaluations for GEBVs might be the main selection criterion across country borders in the near future, and genetic correlations will determine the rank of foreign sires on the national scale, and the significance of domestic breeding program designs.

The relatively simple selection strategy, i.e. selection of natural service sires in the organic population based on EBV (= pedigree index), resulted in lowest average TBV. Selection according to EBV (O_EBV_NS) was only comparable to scenario O_GEBV_NS for a low accuracy of GEBV of value $r_{mg} = 0.5$ (Figures 2a and 2b). Genomic breeding values based on a multitude of SNP- effects depict an animals' individuality. Consequently, GS definitely aids in avoiding the observed practical drawback of so called 'pedigree slippage' (Everett, 1984). The phenomenon of 'pedigree slippage' indicates biases in estimated breeding values of young sires when selection was based on pedigree indices due to over-estimated EBV of bull dams. Possible reasons for over-estimation were preferential treatment of potential bull dams (Kuhn et al., 1994), or the impact of heterogeneous within-herd variances on cow EBVs (e.g. Garrick and Van Vleck, 1987).

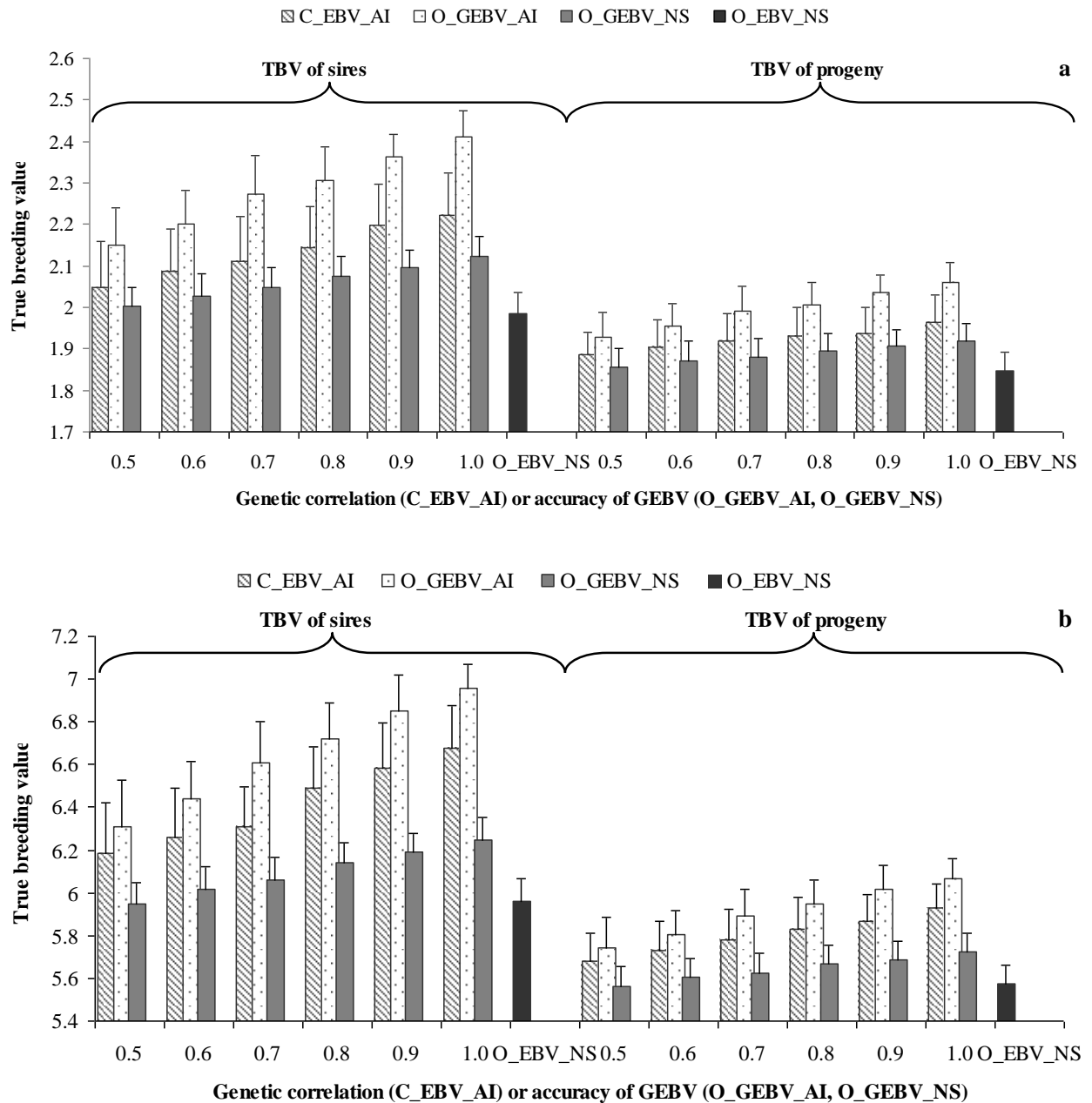


Figure 2. Average and standard error of true breeding value of selected sires and their progeny for four different scenarios (C_EBV_AI, O_GEBV_AI, O_GEBV_NS, O_EBV_NS as explained in Figure 1) for $h^2 = 0.05$ (a) and for $h^2 = 0.30$ (b).

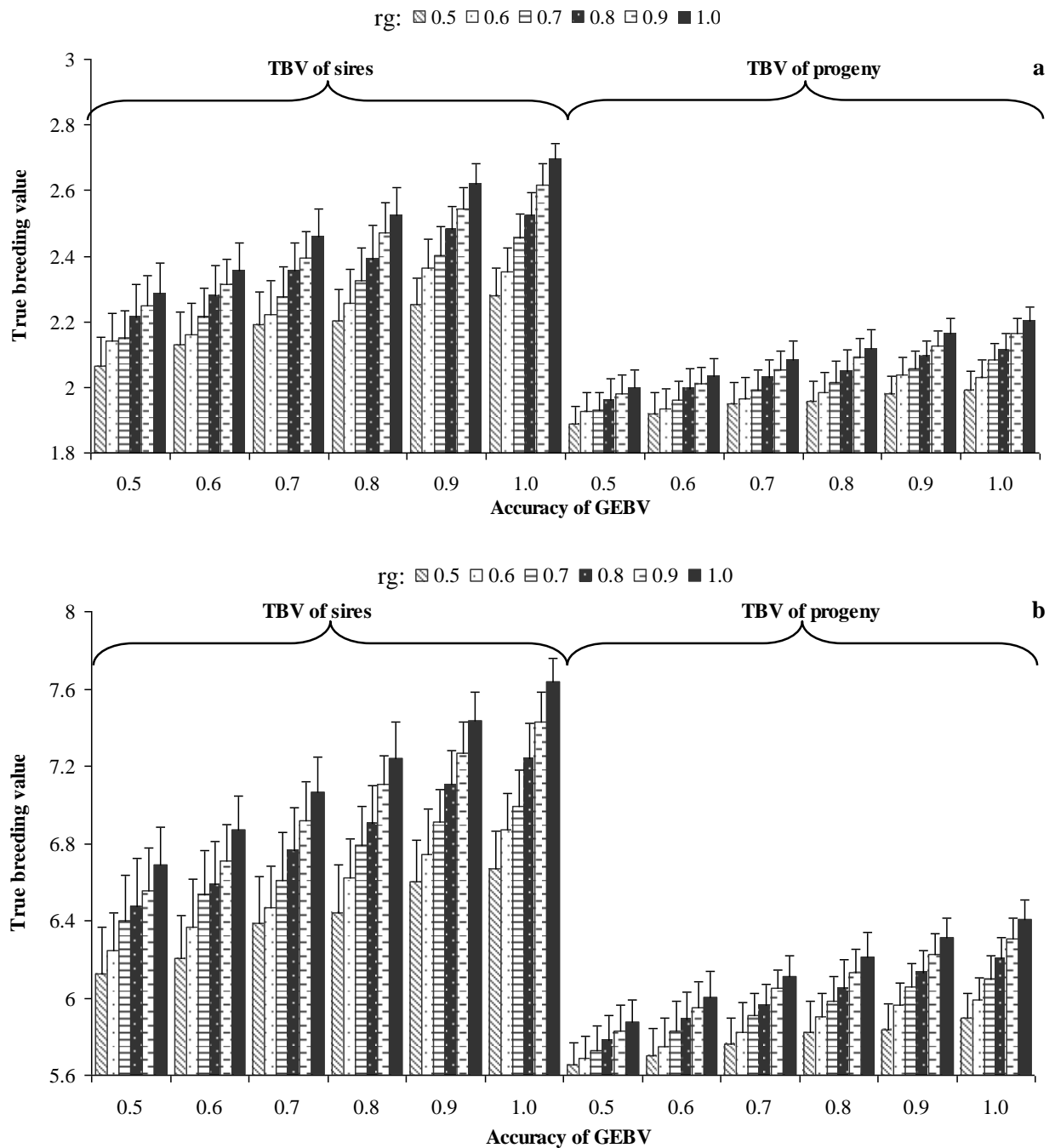


Figure 3. Average and standard error of true breeding values for selected sires and their progeny for scenario of C_GEBV_AI (explanation: Figure 1) for $h^2 = 0.05$ (a) and $h^2 = 0.30$ (b). (r_g = genetic correlation in the same trait between conventional and organic production system)

Inbreeding coefficients of selected sires and their progeny

Mean values and SE of inbreeding coefficients of selected sires and their progeny for all five scenarios C_EBV_AI, C_GEBV_AI, O_GEBV_AI, O_GEBV_NS, and O_EBV_NS are shown in Figure 4a for $h^2 = 0.05$, and in Figure 4b for $h^2 = 0.30$. Taking the average over all scenarios, inbreeding coefficients of selected sires were 0.092 (SE = 0.019) for $h^2 = 0.05$, and 0.056 (SE = 0.012) for $h^2 = 0.30$. For all scenarios, higher inbreeding coefficients were observed for the low heritability trait. Several studies in the pre-genomic and in the genomic era support our results. For example, Woolliams (1989) reported an increase of correlations between EBV of related animals, and an increase of probabilities of their co-selection with decreasing heritabilities. Due to higher weight on family versus individual information, also Strandén et al. (1991) noted that inbreeding accumulated most rapidly when selection was focused on a low heritability trait. For different strategies of pre-selection of young sires in genomic breeding programs, Wensch-Dorendorf et al. (2011) found substantially higher inbreeding coefficients with decreasing heritabilities.

In the present study, genomic selection scenarios C_GEBV_AI, O_GEBV_AI, O_GEBV_NS resulted in lower inbreeding coefficients of selected sires compared to the conventional scenario C_EBV_AI (Figure 4a and 4b). For $h^2 = 0.05$, inbreeding coefficients of sires were 0.09 for scenarios C_GEBV_AI, O_GEBV_AI, and O_GEBV_NS, and 0.12 for scenario C_EBV_AI. König et al. (2011) concluded that a pattern of single markers combined in a GEBV clearly depicts the individuality of a selection candidate instead of basing selection decisions on conventional BLUP-EBV. For the management of inbreeding in genomic breeding programs, Schaeffer (2006) recognized early the possibility to calculate heterozygosity indices based on marker genotypes. Pedersen et al. (2009) reported that marker-assisted selection might reduce identical by descent probabilities as well as pedigree-estimated inbreeding. Lillehammer et al. (2011) also found that the genomic breeding schemes could reduce the rate of inbreeding and still increase genetic gain, compared to the conventional breeding scheme. Daetwyler et al. (2007) summarized that genome-wide selection achieves high accuracies in predicting Mendelian sampling terms, which allows for a better differentiation between sibs. Weigel (2001) focused on the increased likelihood of co-selection of related animals when using EBV as the ultimate selection criterion, and consequently when selecting related animals, inbreeding will increase faster.

In conventional dairy cattle breeding programs in Germany, pedigree indices were used as a main criterion for bull dam selection regarding the young category "heifers without own performance". Analyses of top lists of potential bull dams revealed a multitude of heifers with similar or even identical genetic background (König, 2001). In the present study, EBV was selection criterion for natural service sires within herds, and for selecting 5 young bulls in the conventional population. A large number of selected natural service sires for each of the 60 organic herds depict a broad genetic diversity. Consequently, realized inbreeding coefficients in scenario O_EBV_NS were lower compared to scenario C_EBV_AI. Inbreeding coefficients were slightly higher for scenario O_EBV_NS than the comparable natural service sire scenario O_GEBV_NS.

However, compared to inbreeding coefficients of sires in the starting phase of GS, the development of inbreeding or of genetic relationships in the long term is of higher relevance. In the next generation after one round of matings, inbreeding coefficients of conventional and genomic selection strategies were almost identical, but on a lower level than in selected sires. This is valid for the low (Figure 2a) and the moderate heritability trait (Figure 2b). Inbreeding coefficients in selected groups of elite animals, i.e. bull dams and bull sires, are generally higher than in milking cows in the population (König and Simianer, 2006), but those groups of elite animals determine accumulation of inbreeding in the long term. In genomic breeding programs, results for inbreeding should be seen in close relation to generation intervals. A stochastic simulation by de Roos et al. (2011) clearly showed that GS has the potential for doubling the rate of genetic gain per generation without further increase of inbreeding per generation. However, due to the substantial shortening of generation intervals, rate of inbreeding per year increased. Genomic selection makes it possible to select sires with low inbreeding coefficients, but for controlling inbreeding in the long-term, genomic relationships among selection candidates should be used in mating designs determined by breeding organizations (Schierenbeck et al., 2011).

Selection criterion for scenarios O_GEBV_AI and O_GEBV_NS was the same, but inbreeding coefficients were slightly higher for O_GEBV_AI, because 5 sires were selected for O_GEBV_AI versus 120 sires for O_GEBV_NS. The result is in agreement with Pryce et al. (2010). They found that the number of selected sires has a major impact on levels of inbreeding. Weigel (2001) also stated that inbreeding is primarily a function of selection intensity, rather than population size. Moreover, creation of sub-lines as done in scenario

O_GEBV_NS may also reduce inbreeding substantially, albeit with a slight decrease in genetic gain (Terawaki et al., 1998).

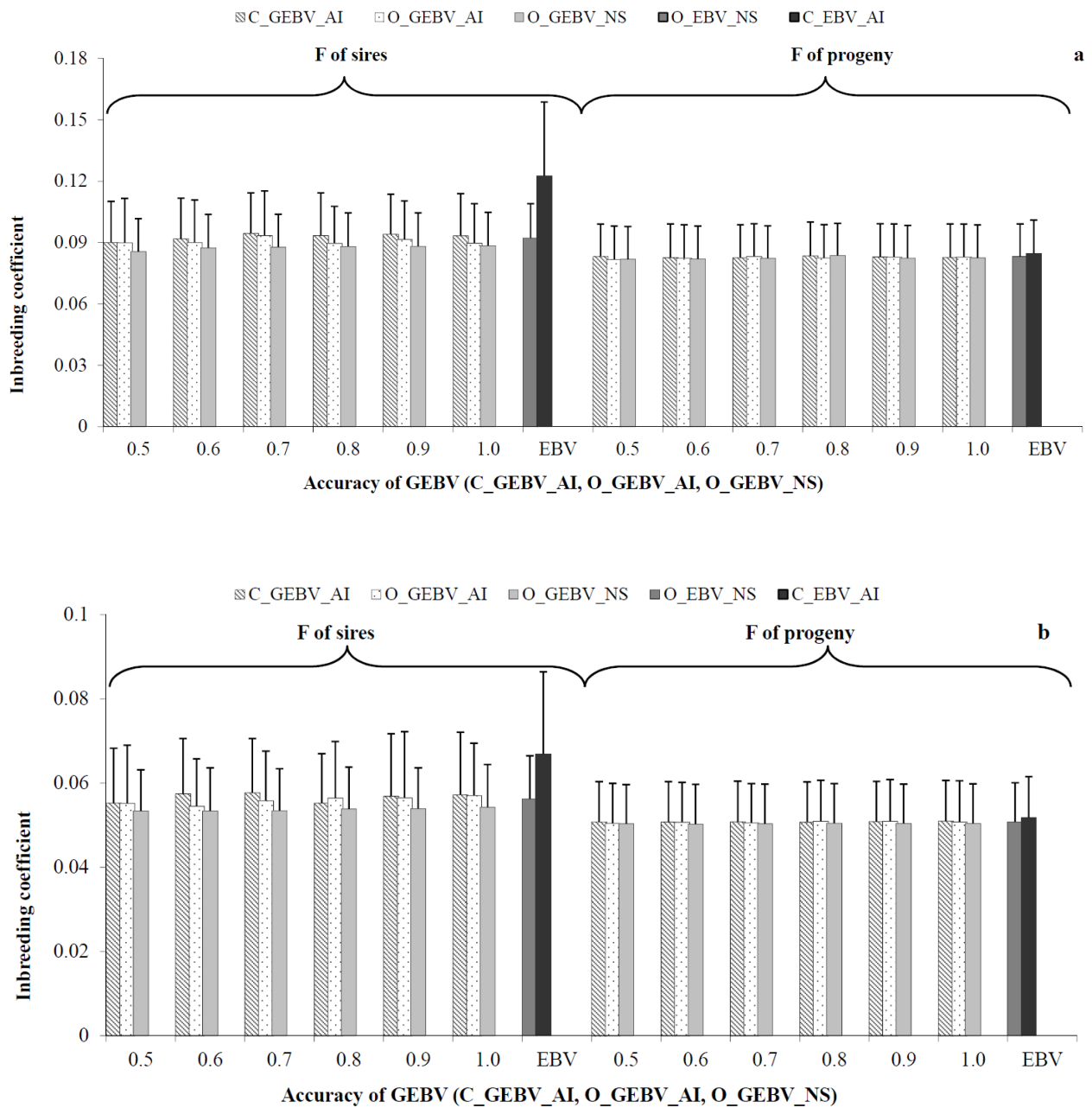


Figure 4. Average and standard error of inbreeding coefficients of selected sires and their progeny for five different scenarios (C_EBV_AI, C_GEBV_AI, O_GEBV_AI, O_GEBV_NS, O_EBV_NS as explained in Figure 1) for $h^2 = 0.05$ (a) and $h^2 = 0.3$ (b).

Sub-scenario for genotyped natural service sires

Organic dairy cattle farmers prefer a breeding system with a strong focus on cow families (Baars, 2002). Female offspring from influential cow lines are used for replacements within farms, and male offspring are used as natural service sires. On the maternal side, the scientific reason underlining the importance of cow families or maternal lineage is due to cytoplasmic effects that explain a small fraction of the phenotypic variance of the trait of interest (e.g. Albuquerque et al., 1998). The argument for using natural service sires grown up in the own herd is based on farm environment adaptation. However, always using natural service sires from the same cow family in the herd makes it difficult to avoid matings between close relatives. This is the reason for a detailed comparison of scenario O_GEBV_NS (no matings between close relatives) with scenario O_GEBV_NS_II (matings between close relatives may occur). Inbreeding coefficients for progeny of selected sires from both scenarios are shown in Figures 5 for $h^2 = 0.05$ and $h^2 = 0.30$, respectively. For identical heritabilities and same values for r_{mg} , no differences in TBV between these two selection strategies were observed (Figures not shown). In contrast, realized inbreeding coefficients from scenario O_GEBV_NS_II were 13.69 % and 23.91% higher compared to scenario O_GEBV_NS for $h^2 = 0.05$ and $h^2 = 0.30$, respectively. Hence, there is potential for realizing identical genetic gain by restricting mating designs, pointing to the application of 'optimum genetic contribution' in the genomic era (Sonesson et al., 2010; Schierenbeck et al., 2011).

Suggestion: Breeding strategy in small organic populations

For new phenotypes or scarcely recorded traits, especially in small populations, the most promising strategy for improving genetic gain will be realized via the implementation of own genomic selection strategies. A possible approach might be the application of scenario O_GEBV_AI. Organic breeding focuses on improvements of animal health and product quality, and only direct selection on the trait of interest, instead of using indicator traits, will ensure sufficient selection response (König and Swalve, 2006). Conventional breeding on health traits currently is mostly based on indicator traits, e.g. SCC for clinical mastitis, or conformation traits for claw disorders. EBVs of those indicator traits are also used in large reference populations for the estimation of SNP effects and of GEBVs. Pimentel and König (2011) verified results for selection response in the genomic era by applying selection index calculations: genetic gain was higher when using GEBVs from the trait of interest instead of

using GEBVs from indicator traits. Organic breeders could take the lead in breeding on dairy cattle health when implementing a calibration group for new phenotypes as pre-requisite for genomic selection. Also GEBVs for new health traits with sufficient reliability increase competitiveness of natural service sires, and consequently the competitiveness of organic breeding programs. In the present study, costs for different breeding strategies were not taken into account. However, implementation of an own genomic breeding program might be cheaper than implementing an own conventional breeding program including a large amount of fixed costs due to necessary capacities for test bulls and waiting bulls. Additionally, König et al. (2009) have shown that the costs for genotyping are of minor importance in a genomic breeding program when applying a comprehensive cost calculation, e.g. considering costs for performance tests or herdbook registration.

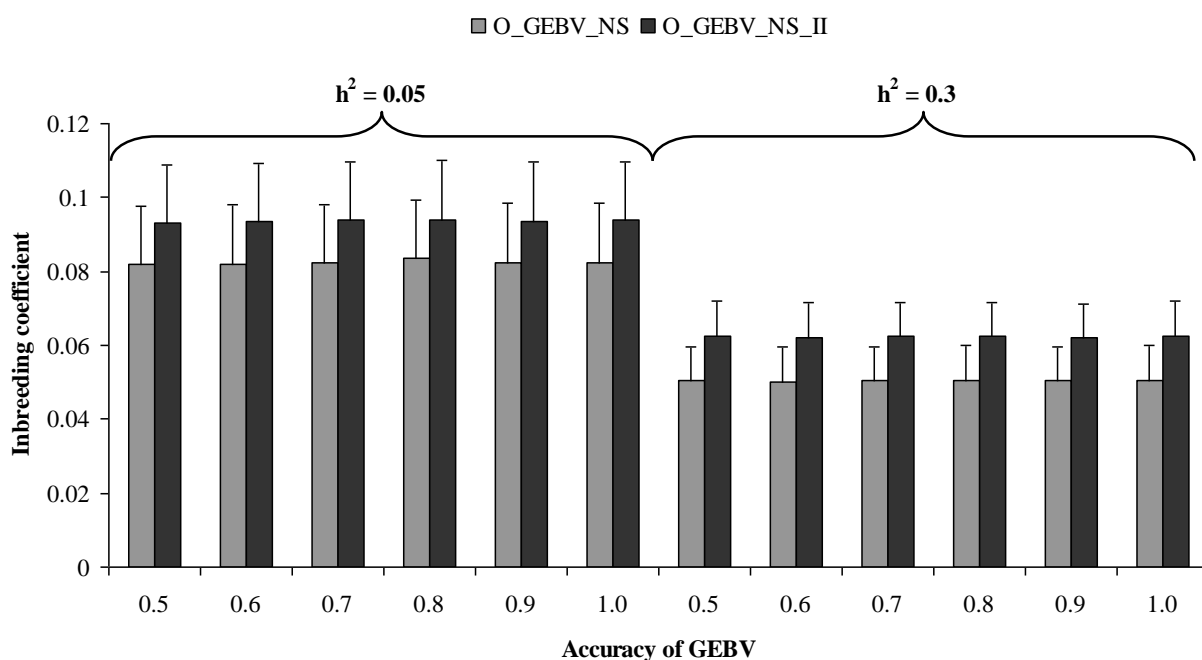


Figure 5. Average and standard error of inbreeding coefficients for progeny of selected sires for scenario O_GEBV_NS (explanation: Figure 1) for $h^2 = 0.05$ and $h^2 = 0.30$. (Scenario O_GEBV_NS_II is identical compared to scenario O_GEBV_NS, but matings between close relatives were allowed).

Generally, in small populations with a small effective population size, a high risk of inbreeding exists. Compared to conventional dairy cattle breeding programs, organic populations are characterized by a small population size. Genomic selection has the potential to combine both genetic gain and acceptable rates of inbreeding. Inbreeding coefficients of sires and of their progeny in the next generation from organic genomic scenarios

O_GEBV_AI and O_GEBV_NS were on the same level or lower compared to conventional scenarios C_GEBV_AI and C_EBV_AI.

CONCLUSIONS

This is a first study addressing the aspects of natural service sires and G x E interactions in genomic breeding programs, which has strong relevance for the optimization of organic breeding program designs. For making decisions about the optimal strategy, crucial parameters are genetic correlations in the trait of interest measured in different production systems, and accuracies of GEBVs. When selecting sires in the larger conventional population based on GEBV, higher TBVs of sires and their offspring compared to organic genomic breeding programs were only realized by neglecting G x E interactions and assuming a genetic correlation close to one. For health traits, we expect genetic correlations between conventional and organic environments below the critical 'threshold' of 0.80, which indicate G x E interactions, and support the idea for implementing an own organic genomic breeding program. A breeding concept based on genotyped natural service sires is competitive with a conventional breeding program for sufficiently reliable GEBV ($r_{mg} \geq 0.80$) and genetic correlations of $r_g < 0.80$ between production systems. Furthermore, we showed that selection of natural service sires based on GEBV resulted in lower inbreeding coefficients than conventional selection strategies in the large conventional population, or selecting natural service sires in the organic population based on pedigree indices.

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6th CHAPTER

GENERAL DISCUSSION

This thesis provides descriptive statistics and genetic parameters for conventional and innovative traits of Brown Swiss cows located in low input farms in Switzerland. In addition, two simulation studies addressed the chances and the risks of breeding programs using genomic selection. Chapter 2 found that heritabilities for production traits in organic farms were similar to those of conventional production systems. However, genetic parameters for reproduction traits were partly different across the two systems. Chapter 3 presented the low disease incidences for new health traits in organic farms and the genetic parameters for these traits using a variety of trait definitions and statistical models, i.e. animal and sire models, repeatability models and random regression models (RRMs). Chapter 4 focused on genomic breeding program designs and evaluated selection strategies for young sires. Pre-selection of bull dams and of bull calves based on genomic breeding values (GBV) could achieve a genetic gain as good as an ideal situation. This is especially valid for lowly heritable traits. The "ideal situation" implied that all male calves in the population were genotyped. In Chapter 5, we showed that if genotype by environment (G x E) interactions exist, (i.e. the genetic correlations were lower than 0.8), an organic breeding program with artificial insemination (AI) was competitive with a conventional breeding program. Therefore, establishing a breeding program for organic farming systems might be a viable alternative, especially to improve traits not currently considered in overall breeding goals (Chapter 5).

Descriptive statistics in organic dairy farming systems

The phenotypic records of Brown Swiss indicate that test-day milk yield increased with increasing age of the cows. However, an increased disease incidence in later lactations was also observed and this finding was supported by previous studies. For example, Lin et al. (1989) found an increased incidence of clinical mastitis in later parities. Compared to other studies conducted in conventional Holstein cows (e.g. Gengler et al., 2004; Nixon et al., 2009), test-day milk yields of organic Brown Swiss cows were relatively low (e.g. 19.04 kg in parity 1, 21.87 kg in parity 2 and 23.61 kg in parity 3). However, fat, protein and lactose content was greater in milk from organic Brown Swiss compared to those from conventional dairy farms across the first three parities (Miglior et al., 2007; van Straten et al., 2011). At least two reasons can explain the low milk yield and high fat, protein and lactose percentages for organic cows. Firstly, organic farming focuses on alternative feeding strategies, with increased dry matter intake from roughage and reduced concentrates. Roughage intake is associated with the increase of fat percentage, while concentrates strongly increase test day

milk yield. Secondly, Brown Swiss is a breed that produces high quality milk when fed diets based on hay instead of silage for cheese production. Brown Swiss cows have the optimal kappa casein genotype for cheese production. Furthermore, milk urea nitrogen (MUN) can be used as an indicator of energy intake. Lower MUN represents lack of energy in diets, while higher MUN may have toxic functions for cows. A comparatively high MUN was found in low input dairy farms in Switzerland, reflecting diets that were high in degradable protein, and deficient in fermentable carbohydrates.

The descriptive statistics for reproduction traits in organic farms were partly different from those of conventional dairy farms. For example, age at first calving for organic Brown Swiss cows was greater than 31 months, but conventional Brown Swiss cows have a value of less than 30 months (Garcia-Peniche et al., 2005; Hare et al., 2006). These data indicate that cows in organic farms may reach sexual maturity later than those in conventional farms, and it may be related to increased dietary roughage and extensive management practices. Interestingly, calving interval was larger in conventional compared to organic production systems (Dal Zotto et al., 2007; Hare et al., 2006), indicating that days open and calving to first service are shorter for organic cows.

Compared to conventional farms, incidences of mastitis, metritis, retained placenta, ovarian cysts and acetonemia are relatively low in the Brown Swiss organic farms (Gernand et al., 2012; Koeck et al., 2012). Functional traits including udder health, fertility, character, calving ease and durability were proven to be more important in breeding goals for organic cows than those for conventional cows (Nauta et al., 2009a). Therefore, the lower disease incidence in organic farms may result from the application of selection strategies supporting the breeding goal (Kijlstra and Eijck et al., 2006). However, there were studies which revealed that health and fertility problems were of the same or even of higher relevance in organic than in conventional farms (Borell and Sorensen, 2004; Weller and Cooper, 1996). Different genetic backgrounds or feeding and management strategies could explain the contradictory results found in the literature. For example, extensive management systems on organic farms may limit medical treatments in organic farming systems. In fact, hand milking may be used instead of antibiotics in some mastitis cases, resulting in reduced mastitis occurrences reported by veterinarians.

Genetic parameters in organic dairy farming systems

Basically, heritabilities for production, reproduction and health traits of Brown Swiss in low input farms are similar with those of conventional farms (Chapter 2). As expected, heritability estimates for production traits were moderate, and reproduction and health traits had low heritabilities (Chapter 3). Interestingly, daily genetic correlations between milk yield and somatic cell score (SCS) varied substantially by days in milk in different parities (Chapter 2). Excluding a weak positive genetic correlation at the very beginning of first parity, the genetic correlations were negative throughout the first three lactations. This result disagrees with several studies showing genetic antagonism between milk yield and SCS (Carlén et al., 2004; Koivula et al., 2005). Generally, lactose percentage had positive genetic correlations with test-day milk yield, and heritabilities for lactose percentage in the first three lactations were moderate. Therefore, adding lactose percentage to the overall breeding goal may be of benefit for organic breeding schemes.

Functional traits including udder health, fertility and calving ease will have higher economic weights in the overall organic breeding goals (Nauta et al., 2009a; Rozzi et al., 2007). Conception rate is one of the important fertility traits. Moderate to high negative genetic correlations between conception rate and test-day milk yield indicate that a higher weight on conception rate would probably reduce milk yield on the genetic level. Meanwhile, fat percentage and protein percentage will increase since conception rate has moderately positive genetic correlations with fat percentage and protein percentage. Milk with higher quality, (e.g. higher fat and protein percentage), should fulfill demands of organic farmers and consumers. Perhaps because higher levels of MUN have toxic effects on cows, MUN was negatively correlated with conception rate. Therefore, selection on conception rate might reduce MUN on the genetic level.

Strictly speaking, the quality and quantity of data from low input farms in Switzerland are not sufficient to estimate reliable genetic parameters. Heritabilities of traits can be influenced by the quality of data. For example, Buch et al. (2011a) reported that higher occurrence of hoof diseases was reported by hoof trimmers than by veterinarians (Laursen et al., 2009). Consequently, heritability was also higher for the hoof diseases reported by hoof trimmers (Buch et al., 2011a). Therefore, improvement of data quality from organic farms is necessary to precisely estimate genetic parameters and predict genetic gain. Furthermore, direct selection

on traits of interest can more efficiently improve selection response compared to indirect selection via indicator traits (König and Swalve, 2006). Therefore, direct measurements on functional traits, e.g. mastitis, metritis and ovarian cysts, might positively influence genetic progress.

Comparison of breeding strategies for organic dairy populations

As proposed in chapter 5, three breeding strategies could be applied for organic farms. The first strategy is to use bulls selected from conventional populations into organic farms taking G x E interactions into account. In another alternative, a closed organic breeding chain can be built up and organic AI bulls are only selected from the organic population. The third option is to select natural service (NS) sires based on farms and regions. There are advantages and disadvantages for each breeding scheme.

In the first breeding scheme, sires used in organic farms are selected from conventional farms. This scheme is relatively easy to apply because semen of sires can be bought from breeding companies for conventional populations and there will be no cost to building up new breeding programs. However, due to G x E interactions between the two production systems, rank of breeding values of sires may change. Therefore, breeding values adjusted to G x E interactions should be given for sires provided for organic farmers. In addition to G x E interactions, breeding goals between organic and conventional dairy farming are also very different. Conventional farmers prefer higher production yield, while functionality is the most important aspect to organic farmers. Using conventional sires in organic farms may not help achieve the goal of improving functionality for cows in organic farms, even when adjusted breeding values to G x E interactions are given. Overall ecology breeding values, as offered by some breeding organizations in Germany and Austria (Krogmeier, 2003), could benefit organic farms greatly. Therefore, it might be worthwhile to re-estimate the overall ecology breeding values of sires in conventional farming systems based on the data coming from organic farms.

Utilization of modern reproduction technologies for producing bull calves, such as multiple ovulation and embryo transfer (ET), is also a disadvantage of using sires selected from conventional farms in organic production systems, because the technologies contradict the naturalness of organic production. Based on organic farming regulations, artificial

reproduction technologies are prohibited in organic dairies. Therefore, farmers in organic systems prefer to use semen of sires without the application of ET, but sometimes information of ET is not available for all bulls. Moreover, conventional breeding of commercial breeds is based largely on ET and complementary technologies (Nauta, 2009b). The farmers in organic farms can only choose sires which are not produced by ET themselves without considering the use of ET in previous generations. If ET in previous generations was banned as well, only very few bulls would remain eligible for use on organic farms.

In the second breeding scheme, organic breeding programs are established within the organic farming systems. Like breeding programs in conventional production systems, a relatively small number of AI bulls are selected based on EBV estimated from data recorded in organic farms. This breeding scheme maintains naturalness of organic breeding, because all genetic material comes from organic production systems and ET-free AI bulls can be supplied to farmers. Additionally, as a result of high weight on functionality, sires selected from organic populations tend to improve udder health and fertility of cows directly, which implies that there is no need to adjust breeding values estimated from this breeding scheme.

However, there are many shortcomings for establishment of breeding programs with AI bulls in organic populations. First of all, the amount of data from organic populations is very small compared to conventional populations. Therefore, accuracy of selection in organic populations is not comparable with the corresponding accuracy in commercial dairy cattle populations. For example, there were more than 100,000 certified organic dairy cows in Germany in 2007, and this was the largest organic dairy population in Europe. Austria had the second largest organic dairy population in Europe, which had around 80,000 organic dairy cows (An analysis of the EU organic sector, 2010). Harder et al. (2004) reported that a conventional breeding program was superior to an organic breeding program in terms of genetic gain, return of costs and profit, assuming 50,000 cows. Better results in conventional breeding programs are attributable to larger population size of conventional populations and the frequent use of reproduction technologies, such as ET. Apart from the lower selection intensity, AI bulls will be used in organic breeding programs. Although AI is still allowed in organic dairy farming, according to EU regulations on organic farming, the proportion of AI in organic farming systems should be reduced as much as possible. Nauta (2009b) also suggested that AI disturbs a natural process of reproduction and natural mating can achieve better fertility results than AI.

In the third breeding strategy, sires are also selected within organic farms, and AI is completely discarded. In this strategy, NS sires are selected within each herd or region and selection of bull dams can be applied within female lines in the herd. Among the three breeding schemes described above, the third one is the most natural way, therefore confirming to the natural aspect of organic farming. Because NS is carried out at farm level or small region level, G X E interactions for the third scheme should be the lowest in the three breeding strategies. Furthermore, there might be an increase in genetic diversity because more service sires are kept in organic populations. Breeding at farm level will also increase differences between herds, since each farmer has a unique opinion on the best type of animal for the specific farm and management. Therefore, vigor of cows may be increased by exchanging genetic materials regularly between organic farms.

Breeding programs with natural mating pose various challenges. First of all, keeping bulls in organic farms may be dangerous and expensive for farmers. Additionally, a great deal of practical knowledge for working with bulls is needed (Nauta et al., 2005), because breeding at farm level is more complicated than choosing semen of AI bulls provided by breeding companies. However, because many organic farms converted directly from conventional farms, many farmers do not have breeding experience. Most importantly, only a very small number of cows are available in each organic farm, commonly ranging from 45 to 140 cows (Rotz et al., 2007) and around 24 (Chapter 2) in our study. A breeding program with a small population will reduce genetic variation because of close genetic relationships and genetic drift (Falconer and Mackay, 1996). Selection intensity of NS bulls also declines because only a limited number of candidates are available at farm level. Furthermore, a reduction in accuracy of selection might be observed as well because number of daughters used for estimating EBVs of bulls is smaller compared to the first and the second breeding schemes. Genetic progress of traits of interest may be reduced when implementing the third breeding scheme in herds with small populations compared to that of larger herds because of decreased genetic variation, selection intensity and accuracy of selection.

Several studies showed that breeding programs with genomic information could increase genetic gains of functional traits. For example, Egger-Danner et al. (2012) found a clear shift of annual monetary genetic gain towards fitness and health traits when applying genomic selection. Buch et al. (2012a) also reported that breeding schemes with genomic selection

resulted in higher annual genetic gain, greater contributions of functional traits to the gain and lower rate of inbreeding per generation than breeding schemes without genomic selection. Results from Chapter 4 also revealed that selection response would be doubled if GBV was a selection criterion in breeding programs for dairy cattle. Hence, application of genomic breeding programs in organic breeding schemes (the second and the third schemes) may increase accuracy of selection. Generation interval may also decrease with frequent use of young bulls in a genomic breeding program. Therefore, incorporating genomic selection into organic breeding programs should increase genetic progress because of improved accuracy and shorter generation interval.

The results from studies of Egger-Danner et al. (2012) and Buch et al. (2012a) were based on relatively large population sizes. Therefore, the potential of genomic selection in small organic populations was tested in Chapter 5 by combining organic breeding scenarios with genomic selection. True breeding values (TBV) of AI sires selected from an organic population based on GBV were higher than TBV of AI sires selected from a conventional population based on pedigree information, although the numbers of cows in the organic and conventional populations were 1,200 and 148,800 respectively. Only if a small G x E interaction existed between two environments (genetic correlation ≥ 0.8), TBV of AI sires selected from a conventional population based on pedigree information were greater than TBV of genotyped AI sires selected from organic farms with accuracy of GBV equals to 0.5. This was especially evident for low heritable traits ($h^2 = 0.05$). Buch et al. (2012b) reported that when 2,000 genotyped cows were added to the reference population annually, accuracy of direct genomic value was around 0.32 for a lowly heritable trait after 10 years. However, the study also showed that the accuracy increased to 0.45 if 30 sires, 2,000 cows and 170 test bulls were genotyped and added to the reference population every year. Verbyla et al. (2010) also found the accuracy of direct genomic value was 0.52 for energy balance, based on data from 527 primiparous cows. This indicates that an accuracy of 0.5 was achievable if more cows were available in organic populations. However, creating an informative reference population for small organic populations is difficult because only a limited number of organic cows are available (Buch, 2011b) Therefore, implementation of an organic breeding program with AI bulls might be possible if the program was applied on organic cattle in the whole country or internationally.

Assuming equal accuracy of GBV, the TBV of genotyped organic AI sires were higher than those from conventional farms if the genetic correlation of the trait was lower than 0.8. Genetic correlations between organic and conventional dairy production for a variety of traits ranged from 0.6 to unity (Ahlman et al., 2011; Nauta et al., 2006; Sundberg et al., 2010). However, selection is based on an index rather than individual traits and the composition of conventional and organic selection indexes are very different (Nauta et al., 2009a). Employment of different breeds between organic and conventional farms will further increase G x E interactions in the future. Therefore, it might be necessary to create a breeding program for organic production system. As suggested in Chapter 4, pre-selection of bull dams based on phenotypes for new functional traits would increase genetic gains compared to selection of bull calves based on a pedigree index. Buch et al. (2012b) also stated that adding genotyped cows with phenotypic information into breeding programs would increase accuracy of selection for new functional traits. Facing so much information, breeding organizations servicing organic farmers should be set up to design optimal breeding schemes and coordinate organic farms to fulfill desires from consumers, organic farmers and the regulations of the organic Council.

Genetic gain of NS sires was greater by incorporating genomic information into the breeding scheme applied at farm level. For example, despite the fact that accuracy of GBV was 0.5, TBV of genotyped NS sires was higher than TBV of NS sires selected on EBV. Nevertheless, selection of NS sires within herd obtained the lowest genetic gain (Chapter 5) in the three breeding schemes. However, genetic gain is not the sole criterion for evaluating breeding programs in organic production systems, naturalness and wishes of organic farmers are also important. The breeding scheme completely using NS sires is the most natural scheme, but may require additional work to maintain genetic vigor. For example, mating information should be recorded in detail and number of bulls kept in the farm should be decided carefully to avoid mating between relatives within 3 generations and prevent inbreeding depression (Chapter 5).

Rate of inbreeding per generation was higher in breeding schemes without the use of genomic selection (Chapter 4 and Chapter 5). There are two reasons summarized by Daetwyler et al. (2007) for lower inbreeding in genomic selection. First of all, genome-wide selection is expected to reduce the between family variance and shift the emphasis of estimated breeding values of individuals towards the Mendelian sampling term. Secondly, estimation induced

intraclass correlations of sibs are expected to be lower in genome-wide selection. However, genomic information might increase the fixation rate of the favorable QTL alleles and thereby increase inbreeding (Pedersen et al., 2010). Moreover, the rate of inbreeding based on genomic identity-by-descent was 3 times higher when a pedigree based rate of inbreeding was constrained (Sonesson et al., 2010). Therefore, Sonesson et al. (2012) suggested that management of changes in genomic inbreeding rather than in pedigree-based inbreeding was relevant, when using genomic-based estimates of breeding values. However, in this thesis, only pedigree based rate of inbreeding was calculated for all breeding schemes (with or without genomic selection).

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