Controlling of dairy cattle breeding programs

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Summary

The overall goal of this study was to develop possible controlling approaches for dairy cattle breeding programs. For this reason different topics from practical dairy cattle breeding were studied. Initially, genetic and environmental impact factors on auction prices of first lactation Holstein cows were analysed. Subsequently, a possible selection strategy for informative cooperator herds in progeny test programs was developed and its impact on a breeding program for Holstein cows was studied. Finally, an approach for the management of genetic variability in dairy cattle populations was applied to a set of preselected potential bull dams and sires, using additive genetic and genomic relationships.

For the first study the impact of a variety of traits and effects on auction prices was determined. Data of 1565 cows in first parity were collected at six monthly auction sales and scored by two classifiers in the auction hall. The analysis of variance revealed a highly significant impact of auction date, test day milk yield, stage of lactation, origin of sire, and miscellaneous defects on auction prices. The feet and leg, udder, and body composite also had a significant effect on the price with higher scores being associated with higher prices. Economic weights for type traits were derived by utilizing results from regression analysis. Highest economic weights per genetic standard deviation for linearly scored type traits were rear udder height, front teat placement, and strength. Genetic parameters for linear type traits scored at the auction date were consistent with literature reports. Heritability for the auction price was 0.27, and the auction price was genetically positively correlated to the feet and leg, udder, and body composite. Moreover, a relative breeding value for auction price was estimated for 27 influential sires, and correlated with official indices for production, conformation, somatic cell count, functional herd life, fertility, and total net merit index.

The second objective of this study was to identify informative cooperator herds. An approach based on yield deviations (YD) was used to identify those herds providing the highest content of information in terms of genetic differentiation. The overall YD of 717,377 first lactation cows from two

regions in East and West Germany were used. Daughters were ranked and classified within sire either for protein yield, fat yield, milk yield or somatic cell score (SCS) by extremeness of their YD. A pronounced genetic differentiation in protein yield was associated with high quality herd management characteristics. The same methodology applied for YD in SCS suggested a distinct genetic differentiation in SCS for cows in those herds characterized by a relatively high value for average somatic cell count. Ranks of herd calving years (HCY) and ranks of herds were calculated by averaging YD percentages within HCY, and within herds, respectively. A further partitioning of ranks of herds into quartiles, combined with an association study for descriptive herd parameters revealed that herds belonging to the first quartile had the highest average protein yield, the highest intra-herd standard deviation for the national production index, and the lowest age at first calving. Correlations between daughter yield deviations for the highest and the lowest herd quartile did not support the existence of genotype by environment interaction between test and production environment.

The third part of this thesis addresses the management of genetic variability in dairy cattle breeding. An algorithm using semi-definite programming was either combined with pedigree (a_{ij}) or genomic relationships (f_{ij}) among selection candidates. Selection candidates were 484 genotyped bulls and 499 pre-selected genotyped bull dams passing a central test on station. In different scenarios, separately for production index (RZM) and somatic cell score index (RZS), constraints on the average pedigree relationships among future progeny were applied. Despite the difference for some bulls in genomic and pedigree relationships, similar trends for results in genetic gain and achieved coefficients of relationships were observed for constraints on pedigree and corresponding genomic relationships. Generally, allowing higher values for relationships resulted in an increase of genetic gain for RZM and RZS, as well as in the number of selected sires. More sires were selected for all scenarios when restricting genomic relationships, compared to restrictions on pedigree relationships. Furthermore a simulated annealing algorithm was applied to minimize relationships in the subsequent generation.

1st chapter

General introduction

Economic success and controlling of dairy cattle breeding programs

The implementation of breeding programs based on progeny testing as suggested by Henderson (1964) and Skjervold and Langholz (1964) still has a strong influence on the structure of today's dairy cattle breeding programs. Since its implementation conventional progeny testing has resulted in a substantial genetic progress especially in production traits (e.g.Van Tassell and Van Vleck, 1991, Swalve and Höver, 2003)

For a long time the objective of German breeding programs was not to maximize financial profit, but the optimization of productive efficiency of the dairy population in a specific region. Thus genetic gain was the critical success factor scientific studies focussed on (Grandke, 2002). Increasing economic pressure due to the globalization of Holstein breeding (Dekkers et al., 1996, Miglior et al., 2005) and decreasing governmental financial support increasingly forced breeding programs to consider economic issues in the last two decades.

Grandke and Simianer (1998) compared several German Holstein breeding programs with regard to efficiency. As a measure of success they used the share of bulls within the list of the top 50 ranked by different selection indices in relation to the amount of herdbook cows. Their results show that population size seemed to be an unsuitable parameter when evaluating the success of artificial insemination (AI) organizations, as significant impact of population size on the amount of top bulls could not be confirmed. Breeding programs with medium populations of 50,000 to 100,000 cows had the lowest success rates whereas rather small breeding programs tended to have the highest. A study conducted by Swalve and Höver (2003) comparing genetic trend in four regions of Northern and Eastern Germany also revealed no interrelations between population size and increase in genetic gain. Moreover, an analysis of the use of proven sires showed a very large proportion of bulls getting second crop daughters although often used in a very limited way (Swalve and Höver, 2003). This indeed has a positive influence on genetic variability, but indicates reserves in terms of genetic gain achieved by the use of the best available bulls.

Dekkers et al. (1996) optimized the number of daughters per tested bull for different parameters like maximum genetic gain, number of marketable bulls and net returns from semen sales. The optimal progeny group size for the critical objective, net returns from semen sales, subtracting costs of sampling bulls, was between 95 and 105 daughters. The returns of a breeding program are mainly determined by both the market share and the semen price (Miller, 1988) with market share being the major factor for a long time, as AI companies were unable to develop differentiated products justifying price differences to other companies (Funk, 2006). This has slightly changed with the introduction of new value added products like sexed semen which can also help to reduce breeding costs as a smaller test capacity is needed (Weigel, 2004). Dekkers and Shook (1990) developed methods to quantify returns from breeding programs for a market with complete competition and purchasing decisions of dairy farmers being only based on estimated breeding values (EBV). Market share in such markets is determined by the number of bulls with an EBV above the marketing threshold, the semen price and the number of semen sold per bull. According to Dekkers and Shook (1990) the three ways to affect the market share are to increase the number of bulls sampled, or the number of daughters per bull, or increase the average genetic merit of bulls being tested. Although these are important influences on the market share it is a rather simplified view, as other factors like the AI companies' quality of marketing or their population size have to be considered. For instance about 60% of the cows in Germany are inseminated with bulls owned by the member AI organization of the dairy farmer (ADR, 2005). Moreover, Swalve and Höver (2003) observed that the bull selection of German dairy farmers not only depends on their total merit index, but also on management traits like calving ease.

König et al. (2007) established a new controlling parameter which is suitable to verify selection decisions as well as to explain differences between the success of AI organizations. They used national EBV from 1998 to 2006 for bulls from 12 different AI companies to determine differences in expected and realized selection intensities of cow sire selection. The ratio between realized and expected selection intensities was determined as the controlling value. Low controlling values indicated necessary improvements. When

evaluated according to the national top list, AI organizations with high controlling values were successful in the national competition regardless of population size.

As already pointed out, there often is a discrepancy between maximizing genetic gain and maximizing economic returns of a breeding program. This was also confirmed by Neuner et al. (2006) who found progeny testing of few bulls with 160 daughters per bull to be the scenario with the highest benefit for the AI company. If the focus was on maximizing genetic gain, a daughter number as small as 26 was the optimum. Thus a compromise between both goals should be adapted to the individual situation of the AI company.

Genomic selection as suggested by Meuwissen et al. (2001) will probably also have a serious impact on economic decisions of breeding programs. According to Schaeffer (2006), due to the introduction of genomic selection costs for proving bulls can be reduced by 92% while simultaneously doubling the genetic gain. König et al. (2009) compared a conventional progeny test program with different scenarios of genomic breeding programs. The evaluation criterion was discounted profit reflecting discounted returns minus discounted costs per cow. All genomic scenarios using at least 20% young bulls without daughter records were up to 2.59 times superior to the conventional breeding program, mainly due to a lower generation interval and a decrease of cost. However, the economic superiority of genomic selection is based on the complete abdication of progeny testing and the condition that dairy farmers are willing to use those genomic bulls. If genotyping costs substantially decrease in the future a two-pathway selection strategy including the genotyping of large amounts of bull calves as proposed by König and Swalve (2009) might even simplify the design of breeding programs and reduce their costs to a larger extent.

Influences on auction prices for dairy cattle

Besides income from milk production marketing of breeding cattle is an essential source of income for many German dairy farmers. In the last decade, on average more than 26,000 auction sales of Holstein dairy cattle per year were transacted in Germany (ADR, 2005), and 75% of all sales were from cows in first parity. To assure economic success on local and

global markets for dairy cattle it is of outstanding importance for farmers and their breeding organizations to have comprehensive information on which traits are being demanded in which qualities by potential buyers. With this information farmers as well as breeding organizations would be able to increase revenues by selecting on those traits.

So far, there were only a few studies addressing auction prices in the Holstein breed which might be out-dated today (Placke, 1982, Ruff et al., 1983). More recent studies have been conducted for Simmental and Brown-Swiss cattle in Austria (Fürst-Waltl et al., 2004) and Germany (Krogmeier et al., 2006). Both studies were focussed on deriving economic weights for conformation traits which have a high impact on current selection decisions (Swalve and Höver, 2003). However, the inclusion of conformation traits in a selection index can cause problems as for the derivation of economic weights direct impact of traits on costs and revenues has to be known (Amer et al., 1994). Thus Fürst-Waltl et al. (2004) and Krogmeier et al. (2006) determined the impact of several type traits on auction prices of heifers and cows using regression analysis. Main results were a substantial impact of udder, conformation, frame, and rump structure on the market price. Today the proportion of conformation data in the national selection index RZG is mainly based on ‘political’ decisions. Findings about economic weights derived with sophisticated methods could help placing accurate emphasis to conformation traits and thus improving total genetic gain.

Contract herds in dairy cattle breeding

AI breeding schemes as described by Skjervold and Langholz (1964) including selection of superior cows in a herdbook population, mating them to the best available sires and testing their male progeny by random mating in the whole population have been the most common ways of progeny testing since decades.

Hinks (1978) proposed open nucleus breeding schemes primarily for countries with a poor infrastructure consisting of supplier herds that produce cows for test herds in which milk recording is conducted. After the test most cows return to the supplier herds, whereas the best cows are selected for the breeding nucleus. Nicholas and Smith (1983) combined nucleus breeding

schemes with the intensive use of embryo transfer in a multiple ovulation and embryo transfer (MOET) program. Main elements were the selection of juvenile animals based on ancestor and sibling information and the use of embryo transfer on these animals which leads to a rigorous decline in generation interval. Both approaches were combined by Swalve (1989) in an intensive test herd program. It comprises the use of special bull dam herds where bull dams are tested intensively and embryo transfer is applied to multiply the best cows. Young bulls are progeny tested in cooperator herds, and in the main population only tested sires are used.

Cooperator herds can help to identify superior sires if herds with optimal environments are selected, since keeping animals in superior environments enables them to express their true genetic potential which leads to a higher accuracy of selection (Hammond, 1947, Van Vleck, 1963). As found in several studies, differences in test environments have been associated with differences in estimated variance components with higher additive genetic variances being prevalent in herds with a higher production level (e.g. Van Vleck, 1963, Hill, 1984, Garrick and Van Vleck, 1987). Several aspects like the optimization of management and feeding strategies (Padilla and Keown, 1990), the milking technology and herd size (Weigel et al., 1993) as well as the skills of herdsmen (Short et al., 1990) were identified as possible reasons for increased intra-herd variances.

Another advantage of cooperator herds would be the implementation of recording functional health like mastitis (Philipsson, 1995, De Haas et al., 2002), claw disorders (König et al., 2005) or reproduction diseases (Zwald et al., 2004). Although too expensive and complicated to implement in the whole population, this recording would lead to a higher genetic gain when compared to selection strategies based on indicator traits.

At present, as conventional breeding programs have to adapt to changes associated with the implementation of genomic selection (Meuwissen et al., 2001) the implementation of a system of contract herds gets even more important. Schaeffer (2006) proposed to estimate SNP effects in special cooperator herds while simultaneously emphasizing the advantages of genomic selection concerning genetic gain in terms of cost reduction. To achieve accuracies for genomic breeding values of 0.75, as assumed in this

study, a solid database is essential, especially for functional traits (König and Swalve, 2009, VanRaden et al., 2009). This can only be achieved by the standardized recording of these traits in a sufficient amount of selected herds.

Testing bulls in special cooperator herds will also provide sufficient test capacities and reduce costs for logistics, e.g. for type trait classification (Swalve and König, 2007).

Due to the above mentioned arguments and to the increasing economic pressure caused by the higher competition on the semen market (Dekkers et al., 1996) and the decline of governmental subsidies for performance testing several German breeding programs are considering to establish contract herd systems or have already established them. However, until now there are only few sophisticated approaches to select informative contract herds. Some studies have focused on single aspects like the number of usable records (Meinert et al., 1997), or herd size and herd production level (Vierhout et al., 1999). A cluster analysis was suggested by Gernand et al. (2007) to combine favourable effects of large herd size, high production level, and low age at first calving. Brügemann (2008) and Dechow et al. (2008) focussed on genetic analyses and variance component estimation within herds. Brügemann (2008) found increasing additive genetic variances and heritabilities with increasing herd size and improving farm management. In the study by Dechow et al. (2008), intra-herd heritability was additionally negatively correlated with sire misidentification rates. Due to relatively large standard errors of estimates from intra-herd analyses, these approaches are only applicable for very large herds.

Impact of inbreeding and management of genetic variability in dairy populations

Selection leads to losses of genetic variability and increases of inbreeding rates, associated with negative effects on the sustainability of breeding schemes.

However, due to a considerable genetic progress achieved by intensive selection the rate of inbreeding in dairy populations has risen substantially (e.g. Sorensen et al., 2005, König and Simianer, 2006, Mc Parland et al.,

2007). Mrode et al. (2009) calculated inbreeding coefficients and average relationships in the top 4,000 index in three different countries. Average inbreeding was approximately 2% in Great Britain and Italy, and 1% in Ireland. When a joint pedigree was used, inbreeding was slightly higher than 2%. Relationships within the Top 4000 index cows in 2006 from Great Britain, Italy and Ireland were 0.083, 0.087 and 0.107 respectively. Kearney et al. (2004) found an increased rate of inbreeding in UK Holsteins, especially since 1990 when, compared to previous time periods. This was a result of the large influence of a few related sires on the breed. In registered US Holsteins born in 1990 two sires accounted for nearly one quarter of the genes (Young and Seykora, 1996). Moreover several authors found negative associations between production traits and inbreeding. Cassell et al. (2003) observed the summit milk yield in Canadian Holsteins to be decreased by -0.12 to -0.06 kg/d per 1% increase of inbreeding. In Belgian Holsteins inbreeding decreased yield of milk, fat, and protein during a lactation by 19.68, 0.96, and 0.69 kg, respectively, per each 1% increase in inbreeding in a study conducted by Croquet et al. (2006). Milk production losses per lactation in US Holsteins caused by inbreeding were about 35 kg per percentage of inbreeding level above 0.01 but increased to 55 kg per percentage inbreeding level from 0.07 to 0.10.

Negative consequences associated with inbreeding apart from the loss of genetic variation are an increase of undesirable genetic disorders like complex vertebral malformation (CVM) and inbreeding depression. Several studies have been conducted to study the impact of inbreeding on different traits in dairy populations. For production traits as well as for functional traits a negative impact of inbreeding was found (e.g. Miglior et al., 1995, Wiggans et al., 1995, Wall et al., 2005). Adamec et al. (2006) reported a relatively small increase of stillbirths of 0.25 and 0.20% for male and female calves per 1% increase in inbreeding for first parity births. Although effects of inbreeding on stillbirths even declined with increasing parity, effects of inbreeding were consistently unfavourable. In Danish Holsteins Sørensen et al. (2006) found an increase of 1,500 cells/ml in first lactation cows. Furthermore, comparing a cow with 5% inbreeding with a cow with 2% inbreeding, the incidence of mastitis increased by 1.08%, 0.55% and 0.98% in first, second, and third

lactation, respectively. These results are in line with Miglior et al. (1995) who reported an effect of 0.012 per percentage inbreeding on linear SCS. However, other studies conducted by Smith et al. (1998), Thompson et al. (2000) and Croquet et al. (2006) found no or very little impact of inbreeding on SCS.

For risk of culling Sewalem et al. (2006) found only a small impact of inbreeding, whereas other studies found fewer day of productive life, higher age at first calving and longer calving intervals (e.g.Smith et al., 1998, Thompson et al., 2000, Adamec et al., 2006). Especially cows with extreme inbreeding coefficients show inbreeding depression. For example González-Recio et al. (2007) observed that cows with an inbreeding coefficient of greater than 25% had lower pregnancy rates and higher dystocia rates (–6.37 and 1.67%, respectively) than low or non-inbred cows.

Meuwissen (1997) developed the optimum genetic contribution selection strategy (OGC) to maintain variability in populations under selection. This method is based on a series of relaxed optimizations using Lagrange Multipliers to maximize genetic progress under the constraint of fixed maximum relationship. Meuwissen and Sonesson (1998) extended this selection rule to overlapping generations and Hinrichs et al. (2006) developed an algorithm enabling the calculation of optimal genetic contribution for large numbers of selection candidates. The optimal genetic contribution theory has been used successfully in many applications (e.g. Kearney et al., 2004, König and Simianer, 2006). König and Simianer (2006) for example applied OGC for elite matings in a breeding program embracing 30 young bulls and found an increase in genetic gain of 13.1% with the same rate of inbreeding as a conventional breeding program. Moreover, they recommended controlling inbreeding when mating bull sires to bull dams, because these genetic groups have a sustainable impact on the development of genetic relationships in dairy cattle breeding programs. Sonesson and Meuwissen (2000) proposed minimum coancestry matings by applying a simulated annealing algorithm using the results of OGC to minimize inbreeding in a short-term view.

However, Pong-Wong and Woolliams (2007) showed that the use of Lagrange Multipliers fails to identify a global optimum solution in some cases, as invalid negative genetic contributions could be assigned to some individuals which are consequently fixed to zero and excluded from the set of selection candidates. As an extension Pong-Wong and Woolliams (2007) suggested an algorithm based upon semi-definite programming (SDP) for maximizing genetic gain while restricting inbreeding. They demonstrated that the SDP approach led to substantially higher expected genetic gains in a range of 1.5% to 9% when compared to the method of Meuwissen (1997). The SDP approach is also characterized by being able to accommodate any number of constraints (Pong-Wong and Woolliams, 2007) and could even be used to simultaneously constrain both pedigree relationship and also relationship around a QTL under selection (Roughsedge et al., 2008) which might be useful to maintain genetic variation in specific genome regions close to loci under selection.

The use of tools for the management of genetic variability will probably become even more important in the future, as genomic selection, as proposed by Meuwissen et al. (2001), is revolutionizing dairy cattle breeding programs (Hayes et al., 2009). This approach is based on the selection of animals using breeding values estimated on the effects of single nucleotide polymorphisms (SNP). Schaeffer (2006) compared a genomic breeding program with a traditional Canadian breeding program and found a 92% decrease in breeding costs combined with a substantial increase in genetic gain.

Daetwyler et al. (2007) pointed out that genomic selection will lead to lower inbreeding as amongst others the accuracies of estimated Mendelian sampling terms will be higher which leads to more within family variation and a lower co-selection of sibs. This is in line with the results of several studies that found marker-assisted selection to reduce the rate of pedigree-estimated inbreeding (e.g. Dekkers, 2007, Sonesson, 2007, Pedersen et al., 2009). However, from a practical point of view genomic selection will probably lead to an increased rate of inbreeding per year if not managed correctly. This is due to the fact that high accuracies of estimated breeding values of young animals will probably lead to higher proportions of young animals being

selected and thus to a shorter generation interval (Hayes et al., 2009). Additionally König et al. (2009) economically evaluated genomic breeding programs and found that gain in discounted profit was strongly correlated with the decrease of selection proportions for young sires having been selected, which will also cause an increase in inbreeding.

Scope of this thesis

The major scope of this study was to develop possible controlling approaches for dairy cattle breeding programs. For this reason different topics linked to practical dairy cattle breeding were studied. Initially, genetic and environmental impact factors on auction prices of first lactation Holstein cows were analysed in chapter 2. Subsequently, chapter 3 addresses the issue selection strategy for informative cooperator herds. A selection strategy was developed and its impact on a breeding program for Holsteins was studied. In a last step an approach for the management of genetic variability in dairy cattle populations using genomic relationships was applied to a set of preselected potential bull dams and sires in chapter 4.

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2nd Chapter

Genetic and Environmental Impact on Auction Prices for Holstein Cows

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Abstract

The aim of the present analysis was to determine the impact of a variety of traits and effects (i.e. production, type, health, management effects, pedigree information) on prices of Holstein cows sold at auction, and to estimate genetic (co)variance components between type traits and auction price. Results were used to derive economic weights for type traits. Data of 1565 cows in first parity were collected at six monthly auction sales from August 2005 through January 2006. Seventeen linear type traits and body condition (scale 1 to 9), and four type composites (dairy character, body, feet and legs, and udder; scale 65 to 88) were scored by two classifiers in the auction hall before cows were sold. Analysis of variance revealed a highly significant impact (*P<0.001*) of auction date, test day milk yield, stage of lactation, origin of sire, and miscellaneous defects on auction price. The most expensive cows were sold in August, they were from foreign proven sires, they had a high level of test day milk yield, and they were free from defects related to udder, feet and legs, or milkability. The feet and leg, udder, and body composite also had a significant effect on the price (*P<0.001*), with higher scores being associated with higher prices. The opposite association was found for dairy character (*P<0.01*). Utilizing results from regression analysis, economic weights per genetic standard deviation were highest for linear scored rear udder height (1.23 €), front teat placement (0.97 €), and strength (0.80 €), but were negative for dairy character (-0.69 €). Genetic parameters for linear type traits scored at the auction date were consistent with literature reports. Heritability for auction price was 0.27, and auction price was genetically positively related to the feet and leg (0.55), udder (0.55), and body composite (0.21). A relative breeding value for auction price was estimated for 27 influential sires, and correlated with official indices for production, conformation, somatic cell count, functional herd life, fertility, and the total net merit index. Correlations were 0.15, 0.21, 0.11, 0.03, 0.05, and 0.19, respectively. Auction price in combination with type scores and information related to farm management provide valuable information for genetic analysis in dairy cattle, and results can be used to increase dairy cow profitability.

Introduction

Worldwide, conformation traits are included in most of the national selection indices for Holstein cattle (Miglior et al., 2005). They are generally used for the national genetic evaluation as indicator traits for udder health (Boettcher et al., 1998), or to predict the length of productive life (Bünger et al., 2001; Schneider et al. 2003; Sewalem et al., 2004). Type traits have a long tradition in German dairy cattle breeding programs (Mügge et al., 1999), and a high emphasis on conformation traits in current breeding goals and selection decisions was reported by Swalve and Höver (2003) and König et al. (2007). However, the inclusion of conformation traits in an overall breeding goal through selection index theory can cause problems. Sophisticated methods for the derivation of economic weights (e.g. Amer et al., 1994) demand a direct impact of traits on costs and revenues, but some conformation traits describing the “beauty” of a cow have only a hypothetical weight (Sölkner et al., 1999).

A possible alternative to derive economic weights for type traits is described by Fürst-Waltl et al. (2004) and Krogmeier et al. (2006). These authors determined the impact of several type traits on auction prices of heifers and of cows, respectively. Both studies, recently conducted in the Simmental dual purpose breed and in Brown-Swiss dairy cattle, revealed a substantial impact of udder, conformation, frame, and rump structure on the market price. Regression analysis, i.e. the change in market price per one unit increase in the score (in genetic standard deviations) for the respective type trait, can be used to derive economic weights (Krogmeier et al., 2006).

The incorporation of type traits in complex breeding goals and the early prediction of longevity through type traits is associated with another problem. It is questionable whether subjectively scored type traits are a reliable database for complex statistical analyses. Beside the subjective classification for type traits, several studies (e.g. Weigel and Lawlor, 1994; Gengler et al., 2006) focused on the problem of heterogeneity in variance and covariance components. In the study by Gengler et al. (2006), heterogeneity of variances was found across different subsets stratified by the size of contemporary groups, the parity of cows, and the average classification for the respective type trait. A substantial heterogeneity of heritabilities for type traits within

different regions in Germany was also found by Bethge et al. (2005), mainly for traits such as foot angle which are difficult to score in the field. A further problem is that classifiers varied in their score given for the same animal or in the range of the linear scale they used (Bowden, 1982; Swalve and Flöck, 1990; Veerkamp et al., 2002). Although these factors can often be adjusted before genetic evaluation (Brotherstone et al., 1990), a harmonisation of classification results would contribute to more authenticity. Hence, the advantages of a general classification of type traits at auction are as follows: 1.) Several classifiers can score the same animal and several hundred animals can be scored per day, 2.) cows for selling at auction are prepared and showcased similar to each other which could minimize bias in statistical analyses due to preferential treatment (Kuhn et al., 1994), and 3.) breeding organisations save expenses when data recording is more centralized (Swalve and König, 2007).

In the last decade, on average more than 26,000 auction sales per year of breeding stock were transacted in Germany for Holstein dairy cattle (ADR, 2005), and 75% of all sales were from cows in first parity. Based on these impressive quantities, many breeders generate an additional income by selling surplus female cattle at auction. Knowledge about management related characteristics on auction prices, e.g. the optimal length of days in milk or age at first calving, is valuable information for a more economical sales strategy. So far, there were only a few studies addressing this topic in the Holstein breed, and most of them are somewhat out-dated (e.g. Placke, 1982; Ruff et al., 1983).

The objectives of this study were: 1.) to determine the most important management characteristics to achieve higher prices on sale, 2.) to determine the impact of type traits on auction prices for a further application in deriving economic weights, and 3.) to estimate genetic parameters for the trait ‘auction price’.

Materials and Methods

The dataset comprised auction prices, test day production records, and type scores of 1565 first-lactation Holstein cows marketed at six monthly auctions between August 2005 and January 2006 at one auction place in North-West

Germany. Seventeen linear type traits and body condition (scale 1 to 9), and five type composites (dairy character, body, feet and legs, udder, final score; scale 65 to 88) were scored by two classifiers in the auction hall before cows were sold. Both classifiers worked simultaneously on all auction dates and scored the animals alternating. The final score combines the composites for dairy character, body, feet and legs, and udder by weighting factors of 0.15, 0.20, 0.25, and 0.40, respectively. A more detailed description related to the recorded linear type traits and type composites for genetic evaluation in German Holstein dairy cattle is given by the VIT (2007). All cows were inspected by a veterinarian at the auction date and deficiencies like clinical mastitis, light quarters, udder warts, substantial feet and leg problems, and obvious reproductive failures were announced during the sale by the auctioneer. Official announcements also included the declaration of insufficient milkability below 1.8 kg/min. A second dataset consisted of 305-d lactation records and type scores of dams. Variables related to the sires, such as estimated breeding values (EBV) and origin (i.e. German young sire, German proven sire, foreign proven sire, or natural service) were used from the official database for international genetic evaluation from August 2005. Four different models were applied to investigate the impact of type composites and of linear type traits on auction price, and to estimate genetic parameters.

Model 1 for type composites

The impact of fixed effects as summarized in Table 1 with a main focus on fixed effects of the four type composites (dairy character, body, feet and legs, udder) on auction price was analysed using the GLM procedure (SAS, 1999). Model 1 was:

$y_{ij} = \mu + F_i + e_{ij}$

where

y_{ij} = auction price of the i-th animal

μ = overall mean

F_i = representing all fixed effects for animal i (see explanations in Table 1)

e_{ij} = random residual effect

Table 1. Levels and P-values of fixed effects from model 1 (F-test, sum of squares type III)

Fixed effect	levels of fixed effects	P-value
Date of auction	August, September, October, November, December, January	< 0.001
Stage of lactation	≤ 14 days in milk (dim), 15-28 dim, 29-42 dim, 43-56 dim, 57-70 dim, ≥ 71 dim	< 0.001
Age at first calving	< 25 months, 25-27,9 months, 28-30,9 months, 31-33,9 months, ≥ 34 months	0.059
Test day milk yield	< 26 kg, 26-27,9 kg, 28-29,9 kg, 30-31,9 kg, 32-33,9 kg, 34-35,9 kg, ≥ 36 kg	< 0.001
Somatic cell count	≤ 100,000; 101,000-400,000; ≥ 400,000	0.004
305-d milk yield of dam	< 7000 kg, 7000-8499 kg, 8500-9999kg, ≥ 10,000 kg	0.053
Final score of dam	not scored or ≤ 79 points, 80-82 points, 83-84 points, ≥ 85 points	0.003
Origin of sire	foreign proven sire, German proven sire, young sire, natural service	< 0.001
Announcement of udder deficiencies[1]	present, absent	< 0.001
Announcement of feet and leg deficiencies[2]	present, absent	< 0.001
Announcement of reproductive failures[3]	present, absent	0.069
Announcement of milkability deficiencies	present, absent	< 0.001
Dairy character composite	≤ 76 points, 77-78 points, 79-80 points, 81-82 points, 83-84 points, ≥ 85 points	0.006
Body composite	≤ 76 points, 77-78 points, 79-80 points, 81-82 points, 83-84 points, ≥ 85 points	< 0.001
Feet and leg composite	≤ 76 points, 77-78 points, 79-80 points, 81-82 points, 83-84 points, ≥ 85 points	< 0.001
Udder composite	≤ 76 points, 77-78 points, 79-80 points, 81-82 points, 83-84 points, ≥ 85 points	< 0.001

[1] Announcements of udder deficiencies imply e.g. presence of mastitis or surplus teats

[2] Announcements of feet and leg deficiencies imply e.g. hyperplasia interdigitalis or digital dermatitis

[3] Announcements of reproductive failures imply e.g. retained afterbirth or cleaning still in progress

Model 2 for linear scored type traits

The linear type traits can be separated into four categories (dairy character, body, feet and legs and udder; Table 2). Model 2 was identical to model 1 apart the following changes: a) when analysing the regression of auction price on BCS and dairy character, the fixed effect of the dairy character composite was removed from the model, b) when analysing simultaneously the regression of auction price on stature, body depth, strength, rump angle, and rump width, the fixed effect of the body composite was removed from the model, c) when analysing simultaneously the regression of auction price on rear leg side view, foot angle, hocks, and rear leg set rear view, the fixed effect of the feet and leg composite was removed from the model, and d) when analysing simultaneously the regression of auction price on rear udder height, suspensory ligament, front teat placement, rear teat placement, fore udder attachment, udder depth, and teat length, the fixed effect of the udder composite was removed from the model. This strategy avoids double counting of traits. The four linear traits rump angle, rear leg side view, teat placement rear, and teat length were taken into account with an intermediate optimum. The highest value was given for the score of the intermediate optimum, and deviations from the optimum, regardless below or above, received the same score in the range from 1 to 5. Values closed to the optimum gave a higher price than scores far apart, and this relationship was linear. The impact of all other linear type traits was modeled as a linear regression, because quadratic or cubic terms were not significant at all ($P > 0.05$).

Model 3 and 4 to estimate genetic parameters for auction price and type traits

Estimation of genetic parameters for the four type composites, the final score, and auction price was done using bivariate animal models for all combinations of type traits and auction price and applying the package ASReml (Gilmour et al., 2000). The model 3 for auction price was:

$y_{ijklm} = \mu + SL_i + FC_j + DA_k + a_l + e_{ijklm}$

and for all type composites and final score, the model 4 was:

$y_{ijklmn} = \mu + SL_i + FC_j + DA_k + CF_l + a_m + e_{ijklmn}$

where SL is the covariate of stage of lactation, FC is the covariate of age at first calving, DA is the fixed effect of date of auction, a refers to the random animal effect, and CF is the fixed effect of the classifier. All other effects were defined as in model 1. Model 4 was also used for unviariate analyses to estimate variance components for the eighteen linear type traits scored at auction. For genetic analyses, relationships among animals were considered back to base animals born in 1940.

Results and Discussion

Impact of production, health, management effects, and type composites (model 1)

Significance values from analysis of variance for all fixed effects (type III test of fixed effects) are shown in Table 1. Most of the effects were highly significant (*P<0.001*), apart from the 305-d milk yield of the dam, announcement of reproductive failures, age at first calving, and the dairy character composite.

A general overview for the number of sold cows in combination with least square means for auction price by month of auction is depicted in Figure 1. According to the observed trend in previous years for different market places in Germany (ADR, 2005), the number of cows sold in November was twice as high compared to the number of cows sold in August, but auction prices were lower. Hence, the market price was mainly influenced by the ratio of supply and demand.

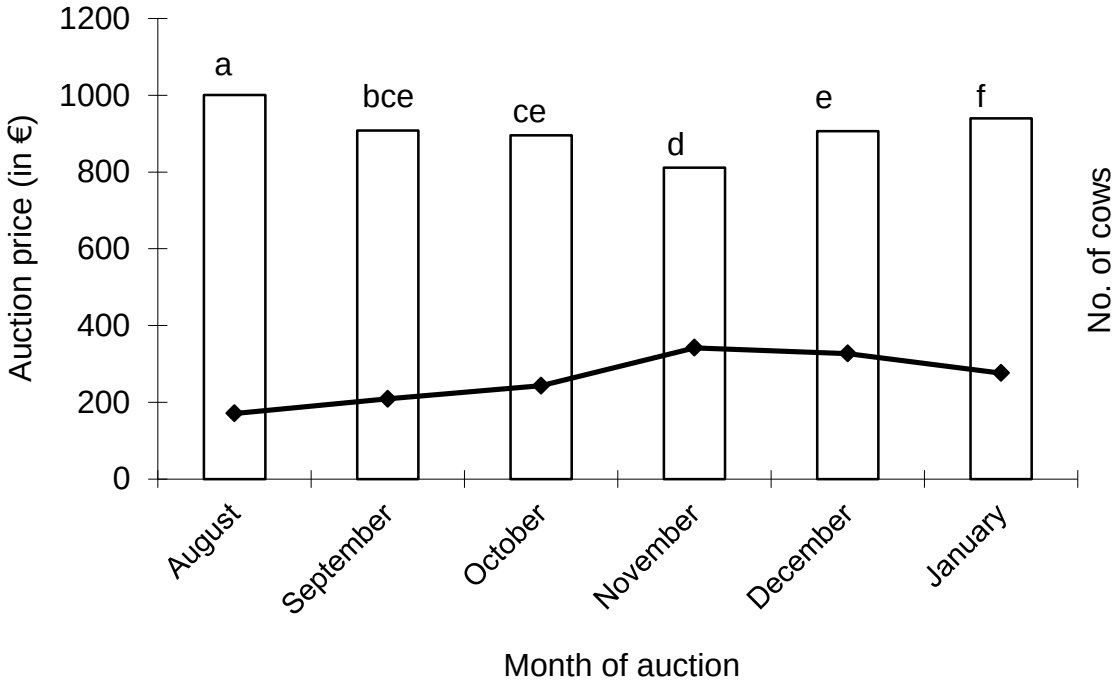

Figure 1. No. of sold cows (black solid line) and LSMeans for the trait "auction price" (in €, white bars) by month of auction. Different superscript indicate significant differences of LSMeans *(P<0.05)*.

Age at first calving, another effect related to farm management, had no significant impact (*P>0.05*) on auction price. Country of origin of the cows' sire (foreign proven, domestic proven, young bull without official EBV, or natural service) had a significant (*P<0.001*) impact on auction price. Prices of daughters from foreign, proven sires were 29 € higher compared to the average market price (Figure 2). As fifty percent of all animals were bought by foreign customers, a reason for this fact might be that those customers favoured daughters from well-known international sires. Lowest prices were paid for daughters from natural service bulls.

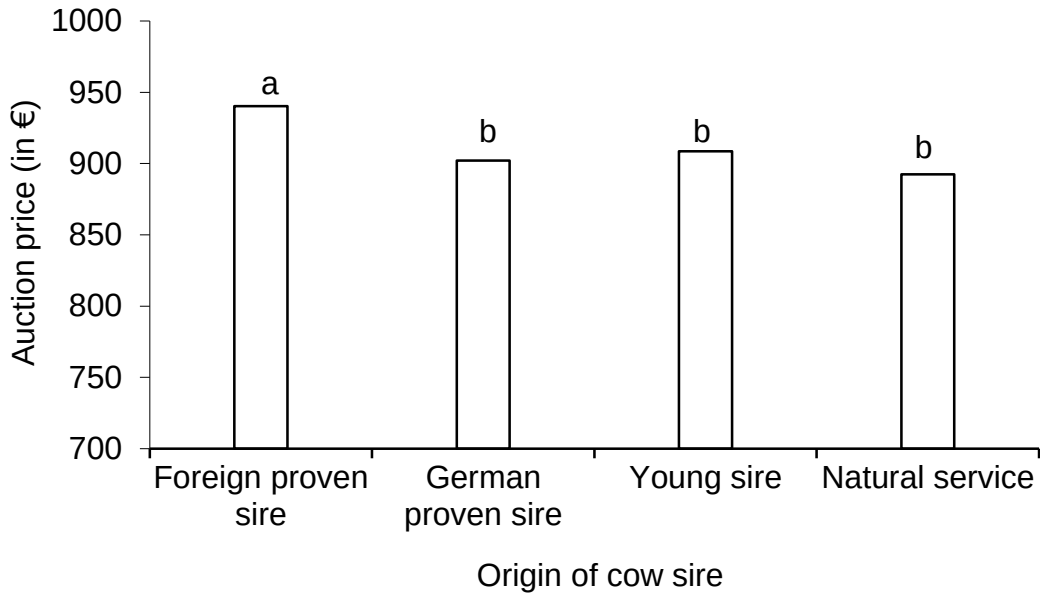

Figure 2. LSMeans for the trait “auction price” (in €) by classes of origin of sire. Different superscript indicate significant differences of LSMeans *(P<0.05)*.

As shown in Figure 3, an increase of days in milk was associated with a decrease in price for more than 43 days in milk. The main intention of customers is to increase the total amount of milk production on their farms to fulfil the fixed fat quota. As a consequence, cows on sale having already exceeded their lactation peak achieved lower prices. Krogmeier et al. (2006) defined three classes for days in milk. In their study, prices for cows sold within the first 30 days after calving were about 30 € higher compared to cows being in a later stage of lactation.

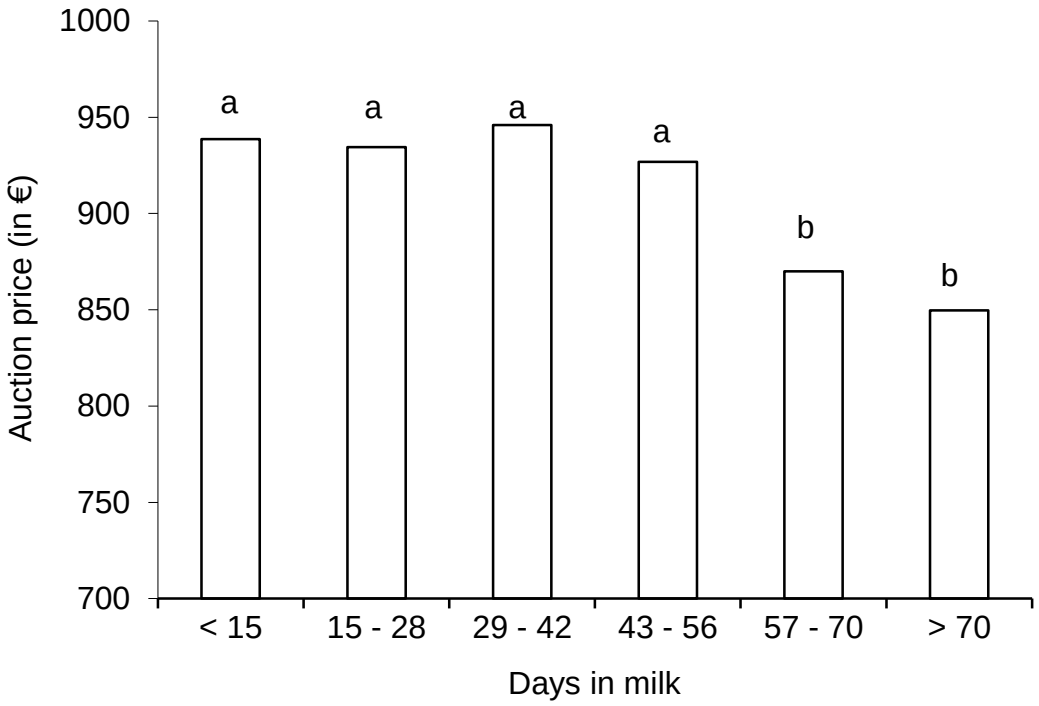

Figure 3. LSMeans for the trait "auction price" (in €) by classes of days in milk. Different superscript indicate significant differences of LSMeans *(P<0.05)*.

The impact of test day milk yield on market prices is supported by results presented in Figure 4. The difference in market price for cows differing 10 kg in test day milk yield, e.g. when comparing prices in milk yield class 1 (< 26 kg) and in milk yield class 7 (> 36 kg), was 311 €. A similar result, i.e. an increase in auction price of 40.5 € per 1 kg of test day milk yield, was reported by Krogmeier et al. (2006). The impact of 305-d lactation milk yield of the dam on auction prices was of minor importance (*P>0.05*), e.g. a difference of only 43 € was observed when comparing extreme classes above 10,000 kg and below 7,000 kg. This result corresponds to those from Krogmeier et al. (2006). Placke (1982) and Fürst-Waltl et al. (2004) found a substantial impact of dams' milk production on auction prices. However, heifers in their analyses did not have any production records. In such a case, customers put more emphasis on pedigree information.

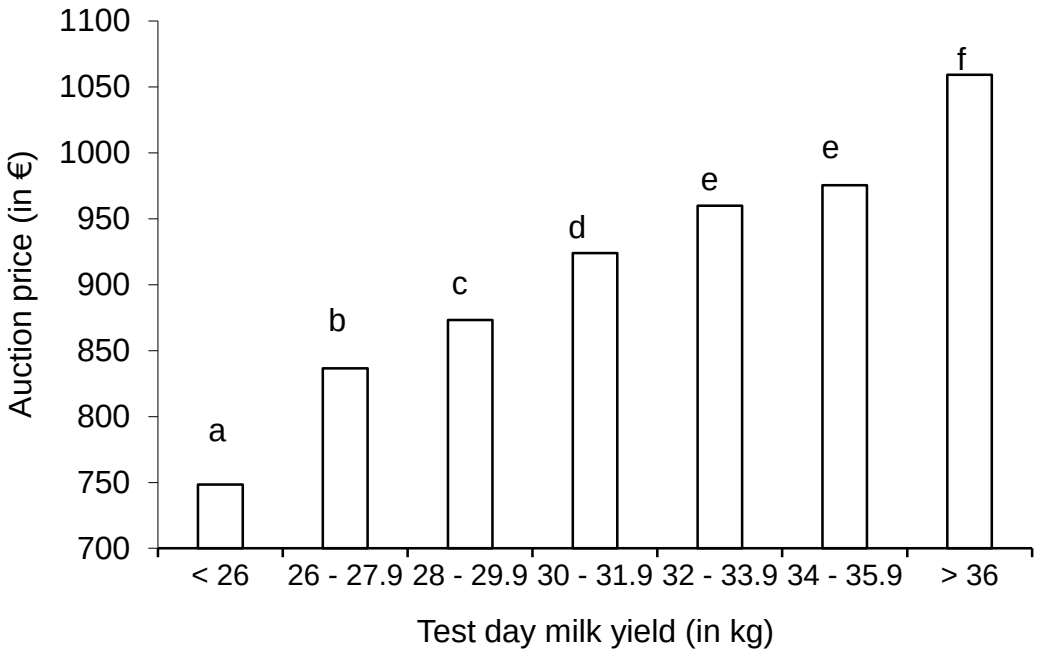

Figure 4. LSMeans for the trait “auction price” (in €) by classes of test day milk yield. Different superscript indicate significant differences of LSMeans *(P<0.05)*.

The current status of a cow’s health strongly determined purchase decisions. Announced deficiencies based on the veterinarians’ inspections, i.e. mastitis, feet and leg problems, and reproductive failures, reduced the average market price by 151.40 €, 121.23 €, and 50.96 €, respectively (Fig. 5). An additional indicator for udder health is SCC (Philipsson et al., 1995). According to guidelines by Smith et al. (2001), SCC of cows in first parity should be below 100,000, whereas the range from 100,000 to 200,000 indicates a possible infection, and 200,000 cells or more is a clear signal that an infection is occurring. In our study, test day SCC below 100,000 cells increased the average market price by 38.60 €. The announcement for insufficient milkability below 1.8 kg/min decreased the market price by 103.92 € (Figure 5): a comprehensible decision, because milking speed of cows is strongly related to labour (Devir et al., 1993) and costs (Trilk et al., 2005) in dairy cattle farming.

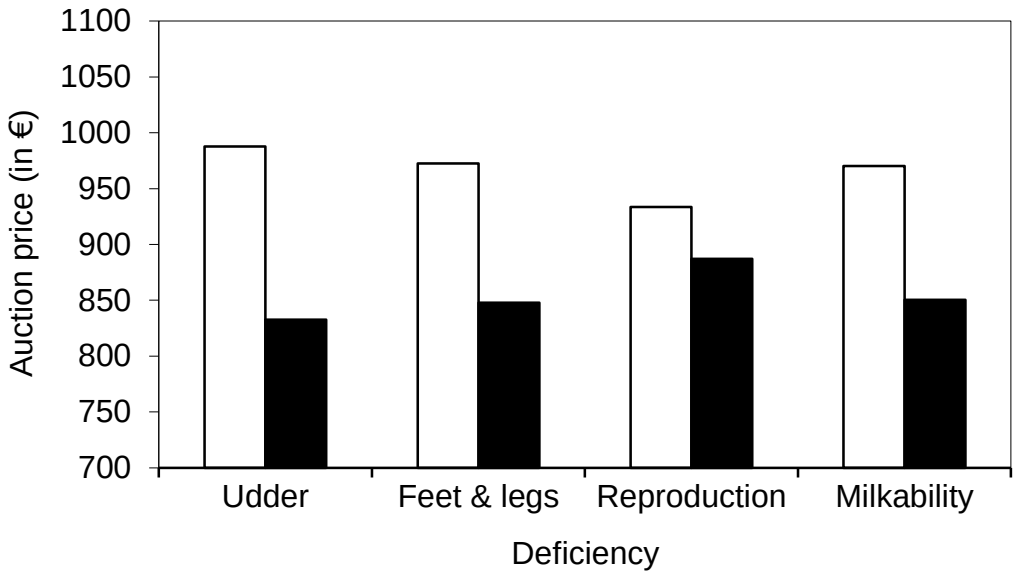

Figure 5. LSMeans for the trait “auction price” (in €) for several kinds of defiency announcements (white bar = no announcement; black bar = announcement). All pair wise differences were significant apart from reproduction *(P<0.05)*.

The impact of type composites on auction price is shown in Figure 6. As depicted, the score for the udder composite had a significant impact on auction price. Scores of 84 points or above resulted in 227 € higher prices compared to udder scores below 77 points. Krogmeier at al. (2006) found a similar price difference between the best and the worst udder class in Brown-Swiss and Simmental. Due to their desirable correlations to longevity (Bünger et al., 2001), and claw disorders (König et al., 2005), also higher scores for the feet and leg composite were associated with higher prices. The price difference between the two extreme classes was 126 €. As shown by Fürst-Waltl et al. (2004), customers also paid significantly higher prices for cows having higher scores for the body composite. Somewhat surprising were higher prices for lower scores for the dairy character composite. Customers favoured well-conditioned cows, but sharpness at the withers (a main criterion for high scores for dairy character) is highly correlated with less strength and body weight (Dechow et al., 2003).

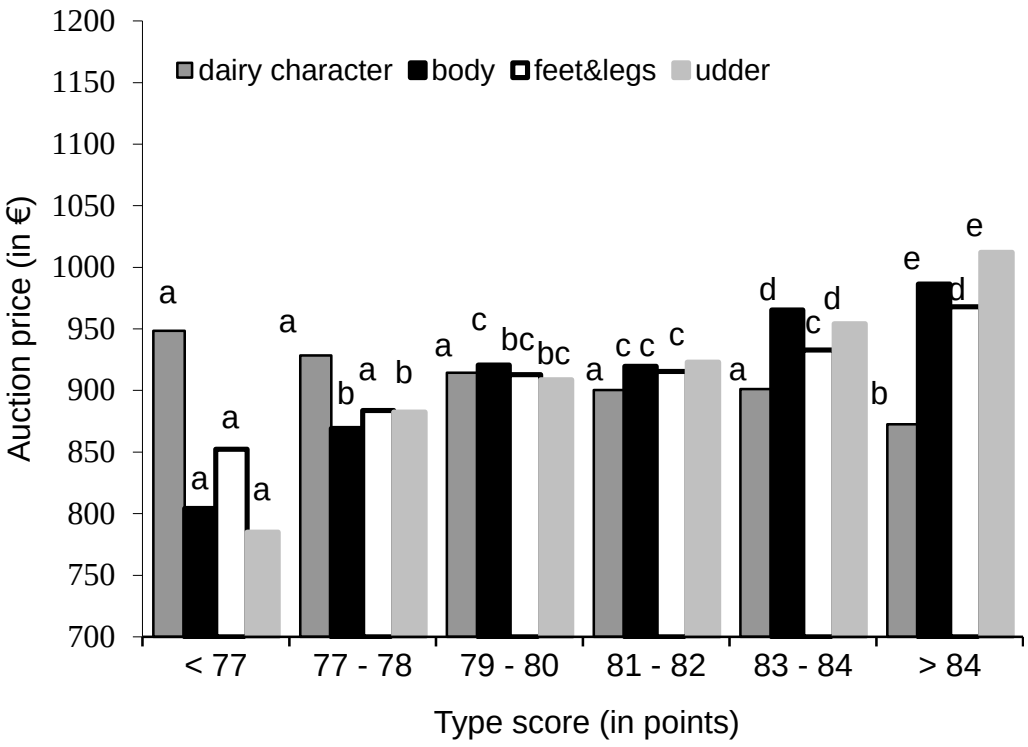

Figure 6. LSMeans for the trait "auction price" (in €) by classes of scores for the type composites dairy character, body, feet & legs, and udder. Different superscript within type composites indicate significant differences of LSMeans *(P<0.05)*.

Impact of linear type traits and economic weights

A main focus of this study was to determine the impact of linear type traits on auction price through the application of linear regression in model 2. Estimated regression coefficients for all linear scored type traits and BCS are provided in Tab. 2. Among all type traits, the largest regression coefficient was estimated for rear udder height (29.78 €/point), followed by body depth (14.76 €/point), and strength (14.60 €/point). In addition to body depth, all other traits related to the body composite, i.e. stature, strength, rump angle, rump width, and BCS, had positive regression coefficients, indicating that customers favoured higher weights and more capacity of sold cows. As reported for the dairy character composite, also linear scored dairy character had a negative impact (-9.49 €/point) on auction price. This poses the question whether scoring of dairy character should be continued. Dairy character is an indicator for milk production, but objectively measured test

day milk yield is a much more accurate trait. The additional genetic gain in an overall breeding goal seems to be limited or even counterproductive when including the dairy character component as a predictor for milk yield.

Table 2. Regression coefficients on auction price (standard errors in brackets), variance components, heritabilities[1], and economic weights for body condition score and 17 linear type traits.

Linear type trait	Regression coefficient (€ / score point)	σ^2_a	σ^2_e	h^2	Economic weight (€ / σ_a)
Body condition score	5.10 (2.40)	0.32	1.24	0.20	0.29
	Dairy character				
Dairy character	-9.49 (2.39)	0.54	1.30	0.29	-0.69
	Body				
Stature (in cm)	1.95 (1.04)	9.19	7.95	0.54	0.59
Body depth	14.76 (3.97)	0.17	0.92	0.16	0.61
Strength	14.64 (3.95)	0.30	0.90	0.25	0.80
Rump angle	1.93 (3.25)	0.33	0.73	0.31	0.11
Rump width	2.31 (3.28)	0.35	0.74	0.32	0.14
	Feet and Legs				
Rear leg side view	2.13 (2.96)	0.15	1.13	0.13	0.08
Foot angle	3.09 (2.09)	0.11	0.87	0.11	0.10
Hocks	9.18 (2.63)	0.42	1.50	0.22	0.59
Rear leg set rear view	9.61 (3.03)	0.17	1.46	0.10	0.40
	Udder				
Rear udder height	29.78 (3.61)	0.17	0.88	0.16	1.23
Suspensory ligament	1.04 (2.51)	0.30	1.89	0.14	0.06
Front teat placement	15.14 (3.63)	0.41	0.61	0.40	0.97
Rear teat placement	8.39 (4.01)	0.32	0.64	0.33	0.47
Fore udder attachment	5.81 (3.28)	0.45	1.35	0.25	0.39
Udder depth	-3.76 (2.97)	0.49	0.60	0.45	-0.26
Teat length	14.14 (3.69)	0.23	0.84	0.22	0.67

[1]Standard errors of heritabilities were in the range from 0.07 to 0.11

Regression coefficients revealed a positive impact for all linear traits belonging to the feet and leg composite in the range from 2.13 €/point (rear leg side view) to 9.61 €/point (rear leg set rear view) on auction price. Heterogeneous results were found for linear traits of the udder complex, i.e. a pronounced positive impact of rear udder height on auction price (29.78 €/point), but neutral or slightly negative regression coefficients for suspensory ligament (1.04 €/point), and udder depth (-3.76 €/point), respectively. Harris et al. (1992) and Short and Lawlor (1992) reported moderately negative genetic correlations between fore udder attachment and udder depth with the three milk production traits. These results suggest that selection for improvement of milk production, which was the main criterion when making purchase decisions about cows at auction, will lead to unfavourable correlated response for udder depth. Hence, purchase decisions were not inevitably related to sustainable breeding strategies. The magnitude of front (14.14 €/point) and rear teat placement (8.39 €/point), as well as teat length (14.89 €/point) could be expected, because these "workability" traits are important for the optimisation of the milking process (Rogers and Spencer, 1991), and they are positively correlated with udder health (Lund et al., 1994).

Regression coefficients from model 2 and additive genetic standard deviations (σ_a) from model 4 (Table 2) were used for an approximate calculation of economic weights for linear type traits. Economic weights expressed in €/σ_a enable a neutral comparison of the importance of individual type traits rather than simple regression coefficients. Additionally, economic weights presented in Table 2 were accounted for the probability of an auction sale or of an exported heifer per average Holstein cow. According to Fürst-Waltl et al. (2004), economic values estimated from a selected pool of auction cows have to be transformed to values representing the whole population or an average cow in the herd. Hence, a realization factor of 0.1 was assumed, i.e. it was considered that on average ten per cent of the heifers in the population were sold. This means a multiplication of economic weights obtained from regression analyses by factor 0.1.

The two most important traits were rear udder height (1.41 €/σ_a) and strength (0.80 €/σ_a). Fürst-Waltl et al. (2004) discussed the disadvantages of this

approach, especially the differences in purchase decisions of cows sold in first parity at auction compared to pregnant heifers sold via “conventional” export. Further restrictions have to be applied if a sectoral model is used to derive economic weights. Within a sector, e.g. within the same country, higher prices for cows sold at auction (increased income for some milk producers), have to be compensated by higher costs for customers (increased costs for some other milk producers). An advantage of increased income (higher prices at auction) for some sellers implies the disadvantage of higher costs for buyers. Economic weights derived in this present study show the importance of individual type traits among each other, but additional and more sophisticated steps have to be applied to construct distinct sub-indices for conformation traits in an overall breeding goal. These steps, such as sensitivity analyses, are part of an ongoing research project (Lind et al., 2007).

A strict derivation of economic weights for conformation only based on the influence on auction prices will probably lead to an underestimation of conformation in a combined breeding goal. It should be considered that conformation has additional effects on dairy cow profitability. For example the improvement of the udder composite by one standard deviation was associated with labour time reduction by 54 min per cow and lactation (Blake and McDaniel, 1979).

Genetic analyses

Heritabilities for 17 linear type traits and BCS as shown in Table 2 were in the wide range reported by Bethge et al. (2005) when analyzing type traits in 15 different regions within Germany. For example for foot angle, Bethge et al. (2005) estimated heritabilities in the range between 0.06 and 0.17. The largest heritability among all linear type traits when using auction data was found for stature. Stature was the only objective measurement (in cm), whereas the remaining traits were subjectively scored on the scale from 1 to 9. Hence, accurate measurements can reduce the residual component and increase repeatabilities and reliabilities as well. Heritabilities for type composites scored on a 100 point scale were 0.26 for dairy character, 0.11 for body, 0.11 for feet and legs, 0.10 for udder, and 0.11 for the final score

(Table 3). Heritabilities were relatively small, but, apart from the lower value for the body composite, similar to the results reported by Betghe et al. (2005). As shown in the previous sections of the present study, auction price is determined by a multitude of traits, e.g. milk production, health, and type traits. From the genetic perspective, these results raised the idea to consider the trait “auction price” as an overall breeding goal, and to estimate genetic relationships between currently used national official indices and auction price. Heritability for auction price was 0.27 (Table 3) and therefore larger than all type composites. We found moderate to high genetic correlations between auction price and feet and legs (0.55), and auction price and the udder composite (0.55). The genetic correlation between auction price and dairy character was close to zero. From the genetic point of view, there is no additional contribution of dairy character when defining the trait “auction price” as an ultimate breeding goal.

Table 3: Variance components and heritabilities (h^2) for auction price and type composites, and genetic correlations (r_g) between auction price and type composites

Trait	σ^2_a	σ^2_e	σ^2_p	h^2	r_g to price
Auction price	7,375	19,991	27,366	0.27±0.06	-
Dairy character	1.49	4.22	5.71	0.26±0.07	0.10±0.16
Body	0.69	5.79	6.48	0.11±0.05	0.21±0.14
Feet and legs	0.80	6.71	7.51	0.11±0.03	0.55±0.19
Udder	0.70	6.22	6.92	0.10±0.04	0.55±0.20
Overall conformation	0.35	2.89	3.24	0.11±0.03	0.38±0.19

Estimated breeding values for auction price of all animals were standardised to a mean of 100 points and a standard deviation of 12 points. The newly constructed relative breeding value for auction (RZA) was correlated with all official relative breeding values, i.e. the German total merit index (RZG), the production index (RZM), the conformation index (RZE), the somatic cell count index (RZS), the reproduction index (RZZ), and the functional herd life index (RZN). The relative weights of the sub-indices RZM, RZE, RZS, RZZ and RZN in the overall index RZG are 50%, 15%, 5%, 5%, and 25%, respectively. Details for the construction of all sub-indices are given by König et al. (2007). Table 4 shows the correlation coefficients between RZA and remaining relative breeding values for 27 bulls with at least 10 daughters sold at auction (reliability of RZA > 0.60), and for the sold cows itself. The correlations were moderate for RZG, RZM, and RZE in the range between 0.15 (RZM of bulls) and 0.33 (RZE of cows), but close to zero for RZN and even negative (-0.03) for RZZ of cows. However, when interpreting results, the limited sample size for bulls and the low reliabilities of EBVs for cows should be kept in mind. The low correlations between RZA and RZZ could be expected, because the customer has, apart from the announcement of reproduction deficiencies, no information available related to fertility of cows.

Table 4: Correlations between the relative breeding value for auction price (RZA) and German national official relative breeding values[1] for bulls and cows

Relative breeding value	Bulls (> 10 daughters sold at auction)	Cows sold at auction
total merit index (RZG)	0.19	0.29
production index (RZM)	0.15	0.21
conformation index (RZE)	0.21	0.33
somatic cell count index (RZS)	0.11	0.10
functional herd life index (RZN)	0.03	0.04
fertility index (RZZ)	0.05	-0.03

Based on the high number of more than 20,000 sold Holstein cows at auction per year, it seems to be a reasonable approach to store auction prices in a national electronic database, and to use this information as indicator traits for the improvement of accuracies of correlated national EBVs. For several dairy cattle breeders, auction sales substantially contribute to their monthly income. Profitability could be increased through the knowledge of RZA of individual sires.

Conclusion

As shown in this study, prices of cows sold at auction reveal several possibilities for analyses related to dairy cow profitability. First of all, the optimisation of management strategies for sales can contribute to additional income for dairy cattle farmers. The most important management effect to achieve higher prices was the choice of a market date early in lactation. A further opportunity, due to the reduced supply of cows on market during the summertime, could be to focus on auction sales in August or September. However, such a strategy implies inseminations in October or November, where heifers are usually kept outdoors. In addition to the identified management effects, there was a moderate genetic contribution to auction prices. Based on the moderate heritability of 0.27 for auction price, it is recommended to provide a relative breeding value for auction price (RZA), or to use auction price as an indicator trait for the improvement of the udder (r_g = 0.55) and the feet and leg composite (r_g = 0.55). The success in breeding programs in Nordic countries, e.g. reduced disease incidences and lower costs, was only possible due to the detailed and extended recording system (Heringstad et al, 2000). This implies the evaluation of all available information sources, also including auction prices, for the general improvement in dairy cow profitability.

It is also possible to derive economic weights for type traits based on their impact on auction prices. However, important type traits identified in the present study through multiple regression analyses (e.g. body depth), are negatively related to functional herd life. Further concerns when deriving economic weights include eventual double-counting of type traits, or

additional direct impact of type traits on dairy cow profitability such as reduced labour time.

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3rd Chapter

Identification of Informative Cooperator Herds for Progeny Testing Based on Yield Deviations

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Abstract

There are several arguments for breeding organizations to focus on cooperative herds for progeny testing, but there is a substantial lack of efficient methodology addressing herd selection strategies. In this study, a new approach based on yield deviations (YD) to identify most informative cooperator herds in terms of genetic differentiation was evaluated. Data comprised YD from 717,377 first lactation cows from two regions in East and West Germany calving between January 2003 and January 2008. Daughters were ranked and classified within sire according to their YD for protein yield, fat yield, milk yield and somatic cell score (SCS). Cows in created YD classes were merged with respective herd-calving year (HCY) characteristics. Cows of extreme YD classes, i.e. such classes including the most extreme daughter contributions, belonged to herds characterized by a high HCY production level, a low value for HCY somatic cell count, and a low HCY age at first calving. Cows with low extremes for YD in protein yield were associated with the lowest HCY production level, a high value for HCY somatic cell count, and a late HCY age at first calving. Ranks of HCY and ranks of herds considering HCY over the whole analyzed period were calculated by averaging YD percentages within HCY, and within herds, respectively. YD percentages (in absolute values so that negative and positive daughter contributions were treated equally) were derived from the rank of the YD of a daughter within sire in relation to all daughters of a sire. A further partitioning of ranks of herds into quartiles revealed the following results: herds in the first quartile had the highest average protein yield, the highest intra-herd standard deviation for the national production index, and the lowest age at first calving. Correlations between herd rankings for different production traits ranged between 0.64 and 0.86, and were 0.65 for West Germany and 0.62 for East Germany between HCY 2006 and the average herd rank of all calving years. Correlations between DYD for the highest and the lowest herd quartile of 0.87 for protein yield disproved concerns regarding genotype by environment interaction between test and production environment. The suggested methodology to identify informative cooperator herds is easy to implement, holds for regions with small herd

sizes, and thus, may help implementing sustainable and competitive dairy cattle breeding programs.

Introduction

Progeny testing (PT) in dairy cattle as suggested by Henderson (1964), and by Skjervold and Langholz (1964), was established in Germany in the late sixties. The original idea included a random mating system for young sires to generate a substantial pool of phenotypes for an unbiased estimation of breeding values (EBV). This random mating system implied a random sample of herds used for PT (or even all herds within the active breeding population), and a random sample of cows within herds for inseminations with young sires. Apart from long generation intervals, PT in this form generated relatively high selection intensities, and highly reliable EBVs for the male pathways of selection. The final improvement for those components was associated with a sustained selection response for traits under intensive selection pressure (König et al., 2007).

Further improvements to identify genetically superior sires could be put into effect by selecting special cooperator herds for PT. This idea was formulated by Hammond (1947), who suggested to keep and to select animals in superior environments, so that animals can fully express their true genetic potential. Other studies also discussed possible genotype by environment interactions when differentiating between test environment and production environment (e.g. König et al., 2008), which underlines the importance of a broad testing scheme in a multitude of herds. As found in several studies (e.g. Hill, 1984; Garrick and Van Vleck, 1987), differences in test environments have been associated with differences in estimated variance components. The impact of heterogeneous variances across regions or herds on results of genetic evaluation for production traits has been discussed intensively (Van Vleck, 1963; Vinson, 1987; Boldman and Freeman, 1990). Former publications (e.g. Van Vleck,1963), as well as more recent studies (e.g. Gernand et al., 2007) found higher additive genetic variances with an increasing production level in herds, and they gave recommendations for optimization of PT schemes. Simulation studies by Hill (1984) and Garrick and Van Vleck (1987) showed an increase of EBVs with

increasing intra-herd variances. The optimization of management and feeding strategies (Padilla and Keown, 1990), the milking technology and herd size (Weigel et al., 1993) as well as the skills of herdsmen (Short et al., 1990) were identified as possible reasons for increased intra-herd variances. Since the unification of the two formerly separated German countries in 1990, the German dairy cattle population is characterized by a dichotomy in housing and management conditions: In West Germany, family farms with herd sizes of around 30 to 100 cows are prevalent, whereas in East Germany large-scale dairy farms with herd sizes of 200 to 2000 cows are common. Also for Germany, heterogeneity in variance components for production traits was found (König et al., 2005a): the larger the farm, the larger the additive genetic variance. A reason for this could be that relationships between genotype and management (e.g. as arising from feeding according to the genetic potential) are higher in large farms.

Due to the increase of competition on the global semen market for dairy sires (Dekkers et al., 1996), some of the 14 different German breeding organizations refresh those ideas towards more selective PT in terms of test environments to achieve more accurate EBVs. Additionally, higher accuracy to identify genetically superior sires among the total pool of test candidates will increase genetic gain as well as production level in the whole population. However, there is a lack of effective methods to identify those informative cooperator herds allowing the highest genetic differentiation. Some studies have focused on relatively simple aspects, e.g. the number of usable records (Meinert et al., 1997), or herd size and herd production level (Vierhout et al., 1999). Gernand et al. (2007) suggested cluster analyses to combine favourable effects of large herd size, high production level, and low age at first calving (AFC). Other studies (e.g. Brügemann, 2008; Dechow et al., 2008a) focussed on genetic analyses and variance component estimation within herds. Brügemann (2008) found increasing additive genetic variances and heritabilities with increasing herd size and improving farm management. In the study by Dechow et al. (2008a), intra-herd heritability was also negatively correlated with sire misidentification rates. Due to relatively large standard errors of estimates from intra-herd analyses, this approach is not applicable for small family farms as prevalent in West Germany.

As an alternative, we evaluated a strategy for selection of cooperator herds based on yield deviations (YD). The derivation and calculation of daughter yield deviations (DYD) and YD was reported by VanRaden and Wiggans (1991) for animal models, and by Mrode and Swanson (2004) for random regression models. DYD have been described as the most independent and most accurate measure of phenotypic performance of a bull, conceptually equivalent to average daughter records (VanRaden and Wiggans, 1991; Liu et al., 2004; Mrode and Swanson, 2004). Utilization of DYD for dairy cattle genetic evaluation and breeding objectives is quite common: DYD are used as controlling instruments at Interbull for validating trends in national genetic evaluations (Boichard et al., 1995), for the identification of preferential treatment (Powell et al., 1994), or for the identification of quantitative trait loci and derivation of SNP effects (Szyda et al., 2005; Neuner et al., 2008).
The specific goal of the present study was to investigate the association between YD and defined herd characteristics. Based on these findings, an approach using YD to select cooperator herds for PT is suggested.

Material and methods

Data

The data consisted of 3,652,113 test day records from 445,819 first lactation cows in 26,651 herd-calving years (HCY) located in the German state Lower Saxony (Northern part of West Germany), and of 2,244,185 test day records from 271,558 first lactation cows in 3,483 HCY located in Saxony (East Germany). Data from West Germany generally represent the typical family farm in this region with an average herd size of 16.7 cows in first lactation. Average herd size for large-scale dairy farms in East Germany comprised on average 68 cows in parity one. Cows calved between January 2003 and January 2008, and test day records for all cows were available for this period. Furthermore, yield deviations for milk yield, fat yield, protein yield, and somatic cell count for these cows were available. Yield deviations were calculated as lactation yield deviations, i.e. based on the cow's performance adjusted for fixed and non-genetic random effects, and for genetic effects of the dam. Details for the calculation of YD and criteria for publication of YD are explained in Liu et al. (2004).

Records from cows that had their first herd test day later than 60 days after calving (presumably due to herd changes) and records from cows without a second calving were excluded from the analyses. An additional requirement for keeping a cow record was a registered sire with more than 50 daughters, resulting in cows from 833 different sires. This strategy also excluded natural service sires. The final data set consisted of 265,667 cows in 22,668 HCY from West Germany, and of 173,567 cows in 3,410 HCY from East Germany. Means and standard deviations averaged over the first five test records for milk yield, fat content, protein content, somatic cell count, calving interval (CI), and age at first calving for both regions are shown in Table 1.

Table 1. Means and standard deviations (SD) averaged over the first five test day records for milk yield, fat content, protein content, somatic cell count, calving interval and age of first calving for the regions West Germany and East Germany within calving years.

			calving year parameters											
Region	Calving year	No. of cows	milk (kg)		fat (in %)		protein (%)		SCC (x1000)		Calving interval		Age at first calving	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
West Germany	2003	64,293	26.57	4.68	4.05	0.49	3.31	0.22	167.26	277.25	417.28	81.64	29.64	3.74
	2004	61,918	26.88	4.71	4.02	0.48	3.30	0.21	165.35	269.83	421.87	86,60	29.53	3.85
	2005	55,079	27.57	4.85	3.99	0.50	3.30	0.21	167.83	279.96	424.30	88.79	29.19	3.81
	2006	59,358	27.82	4.78	3.99	0.49	3.27	0.20	172.84	292.55	422.96	86.07	28.91	3.70
	2007	25,019	28.05	4.79	3.96	0.49	3.26	0.20	176.43	298.74	417.89	70.08	28.49	3.31
East Germany	2003	39,693	27.82	5.21	4.00	0.51	3.35	0.22	179.44	308.71	417.27	81.29	26.96	2.75
	2004	40,178	28.26	5.23	4.00	0.50	3.32	0.22	176.99	301.71	421.92	87.71	26.75	2.81
	2005	39,478	28.94	5.29	3.93	0.51	3.30	0.22	177.58	301.38	423.17	88.39	26.55	2.78
	2006	37,786	29.40	5.36	3.92	0.50	3.28	0.21	193.51	342.31	424.17	88.41	26.32	2.72
	2007	16,43	29.75	5.24	3.92	0.49	3.25	0.21	205.04	358.23	418.23	71.37	26.28	2.61

Method

Ranking of daughters within sire and allocating daughters to HCY

An initial, general analysis was conducted to verify possible associations between YD and respective HCY parameters. For this purpose, cows were classified in seven different YD classes (Table 2). All cows were ranked within sire by the magnitude of their YD. Subsequently, the cows were assigned to different YD classes, e.g. the 10% cows with the highest YD within their sire were assigned to class “highest 10”, and the 20% with the highest YD within sire (from 0 to 20%) were assigned to class “highest 20”. Cow records in defined YD classes were merged with phenotypic observations of their remaining HCY contemporaries to calculate HCY parameters. These were:

1. average HCY protein yield (average of first five test day records)
2. average HCY somatic cell score (average of first five test day records)
3. average HCY calving interval
4. average HCY age of first calving

A study focusing on the first five test day records is in line with criteria for early selection strategies of young sires. Furthermore, genetic differentiation is less pronounced at the end of the lactation due to a decrease in additive genetic variances (Gernand et al., 2007). Analyses were conducted separately for YD classification based on the following traits: 1. YD for milk yield, 2. fat yield, 3. protein yield, and 4. SCS.

Table 2. Yield deviation (YD) classes used to analyze possible associations between YD and respective herd-calving year parameters

YD class	Range	Percentile
lowest 10%	10% of daughters with lowest YD within sire	0 to 9
lowest 20%	20% of daughters with lowest YD within sire	0 to 19
lowest 30%	30% of daughters with lowest YD within sire	0 to 29
average 40%	40% of daughters with low extremes for YD within sire, i.e. those cows between the lowest 30% and the highest 30%	30 to 69
highest 30%	30% of daughters with highest YD within sire	70 to 99
highest 20%	20% of daughters with highest YD within sire	80 to 99
highest 10%	10% of daughters with highest YD within sire	90 to 99

Selection of most informative cooperator herds

For optimization of genetic differentiation, those herds are most informative which include a high fraction of cows with extreme genetic contributions (high or low), e.g. such cows classified in YD-classes “highest 10%” and “lowest 10%”. In terms of the phenotypic expression of the genetic potential, average YD or YD with low extremes as prevalent in YD-class “average 40” within sire are unfavorable. Our approach thus focused on the identification of herds providing extreme YD within sire, treating negative and positive YD equally. Identification of cooperator herds based on this strategy does not focus on the success of a breeding organization with respect to the number of bulls in the national top list rather than a more accurate genetic differentiation.

For treating positive and negative daughter contributions equally, all cows within sire were ranked in percentages by extremeness of their YD, in negative as well as in positive direction. Hence, most extreme YDs in both directions imply high values for daughter rank percentages. In the next step, herd-calving year ranks (HCYrank) were created by utilizing the defined “within-sire percentages” and applying the following formula:

$$HCYrank_{jl} = \frac{\sum | \ perc_{ijkl} \ |}{n_{jl}}$$

where $HCYrank_{jl}$ is the rank of herd j in calving year l; $|perc_{ijkl}|$ is the absolute value of the percentage score of cows i from herd j within sire k in year l; and n_{jl} is the number of cows in herd j in calving year l. Furthermore, the rank of a herd, that considered all available HCY within the entire analyzed period, was calculated as follows:

$$Rank\ of\ herd_{j} = \frac{\sum | \ perc_{ijk} \ |}{n_{j}}$$

where $|perc_{ijk}|$ is the absolute value of the percentage score of cow i from herd j within sire k; and n_j is the number of cows in herd j.

An example for calculating the HCYrank for one specific small HCY with three cows from two different sires in first lactation is given in Fig. 1. As explained, at first cows were ranked by extremeness of their YD within sire. A percentage score of -42.1% was assigned to cow A which implies that this cow represents the 42.1% percentage of all cows below the DYD of the respective sire A. Cow B represents the 80.7% percentage of all cows above

the DYD of sire A. Cow C has a percentage score of 21.2% indicating that within all daughters of sire B that have a YD above the sires DYD cow C represents the 21.2% most positive YD. Subsequently, absolute values of the percentage scores of all cows belonging to the HCY in this example are averaged to calculate the HCYrank of 48%:

$$\text{HCYrank} = \frac{|-42.1\%| + 80.7\% + 21.2\%}{3} = 48\%$$

The procedure as explained in Fig. 1 was subsequently used to calculate the rank of a herd using cows from all HCY.

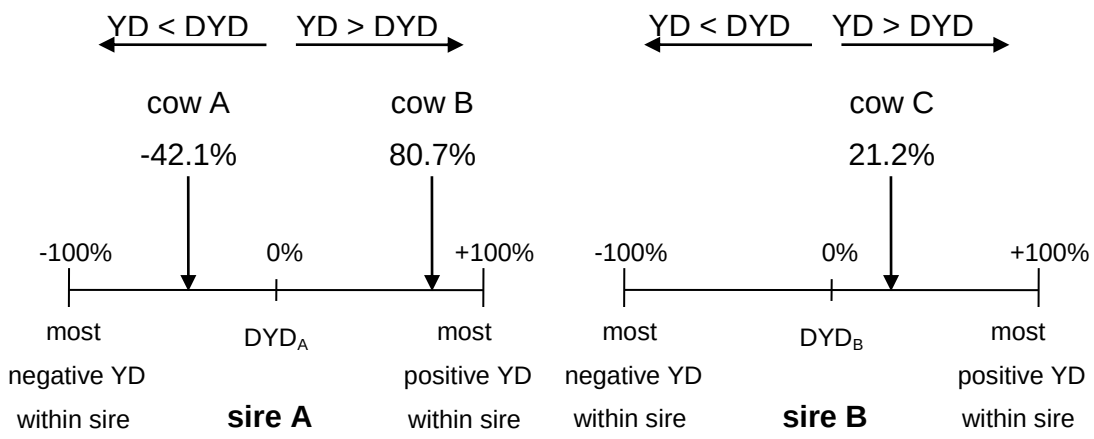

Figure 1. Example for ranking one specific herd-calving year (HCY) including three cows in first parity from two different sires: Cows were ranked by extremeness of their YD within sire. Subsequently absolute values of the percentages within sire were averaged for each HCY to create HCY ranks.

In the last step, herds were classified into quartiles according to their rank of herd. The lower the herd quartile, the more extreme YD were allocated. Low quartile herds were suggested as a cooperator herd for PT with respect to genetic differentiation. For each herd quartile, means for the following herd characteristics were calculated:

- herd size defined as the average number of first lactation cows per HCY
- protein yield (average of first five test day records)
- intra herd standard deviation for the German production index (RZM)
- age at first calving

Analyses were restricted to herds with at least 10 first lactation cows in calving year 2006, and were conducted separately using YD for milk yield, fat yield, protein yield and somatic cell score. Spearman rank correlations were calculated between herd rankings for different traits, and between HCYranks within the same trait.

Analysis of genotype by environment interactions

Possible genotype by environment interactions (GxE) for protein yield and somatic cell count between high and low ranking herds were analyzed by correlating DYD of sires between the highest and lowest herd quartile. Data comprised 54,346 cows in the 1st herd quartile and 39,951 cows in the 4th herd quartile for West Germany, as well as 40,193 cows in the 1st herd quartile and 22,276 cows in the 4th herd quartile for East Germany. DYD for a sire was the average of YD of his daughters in the respective herd quartile. Subsequently, Spearman rank correlations were calculated between sire's DYD in different herd quartiles and different regions. The first analysis considered all sires, and was restricted in a second analysis to sires with at least 50 daughters in both environments. In absence of GxE, ranking of sires is expected to be similar in both environments.

Results and Discussion

Associations between YD and herd parameters

Means for HCY test day protein yield, HCY somatic cell count, HCY calving interval, and HCY age of first calving stratified by region and YD classes for protein yield and somatic cell count are shown in Figures 2 to 5.

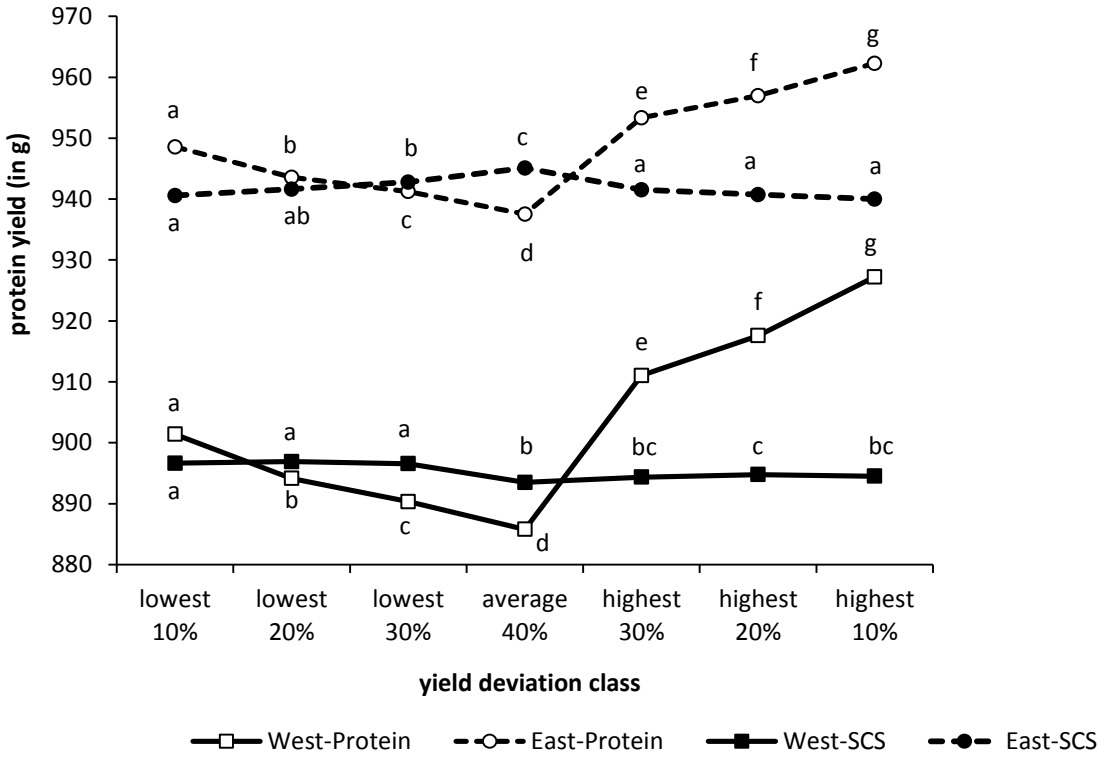

Figure 2. Mean herd-calving year parameters for test day protein yield stratified by region for different yield deviation classes ranked by YD for protein yield and by YD for somatic cell score (SCS). Different superscripts indicate significant differences at P<0.05 within each region and trait combination.

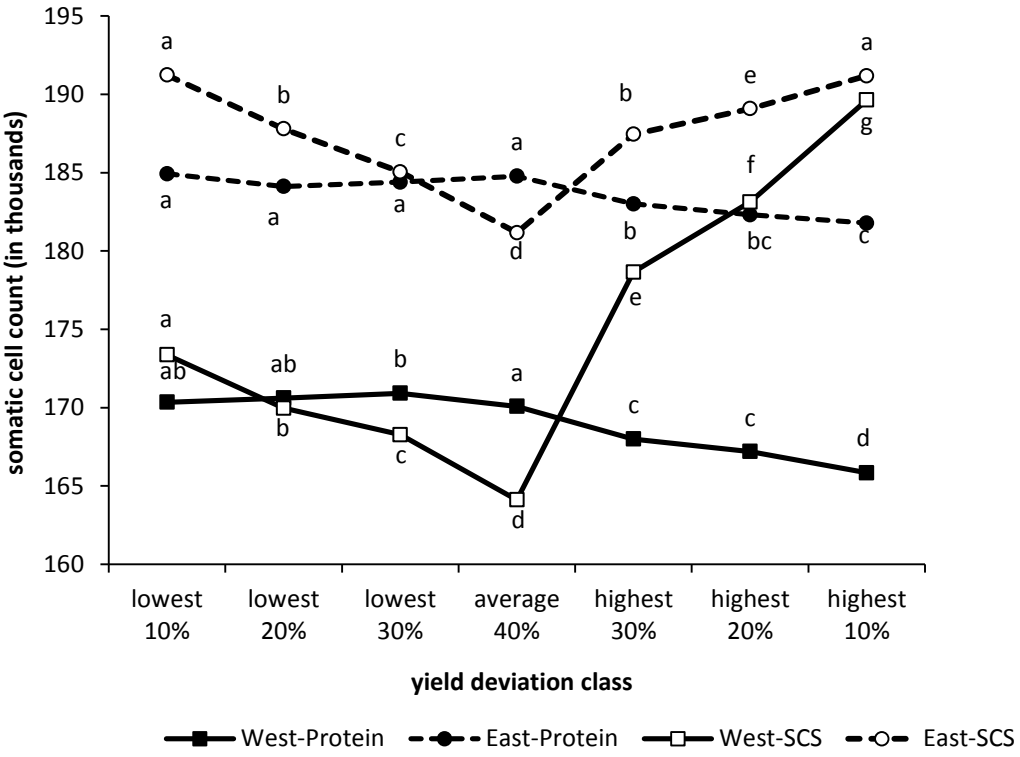

Figure 3. Mean herd-calving year parameters for somatic cell count stratified by region for different yield deviation classes ranked by YD for protein yield and by YD for somatic cell score (SCS). Different superscripts indicate significant differences at P<0.05 within each region and trait combination.

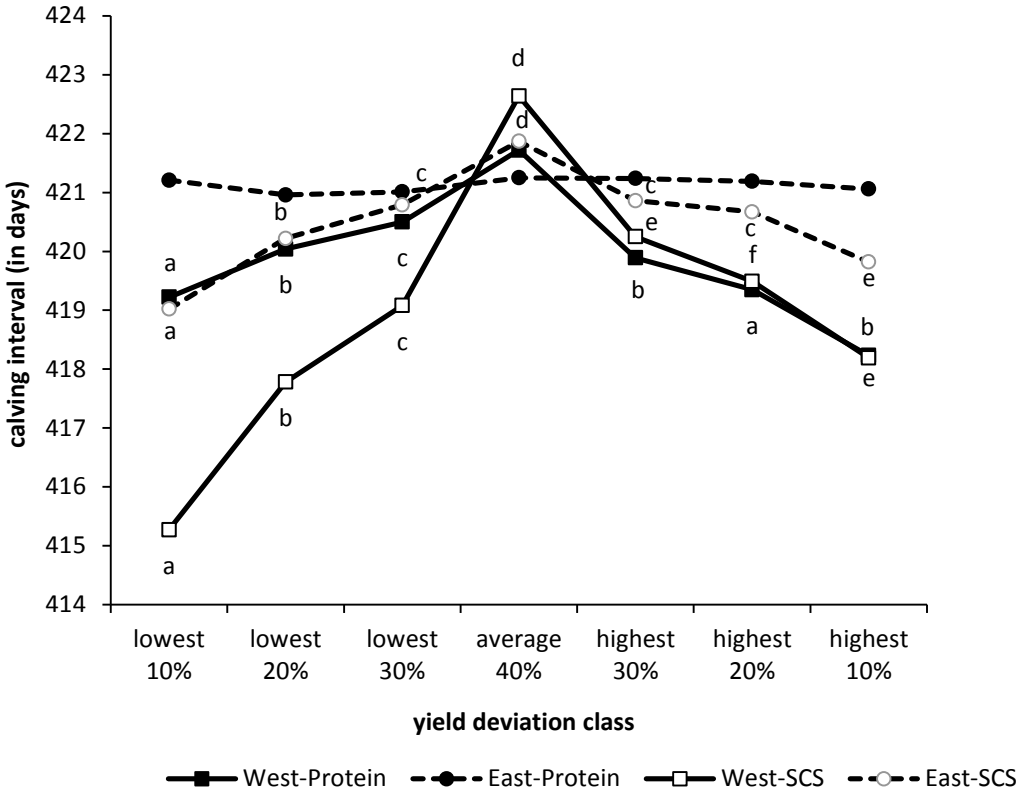

Figure 4. Mean herd-calving year parameters for calving interval stratified by region for different yield deviation classes ranked by YD for protein yield and by YD for somatic cell score (SCS). Different superscripts indicate significant differences at P<0.05 within each region and trait combination. No significant differences (P<0.05) were found within East-Protein.

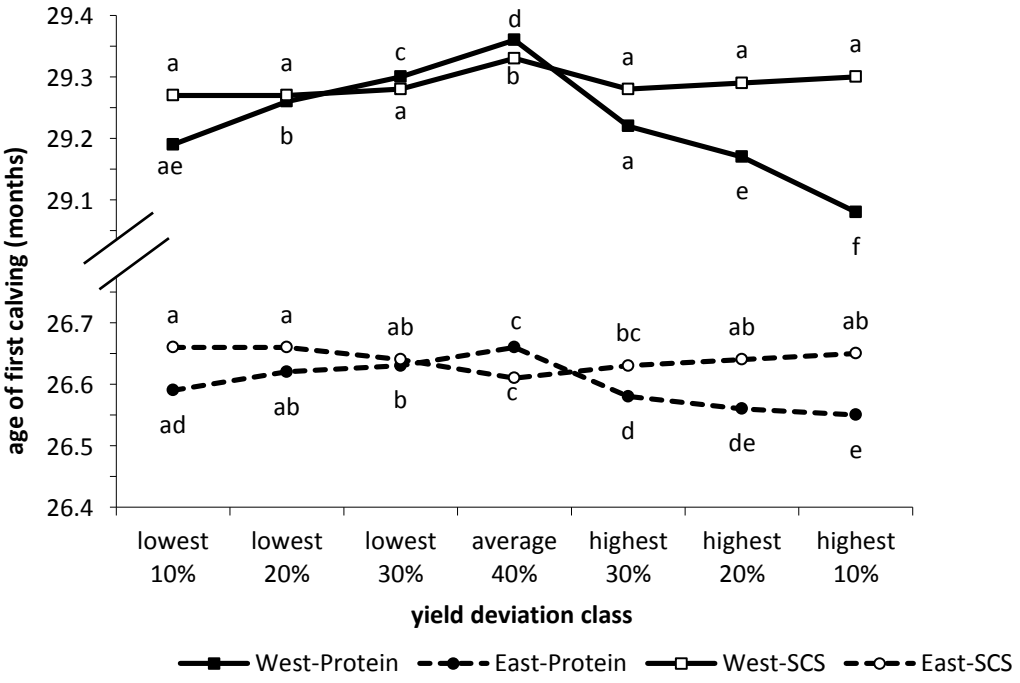

Figure 5. Mean herd-calving year parameters for age of first calving stratified by region for different yield deviation classes ranked by YD for protein yield and by YD for somatic cell score (SCS). Different superscripts indicate significant differences at P<0.05 within each region and trait combination.

When ranking daughters according to YD for protein yield within sire, high YD were generally associated with a higher HCY production level for protein yield. This finding is also in line with the biological nature of traits, i.e. a positive association between the mean of the trait and the variance: a topic that has been investigated in dairy cattle from the perspective of heterogeneous intra-herd variances and selection proportions (e.g. Dong and Mao, 1988; Boldman and Freeman, 1990). High YD for protein yield were also found for a lower somatic cell count, and a lower AFC within herds. We also observed a decrease in the HCY calving interval in West Germany with a more stringent allocation of YD, whereas no significant differences were found in East Germany. Cows with negative daughter contributions (i.e. YD classes “lowest 30 %”, “lowest 20 %”, and “lowest 10%”) were allocated to HCY characterized by a higher production level, a lower AFC, and a shorter calving interval compared to the YD group representing less extremes in YD

(average 40%). Daughters characterized by average genetic contributions were generally kept in herds having a low production level for protein yield, and a late AFC. A low production level in combination with a high AFC, a long calving interval, and a high somatic cell count indicates a suboptimal management in those herds (Gernand et al., 2007). Similar trends were found when ranking daughters within sire according to YD for fat yield or YD for milk yield (results not shown). Hence, these results are in line with results from previous studies using an approach based on variance components (e.g. Dodenhoff and Swalve, 1998; König et al., 2005a; Gerber et al., 2008); i.e., the better the testing environment, the better the phenotypic expression of the genetic potential.

When ranking daughters according to YD for somatic cell score within sire, results from association analyses were completely different. Herd-calving year production level for test day protein yield, test day somatic cell count, and HCY age of first calving were relatively equal for all created YD classes. Only HCY somatic cell count was substantially higher for the lowest and the highest YD classes. Results for YD-SCS grouping showed the same patterns for East and for West Germany. Apparently, the genetic potential for somatic cell count being an indicator of mastitis resistance is better expressed in an environment where the cows' immune system is under challenge. This is a desired effect in terms of a more accurate genetic differentiation for somatic cell count and closely related susceptibility to mastitis (Philipsson et al., 1995), but difficult to combine with a maximization in genetic differentiation for production traits.

Selection of cooperator herds

Table 3 depicts average herd characteristics for the number of cows in first parity, test day protein yield, intra-herd SD for the production index RZM, and AFC stratified by region and herd quartiles based on the rank of the herd for YD in protein yield. In West Germany, herd size was relatively equal for the first three herd quartiles, but herds allocated to the fourth quartile were substantially smaller. Test day protein yield and intra-herd-SD of RZM decreased from the first to the fourth quartile. Cows in the first quartile produced at average 100g protein per day higher than cows in the fourth

quartile. The difference in intra-herd SD for RZM was 2.05 points when comparing these two quartiles. The second quartile was characterized by the lowest AFC, while the fourth quartile showed the highest AFC. Herd sizes, protein yield and intra-herd SD in RZM were higher, and AFC was lower for herd quartiles in East Germany when comparing to the respective quartiles in West Germany. Interestingly, herds in East Germany allocated to the first quartile were smaller than the herds in the second and third quartile, but substantially larger than herds in the fourth quartile. Apart from that, trends for average protein yield and intra-herd SD were similar to those in West Germany. Herds in the first quartile had the highest average protein yield, the highest SD in RZM, and the second lowest AFC. These results support former arguments that potential cooperator herds for PT should have a high production level combined with a high intra-herd variance and a low AFC (Gernand et al., 2007). An early AFC combines several desired effects for improvements in breeding programs, i.e. a distinct genetic differentiation, and additionally a decrease in generation intervals on the cow sire path of selection.

Table 3. Mean herd characteristics and standard deviations (SD) for number of cows in first parity, test day protein yield, intra-herd standard deviation (Intra-herd-SD) in the German production index RZM, and age of first calving stratified by region for different herd quartiles[1] according to YD selection for protein yield. Different superscripts within regions indicate significant differences at P<0.05.

		Herd characteristics								
Region	Quartile[1]	No. of herds	No. of cows in first parity		protein (in g)		Intra-herd-SD for RZM		Age at first calving	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD
West Germany	1st	610	24.68[a]	11.07	943.86[a]	73.98	11.60[a]	1.18	29.10[ab]	2.12
	2nd	610	25.31[a]	12.32	920.73[b]	74.52	10.99[b]	1.10	28.96[a]	2.14
	3rd	610	24.40[a]	13.04	904.27[c]	77.28	10.58[c]	1.23	29.32[b]	2.27
	4th	611	18.32[b]	7.73	844.71[d]	97.54	9.55[d]	1.40	29.82[b]	2.50
East Germany	1st	126	82.62[a]	73.92	981.24[a]	78.00	12.41[a]	1.09	26.67[a]	1.41
	2nd	127	109.61[b]	100.99	950.99[b]	66.48	11.95[b]	0.85	26.53[a]	1.66
	3rd	127	100.20[ab]	102.29	912.13[c]	63.69	11.67[c]	0.89	26.72[a]	1.45
	4th	127	49.41[c]	61.25	848.36[d]	94.62	10.30[d]	1.07	27.97[b]	1.95

[1]Quartiles based on the rank of the herd for genetic differentiation. The higher the quartile, the lower the genetic differentiation in herds based on yield deviations.

Progeny testing in extremely large herds may have some logistic advantages (e.g. an easier coordination of PT especially in terms of conformation classification, or DNA sampling for genotyping in the near future), but a restriction only on herd size does not necessarily maximize genetic differentiation. Of course, a minimum for herd size should be a criterion to ensure a sufficient number of cows in contemporary groups with respect to a reliable genetic evaluation.

Rank correlations between different herd rankings

Herd ranking based on YD for milk yield instead of YD for protein yield revealed almost identical results. The Spearman rank correlations between both alternatives were 0.84 and 0.86 for West and East Germany, respectively (Figure 6). Correlations between herd ranks for protein yield and those for fat yield were 0.64 for West Germany, and 0.69 for East Germany. However, correlations between herd ranks for protein yield and herd ranks for SCS were only 0.09 for West Germany, and slightly negative (-0.05) for East Germany.

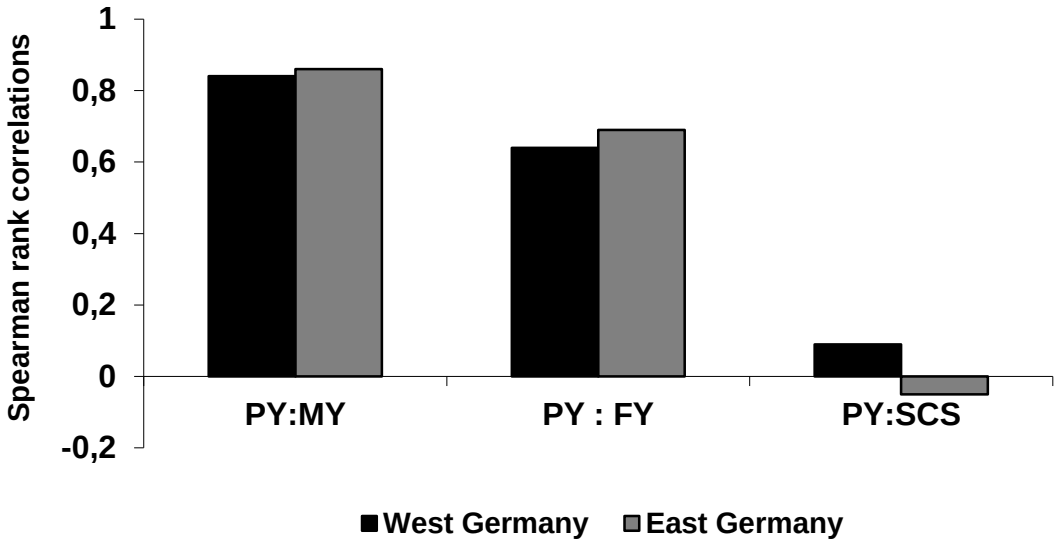

Figure 6. Spearman rank correlations between herd rank for protein yield (PY) and herd ranks for milk yield (MY), fat yield (FY) and somatic cell score (SCS) for two different regions in Germany

Additionally, Spearman rank correlations between the herd rank for YD in protein yield in calving year 2006 and the average herd rank from all calving years (2003-2007) were calculated. Year 2006 was the most recent calving year including a substantial data pool, while data from calving year 2007 was substantially reduced due to the criteria for publishing YD (Liu et al., 2004). Correlations were 0.65 for West Germany and 0.62 for East Germany. Those estimates of correlations suggest that an informative herd for a specific calving year will also be an informative herd in other calving years. Correlations between single years were in the range of 0.19 and 0.45 with correlations between consecutive years being higher than those between

non-consecutive years. Possible reasons for differences in herd rankings in different year are changes in farm management, disease issues, heat stress, or poor quality of roughage in some specific years so that animals cannot express their full genetic potential. However, from the practical and logistic point of view, we do not recommend an update in selection of cooperator herds in short intervals, or a herd selection based only on the information of one specific HCY.

Analysis of genotype by environment interactions

Daughters of young bulls are supposed to be randomly distributed within the test region of an AI station. Hence, daughters are randomly distributed across herd sizes and production levels. Consequently, EBVs of bulls should be unaffected by herd characteristics (Vinson, 1987). A shift towards selective PT in those herds with higher intra-herd variances and a superior herd management, the question of GXE will arise. Genotype by environment interaction occurs when different genotypes are not equally affected by different environments (Falconer, 1952), and can result in differences in the ranking of genotypes. Thus, rank correlations between average DYD for protein yield and SCS in upper and lower herd quartile for West and East Germany were calculated. Correlations coefficients are shown in Table 4. For protein yield, rank correlations ranged between 0.82 and 0.87 within and across different regions. Rank correlations for SCS between different quartiles ranged between 0.67 and 0.83. Rank correlations including only those sires with more than 50 daughters between herd quartiles within the same region and also across different regions were in a range between 0.92 and 0.98 for both traits. Hence, according to the criteria suggested by Robertson (1959), correlations did not reveal any relevant GxE interaction between different herd conditions or regions. Results were also in line with those from Gerber et al. (2008), who found rank correlations in the range of 0.90 when comparing DYD of bulls in high input and low input production systems.

Several studies have focused on GxE (e.g. Van Vleck, 1963; Carabano et al., 1990; Hayes et al., 2003). König et al. (2005a) estimated genetic correlations for production traits between small herds from West Germany and herds from

East Germany to be 0.90 and higher. Only when small family farms in West Germany were compared to large scale dairy farms in East Germany with more than 150 cows in first lactation, correlations dropped to 0.79.

Economic pressure also will force dairy farmers in West Germany to increase herd size. Based on the genetic correlations above 0.95 estimated in this study, and considering the expected future herd structures in Germany, GxE should not be a problem. Currently selected cooperator herds for PT will be representative of the typical structure of German dairy cattle herds being competitive in the future.

Table 4. Spearman Rank correlations between average daughter yield deviations in the 1st and 4th herd quartile[1] for potential cooperator herds in two different German regions

		All sires		Sires with at least 50 daughters	
Compared herd quartiles	Trait	Rank correlation	Sires (n)	Rank correlation	Sires (n)
1st quart. West/ 4th quartile West	Protein (kg)	0.87	785	0.98	84
	SCS	0.83		0.96	
1st quartile East/ 4th quartile East	Protein (kg)	0.82	791	0.97	60
	SCS	0.67		0.95	
1st quartile West/ 1st quartile East	Protein (kg)	0.87	141	0.97	36
	SCS	0.81		0.93	
1st quartile West/ 4th quartile East	Protein (kg)	0.82	137	0.92	24
	SCS	0.67		0.92	
4th quartile West/ 1st quartile East	Protein (kg)	0.86	142	0.97	38
	SCS	0.81		0.95	
4th quartile West/ 4th quartile East	Protein (kg)	0.82	138	0.94	26
	SCS	0.71		0.92	

[1]Quartiles based on the rank of the herd for genetic differentiation. The higher the quartile, the lower the genetic differentiation in herds based on yield deviations

Practical considerations when implementing cooperator herds

Using YD to identify informative cooperator herds for an accurate genetic differentiation among young bulls in PT schemes has three major advantages compared to selection strategies based on the intra-herd estimation of variance components (Brügemann, 2008; Dechow et al., 2008a). Firstly, computing time for the suggested method is substantially lower. Secondly, YD are generally available when computing EBVs in the process of national genetic evaluation. Hence, our algorithm could be incorporated as an additional feature in this routine process. Thirdly, the YD-based approach is applicable also to small herds as prevalent in West Germany. In contrast, an intra-herd variance component estimation approach leads to inflated standard errors of estimates with decreasing herd size. The proposed method is also characterized by a high flexibility to data restrictions, e.g. focusing only on herds using a high quantity of young sires, or for created subsets within distinct regions.

Gernand et al. (2007) suggested a two-step cluster approach to combine herd characteristics such as herd size, protein yield, and AFC for a selection of cooperator herds. This may be an applicable method, but it does not focus in detail on the aspect of optimizing genetic differentiation. Dechow and Norman (2007) used regression techniques to estimate herd-heritabilities more rapidly. Those estimates were moderately correlated with heritabilities estimated with an animal model. The regression technique can be seen as an alternative to stratify individual herds by heritability or additive genetic variance (Dechow et al., 2008b).

An adjustment procedure for heterogeneous variances (Reents et al., 1998) has been implemented in the estimation procedure of German EBV, which might have a slight impact on associations found between genetic contributions and herd characteristics. However, as the adjustment method depends on herd size, it will have a marginal impact only on the results for small herds as prevalent in West Germany.

Cooperator herds will be of major importance in the near future. Especially in the period of genome-wide selection (Meuwissen et al., 2001), program designs of existing breeding programs will be modified intensively. Schaeffer

(2006) suggested using daughter records from cooperator herds as a substantial base to estimate SNP effects. Such a strategy especially is recommended for low heritability traits to ensure sufficient reliabilities of genomic breeding values (VanRaden et al., 2009). Several functional low heritability traits have been incorporated in international breeding goals (Mark, 2004; Miglior et al., 2005). Additional traits such as claw health (König and Swalve, 2006), pathogen-specific mastitis resistance (De Haas et al., 2002; Sørensen et al., 2009), or other metabolic and reproductive diseases (Zwald et al., 2004) might become important in the future. For achieving high reliabilities of EBVs in those low heritability traits, larger numbers of daughters and larger contemporary groups are required, as compared to production traits (Lindhé and Philipsson, 1998; Willam et al., 2002). To date, recording systems for these major health problems are not implemented in Germany. In contrast, in Scandinavia veterinary treatments are monitored on health cards by veterinarians (Philipsson and Lindhé, 2003). When starting such an attempt, it would be easier to concentrate on a certain amount of cooperator herds. Testing bulls in special cooperator herds and contracting farmers also will secure sufficient test capacities and reduce costs for logistics, e.g. for type trait classification (Swalve and König, 2007).

There is one, however minor, disadvantage of our strategy in the current situation: Selected contract herds based on yield traits are not necessarily the best herds for the genetic differentiation for SCS. We recommend a strategy that allows an accurate genetic differentiation for production traits, and using those informative and well managed herds to generate an extensive high quality data pool for functional health traits. When selecting cooperator herds with a high health status (e.g. low somatic cell count), the disadvantage of reduced YD differentiation for SCC may be compensated for by recording mastitis. Genetic gain for animal health generally will increase when using direct health information compared to selection strategies focusing on indicator traits recorded in the entire population (Philipsson, 1995; De Haas et al., 2002; König et al., 2005b). Another strategy to ensure an adequate within-herd variation in health traits would be to maintain a certain amount of herds in progeny testing that are characterized by only

average herd ranks combined with more challenging environments like a higher average SCC.

Conclusions

The strategy to identify herds with maximized genetic differentiation based on YD is a practical method for selecting cooperator herds in dairy cattle breeding programs. In contrast to other herd selection procedures such as the estimation of intra-herd heritabilities, the YD approach is relatively easy to implement, requires less computing time, and is practicable even in the case of small herd sizes. However, the applied theoretical selection strategy for finding cooperator herds implies that farmers are willing to participate in such a system. Financial compensation for participating farmers is necessary, especially when focusing on the accurate recording of additional and new health traits in cooperator herds. Ultimately, the presented approach can be seen as a substantial contribution to the design of competitive and sustainable dairy cattle breeding programs.

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4th Chapter

Controlling Inbreeding and Maximizing Genetic Gain using Semi-definite Programming with Pedigree Based and Genomic Relationships

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Abstract

Due to relatively high levels of genetic relationships among potential bull sires and bull dams, innovative selection tools should consider both genetic gain and genetic relationships in a long term perspective. Optimum genetic contribution (OGC) theory using official estimated breeding values for a moderately heritable trait (INDEX-PROD = production index), and a lowly heritable functional trait (INDEX-SCS= index for somatic cell score) was applied to find optimal allocations of bull dams and bull sires. In contrast to previous practical applications using optimizations based on Lagrange multipliers, we focussed on semi-definite programming (SDP). SDP methodology was either combined with pedigree (a_{ij}) or genomic relationships (f_{ij}) among selection candidates. Selection candidates were 484 genotyped bulls, and 499 pre-selected genotyped bull dams completing a central test on station. In different scenarios separately for PROD and SCS, constraints on the average pedigree relationships among future progeny were varied from a_{ij} = 0.08 to a_{ij} = 0.20 in increments of 0.01. Corresponding constraints for SNP based kinship coefficients were derived from regression analysis. Applying the coefficient of 0.52 with an intercept of 0.14 estimated for the regression pedigree relationship on genomic relationship, the corresponding range to alter genomic relationships varied from from f_{ij} = 0.18 to f_{ij} = 0.24. Despite differences for some bulls in genomic and pedigree relationships, the same trends were observed for constraints on pedigree and corresponding genomic relationships regarding results in genetic gain and achieved coefficients of relationships. Generally, allowing higher values for relationships resulted in an increase of genetic gain for INDEX-PROD and INDEX-SCS, and in a reduction in the number of selected sires. Interestingly, more sires were selected for all scenarios when restricting genomic relationships, compared to restrictions on pedigree relationships. For example, at constraint of f_{ij} = 0.185 and selection on INDEX-PROD, the number of selected sires was 35. In contrast, only 21 sires were selected at the comparable constraint on additive-genetic relationship of a_{ij} = 0.09. A further reduction in relationships is possible when using SDP output (i.e. suggested genetic contributions of selected parents), and applying a

simulated annealing algorithm to define specific mating plans. However, the advantage of this strategy is limited to a short- term perspective, and probably not successful in the period of genomic selection allowing a substantial reduction of generation intervals.

Introduction

The methodology of genomic selection enables the estimation of genomic breeding values of young sires with relatively high accuracies for production as well as for functional traits (e.g. VanRaden et al., 2009). An expected consequence is a further increase of selection intensities in genomic breeding programs on the cow sire and on the bull sire pathways of selection. König et al. (2009) economically evaluated genomic breeding programs based on the general framework of a genomic breeding program design as developed by Schaeffer (2006). Gain in discounted profit was strongly correlated with the reduction in the number of young sires having been selected upon genomic breeding values. For example, when selecting 25 young sires per year to inseminate a population of 50,000 cows, discounted profit per cow and year was 50 Euro. Profit was doubled when increasing selection intensity and selecting only 5 outstanding young sires. Hence, to balance genetic gain and inbreeding in a long-term perspective in the genomic era, König et al. (2009) suggested to use genomic information (i.e. the SNP pattern and genomic EBV) and to focus on both aspects, selection response and constraints in relationships, among selection candidates.

The upward trend of the inbreeding level in different dairy cattle populations mainly due to the widespread distribution of sire semen has been already evaluated in several studies in the past 20 years (e.g. Wiggans et al., 1995; Miglior, 2000; Thompson et al. 2000; Kearny et al., 2004). Due to the effect of selection on phenotypic means, genetic variances, and changes in relationships of individuals to the population, VanRaden (2005) described a method for adjusting expected future inbreeding that can be included in the process of genetic evaluation. According to VanRaden (2005), this adjustment procedure has been introduced in several United States trait evaluations in February 2005. An approach used by König and Simianer (2006) to maximize genetic gain by restricting additive genetic relationships

among bull sires and bull dams was based on quantitative genetics and optimum genetic contributions (OGC) as developed in theory by Meuwissen (1997). König and Simianer (2006) strongly recommended controlling inbreeding when mating bull sires to bull dams, because both genetic groups have substantial impact on the development of genetic relationships in dairy cattle breeding programs. Available mating programs used by breeding organizations or dairy cattle producers suggest cow sires for matings with cow dams. Such a mating strategy implies the management of inbreeding and relationships only in the short term. In contrast, long-term control of inbreeding in a dairy population requires consideration of relationships between young bulls entering AI progeny test programs, or directly selected sires for AI based on genomic breeding values. The program GENCONT (Meuwissen, 2002) was used by König and Simianer (2006) for elite matings in a breeding program embracing 30 young bulls per year to find the optimal allocations of bull sires and bull dams for one specific breeding organization. Compared with the actual breeding program applied in practice, OGC-theory revealed the potential to increase genetic gain under the same constraint for the increase of average relationship by 13.1%.

Algorithms as implemented in GENCONT (Meuwissen, 2002) are based upon a series of relaxed optimizations using Lagrange multipliers. This methodology has been intensively discussed by Pong-Wong and Woolliams (2007), and they focussed on the problem that invalid negative genetic contributions could be assigned to some individuals. As an approximate solution, GENCONT fixes genetic contributions of those individuals to zero, and the algorithms continues in a smaller subset of selection candidates. An alternative suggested by Pong-Wong and Woolliams (2007) for maximizing genetic gain while restricting inbreeding is a method based upon semi-definite programming (SDP). Due to the failure of Lagrange multipliers in some situations, i.e. the possible negative contributions when applying GENCONT, expected gains with SDP for some examples were substantially higher in the range from 1.5% to 9%.

Practical applications of OGC theory in dairy cattle are mainly based on GENCONT and used additive genetic relationship matrices among selection candidates (e.g. König and Simianer, 2006; Kearny et al., 2004). Additive

genetic relationship matrices only use pedigree data to calculate probabilities that gene pairs are identical by descent (Wright, 1922). However, wrong and missing sire information for Holstein dairy cattle in the assumed range from 3% to 23% (e.g. Weller et al., 2004) is a well-known problem for setting up accurate additive genetic relationships. Further problems arise when applying BLUP animal or BLUP sire models, i.e. possibly biased estimated breeding values (EBV), especially for low heritability traits. Paternity errors are due to recording errors by the farmer or by the AI company (Sanders et al., 2006). Alternatively, the use of actual SNP-genotypes for construction of genomic relationship matrices can provide more accurate measures of realized relationships among animals. Pimentel et al. (2011a) estimated the association of kinship coefficients estimated from marker data against relationship coefficients estimated from pedigree data for genotyped bulls in Germany. The R^2 value was only 0.53. Accordingly, the authors suggested to use genomic relationships for further association analyses due to the potential sire and dam misidentification when using pedigree relationships. Furthermore, as pointed out by Schork (2001), relationship coefficients calculated from pedigree data do not take into account the variation in relationships among similarly related individuals. Such variation is accounted for when computing relationship coefficients using marker information. Consequently, the aim of our study was to generate a framework for the combination of SDP methodology with genomic relationships among selection candidates, and to determine optimal genetic contributions for elite mating schemes for the optimization of genomic breeding programs. When restricting selection of candidates according to genomic relationships, also realized additive genetic relationships were monitored, and vice versa.

Material and methods

The data file of selection candidates consisted of 484 German Holstein bulls born in 2002 which were part of the German reference population for the estimation of SNP effects. Thus their estimated breeding values (EBV) were very similar to their genomic breeding values (GBV). All bulls were included without prior selection on EBV. Furthermore, 499 pre-selected potential bull dams born in the years 2001 to 2006 and located at a central station test were included in the data set. All selection candidates had been genotyped, and they had an official national EBV for the overall production index (INDEX-PROD), and for the somatic cell score index (INDEX-SCS). Means and standard deviations for both indices are shown in Table 1.

Table 1: Means, standard deviation (SD), minimum and maximum for the selection criteria production index (INDEX-PROD) and somatic cell score index (INDEX-SCS) for bull sires and bull dams

			Descriptive statistics			
	number	index	mean	SD	minimum	maximum
cows	499	PROD	103.27	6.61	81	121
		SCS	103.24	8.60	79	126
bulls	484	PROD	103.15	12.26	65	141
		SCS	102.23	11.15	67	136

Methods

Coefficients for relationship matrices.

Coefficients of kinship among genotyped bull sires and bull dams were calculated following the similarity index approach proposed by Eding and Meuwissen (2001). For each SNP locus, a genetic similarity index between a pair of bulls x and y was computed as $S_{xy}=0.25(I_{11}+I_{12}+I_{21}+I_{22})$, where I_{ij} is 1, if allele i in x is identical to allele j in y, or 0 otherwise. Under the assumption of unique founder alleles S_{xy} averaged over multiple loci is an unbiased estimator of the kinship coefficient (i.e., the probability of IBD). When founder

alleles are not unique, it needs to be corrected for the probability of alleles being alike in state (AIS).

For a given locus, the kinship coefficient between a pair of animals i and j (f_{ij}) was therefore estimated as:

$$\hat{f}_{ij} = \frac{S_{ij} - s}{1 - s}$$

where s is the similarity index in the founder population, i.e., the probability of two alleles being AIS, but not IBD. An estimate of s can be obtained from data on the founder population as:

$$s = \sum q_k^2$$

where q_k is the frequency of the k^{th} allele of the given locus in the founder population.

Allele frequencies in the founder population were estimated following the mixed model equations method proposed by Gengler et al. (2007) using a pedigree comprising 21,646 animals tracing back to 1906. Final estimates of kinship coefficients between every pair of animals were computed by averaging across all loci. Since estimates of s differed from one locus to another, the inverse of the variance of the estimate was used as weight when taking the average, as proposed by Eding and Meuwissen (2001). Pedigree based relationships a_{ij} were calculated by the tabular method (Emik and Terrill, 1949).

SDP-algorithm

Based on the SDP theory for maximizing genetic gain and minimizing long term inbreeding or relationships as introduced by Pong-Wong and Woolliams (2007), we developed an own computer program. The flexibility of this computer program allows using either pedigree based relationships or kinship coefficients derived from SNP data as an input file. The basic idea of the SDP algorithm originates from Fujisawa et al. (2002). Accounting for minimum contributions was done in an iterative way by fixing the maximum contribution of the animals with the lowest contributions to zero, and then starting the SDP algorithm again. This was done until all animals exceeded the minimum contribution.

The parameter file for the SDP algorithm to describe the outline of the breeding program was set up in the standard SDP form as described by

Pong-Wong and Woolliams (2007). Minimum genetic contributions for bull sires were fixed at 2%, and maximum genetic contributions for individual sires were restricted to 20%, resulting in 10 possible matings. Genetic contributions for bull dams were generally fixed at 2%. This implies an annually generated number of 50 young bulls, assuming that reproduction biotechnologies ensure at least one male offspring per cow and year. This is a realistic success rate of embryo transfer as used by Wensch-Dorendorf et al. (2011) to evaluate genomic dairy cattle breeding programs in Germany via simulation studies.

In different scenarios for INDEX-PROD and INDEX-SCS separately, constraints on the average pedigree relationships among future progeny were varied from a_{ij} = 0.08 to a_{ij} = 0.20 in increments of 0.01. Corresponding constraints for SNP based kinship coefficients were derived from regression analysis. Using the regression coefficient for $b_{f_{ij,a_{ij}}}$ of 0.52 with an intercept of 0.14 produces a corresponding range in genomic relationships from f_{ij} = 0.18 to f_{ij} = 0.24 (Figure 1)

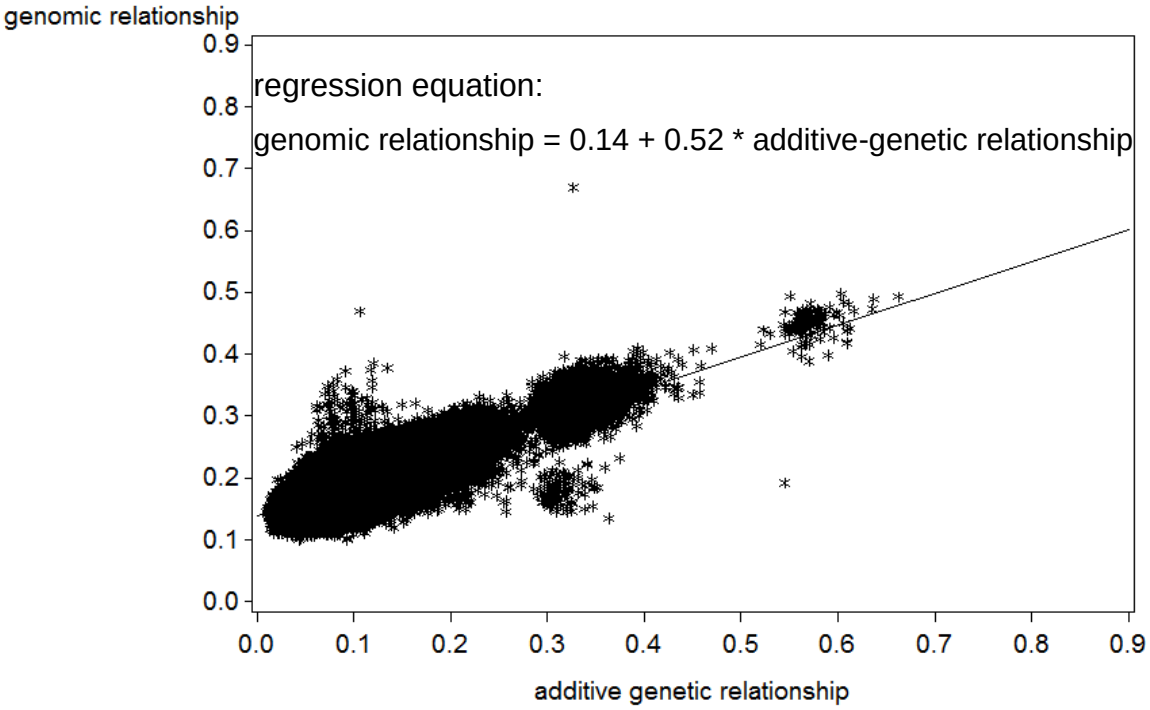

Figure 1. Relationship coefficients estimated from SNP- data (genomic relationship) against relationship coefficients estimated from pedigree data (additive genetic relationship)

Specific mating design

SDP output, i.e. suggested genetic contributions for bull sires and bull dams, was used to identify specific matings with the ultimate goal to minimize the average inbreeding coefficient in the short term in the following generation. For this purpose, a simulated annealing algorithm was applied (Press et al., 1989; Sonesson and Meuwissen, 2000). The essential steps of this algorithm have been summarized by König et al. (2010). Further essential input parameters were all possible relationships between pairs of selected bull dams and selected bull sires. The annealing algorithm was applied to the SDP output from two constraints on additive genetic relationships, and from the corresponding two constraints on genomic relationships. Constraints were a_{ij} = 0.09 and a_{ij} = 0.14, and accordingly f_{ij} = 0.185 and f_{ij} = 0.21.

Results and Discussion

SDP algorithm

Average additive genetic relationship among 983 selection candidates was 0.098±0.040, and average genomic relationship was 0.189±0.035 (Table 2). Average relationships among potential bull dams, among potential bull sires, and among bull dams and bull sires are also shown in Table 2. Additive genetic relationships among the best 4000 index cows in 2006 originating from Great Britain, Italy and Ireland were 0.083, 0.087, and 0.107, respectively (Mrode et al., 2009), and thus comparable to results from our study.

Table 2: Average coefficients of relationship and standard deviations (SD) for selection candidates

Selection candidates	Additive genetic relationship ± SD	Genomic relationship ± SD
484 bull sires	0.105±0.045	0.192±0.029
499 bull dams	0.097±0.045	0.189±0.030
983 bull sires and dams	0.098±0.041	0.190±0.035
484 bull sires with 499 bull dams	0.095±0.035	0.187±0.025

Average values for both indices of selected animals for different constraints on additive genetic and genomic relationships are shown in Figure 2 (INDEX-PROD) and in Figure 3 (INDEX-SCS). An increase in INDEX-PROD was generally associated with an increase in allowed long-term relationships. This is due to the fact that a relaxation in constraints for relationships resulted in a lower number of selected bulls (Figure 4). Hence, higher genetic contributions of genetically favourable single bulls were possible. These findings are in line with those of Kearney et al. (2004) and of König and Simianer (2006) when applying OGC as implemented in GENCONT. Also Weigel and Lin (2002) showed that an increase in allowed relationships decreased the number of selected sires. Kearney et al. (2004) associated genetic contributions and index scores for different levels of constraint on inbreeding for selected males, and they found a higher proportion of selected males with a more stringent constraint on rate of inbreeding. Interestingly, more sires were selected for all scenarios when restricting genomic relationships, compared to restrictions on pedigree relationships. For example at constraint of f_{ij} = 0.185 and selection based on INDEX-PROD, the number of selected sires was 35. In contrast, only 21 sires have been selected at the comparable constraint on additive genetic relationship of a_{ij} = 0.09 (Figure 4).

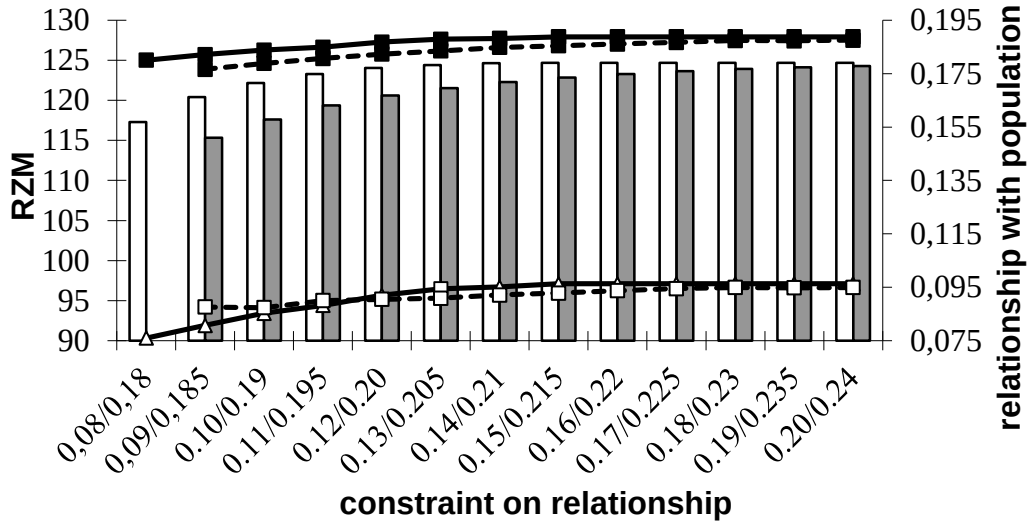

Figure 2. Average production index (INDEX-PROD) of selected bull sires and bull dams and their average relationship at different constraints for additive genetic and genomic relationships (white bars = average INDEX-PROD for constraint on additive genetic relationship; grey bars = average INDEX-PROD for constraint on genomic relationship; solid lines = constraint on additive genetic relationships; dashed lines = constraint on genomic relationships; lines with white squares = realized additive genetic relationships; lines with black squares = realized genomic relationships).

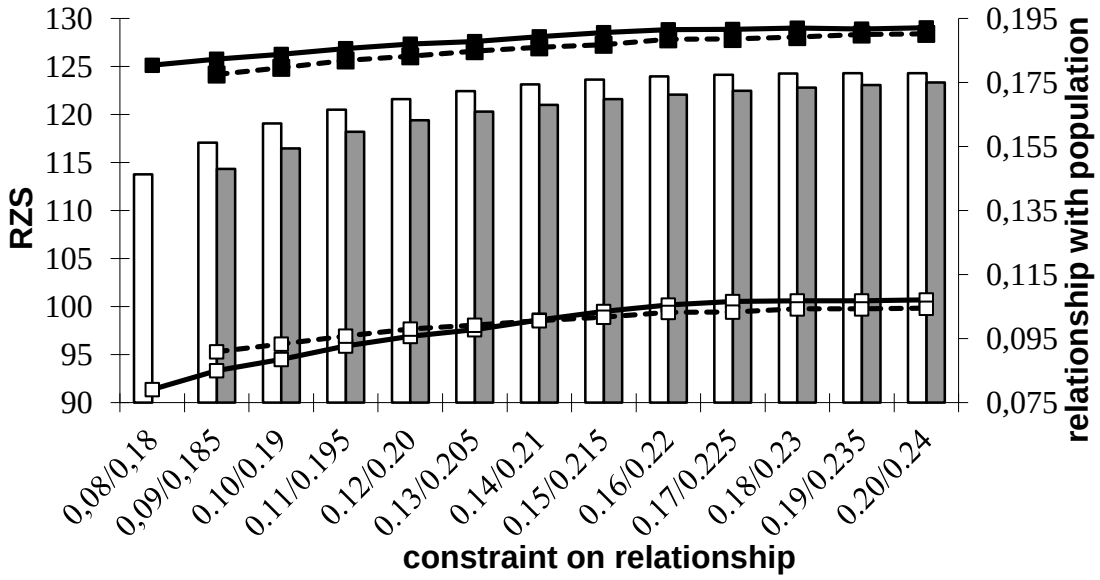

Figure 3. Average somatic cell score index (INDEX-SCS) of selected bull sires and bull dams and their average relationship at different constraints for additive genetic and genomic relationships (white bars = average INDEX-SCS for constraint on additive genetic relationship; grey bars = average INDEX-SCS for constraint on genomic relationship; solid lines = constraint on additive genetic relationships; dashed lines = constraint on genomic relationships; lines with white squares = realized additive genetic relationships; lines with black squares = realized genomic relationships).

When selection was constrained on additive genetic relationships, average INDEX-PROD and average INDEX-SCS of selected animals was maximal for an allowed restriction of a_{ij} = 0.15 (Figure 2 and Figure 3). For constraints on genomic relationships, we observed a continuous increase in genetic gain over the whole range of constraints from f_{ij} = 0.185 to f_{ij} = 0.24. The average value of INDEX-PROD was generally lower when selection was restricted on genomic relationships. This finding is in line with results from a comprehensive simulation study for aquaculture species conducted by Sonesson et al. (2010). In their study, genetic gain was 37 - 60% higher when constraining the increase in inbreeding based on pedigree data compared to constraints in inbreeding based on genomic data. No optimum solution was found for a constraint of f_{ij} = 0.18 on genomic relationships, when the minimum contribution of an individual sire was set to 2%.

For severe constraints on genomic relationships, i.e. in the range from f_{ij} = 0.185 to f_{ij} = 0.195, solutions for additive genetic relationships were more relaxed compared to corresponding restrictions of pedigree relationships (Figure 2 and Figure 3; comparison of lines with white squares). When increasing the allowed relationships from f_{ij} = 0.20 to f_{ij} = 0.24, solutions for coefficients of additive genetic relationships were higher compared to corresponding restrictions on additive genetic relationships (i.e. altering a_{ij} = 0.12 to a_{ij} = 0.20). This was found by Sonesson et al. (2010) for all analyzed scenarios. However, differences in solutions for additive genetic relationships were marginal, probably random, but interesting in its observed trend.

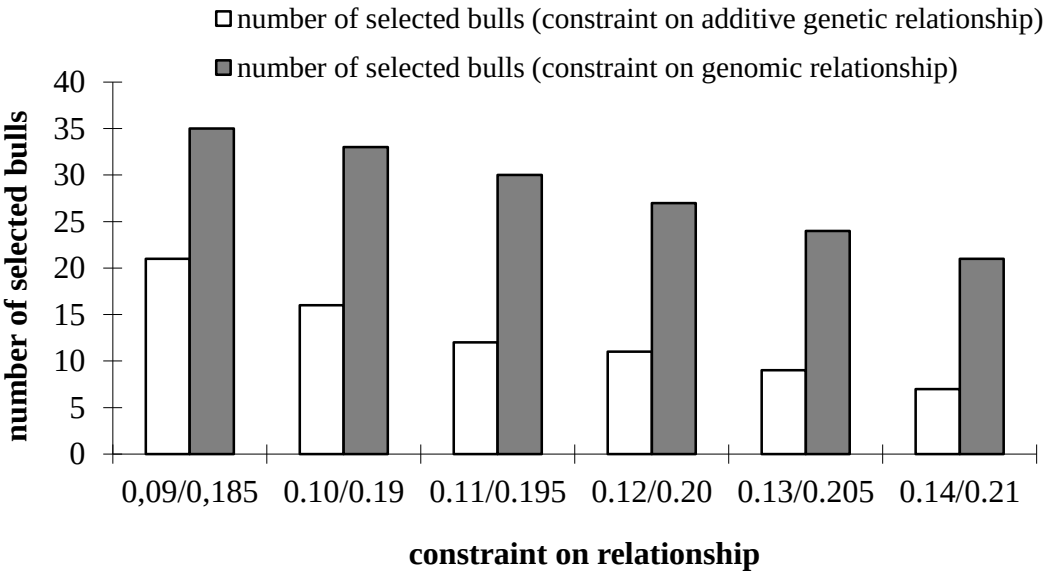

Figure 4. Number of selected bull sires at different constraints on average additive genetic and genomic relationships
(selection criteria: INDEX-PROD)

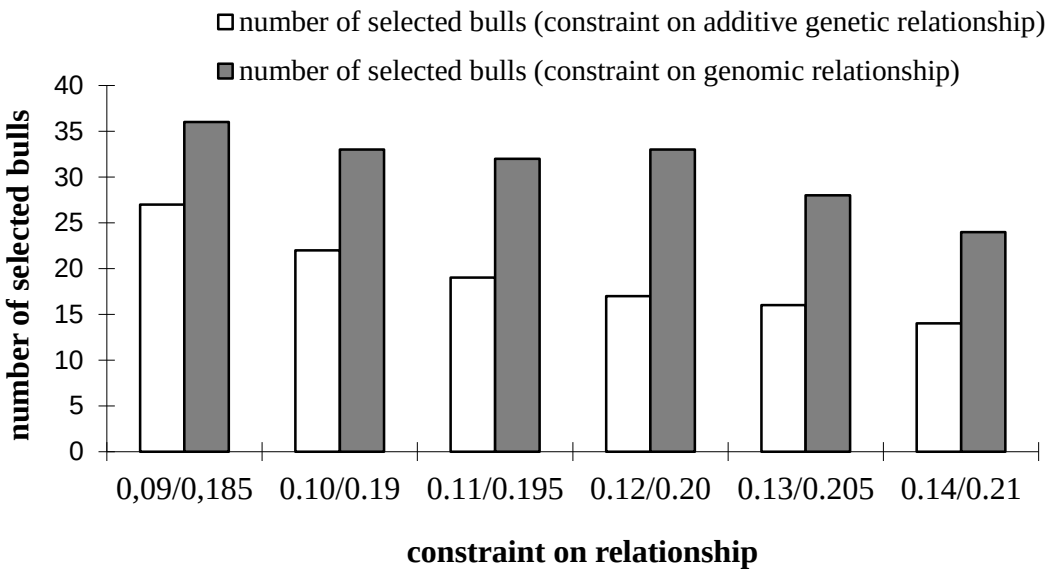

Figure 5. Number of selected bull sires at different constraints on average additive genetic and genomic relationships (selection criteria: INDEX-SCS)

According to Sonesson et al. (2010), solutions for realized genomic relationships were generally lower when restricting selection on genomic relationships compared to restrictions on pedigree relationships (Figure 2 and Figure 3, comparison of black squares). As expected, a target orientated restriction produced more desired results. This desired advantage, i.e. substantially lower solutions for average genomic relationships, decreased with an increase in allowed restrictions. The same trends for solutions in terms of genetic gain and realized relationships were observed for the high heritability trait (INDEX-PROD, Figure 2), and the low heritability trait (INDEX-SCS, Figure 3). Although more bulls were selected in the INDEX-SCS than in the INDEX-PROD scenario (comparison of results in Figure 4 and Figure 5), realized relationships were marginally higher for INDEX-SCS scenarios, maybe due to the lower SD in INDEX-SCS for bull sires.

Associations between genetic contributions of selected sires and their indices (INDEX-PROD, INDEX-SCS) for four different constraints on relationships are depicted in Figure 6 and in Figure 7. Differences in genetic contributions among selected sires increased with a relaxing constraint on coefficients of relationships, which is in line with previous studies (e.g. Kearney et al.,

2004). In our study and in contrast to results by Kearney et al. (2004) and by König and Simianer (2006), selected sires with the highest EBV always had the highest genetic contributions. This was probably a coincidence as those animals had relatively low coefficients of relationship. For example, the four best sires for INDEX-PROD had an average additive genetic relationship with the population of a_{ij} = 0.089, and a genomic relationship of f_{ij} = 0.183. Generally, a wider range for INDEX-PROD (Figure 6) and INDEX-SCS (Figure 7) of selected sires was found when constraining genomic relationships.

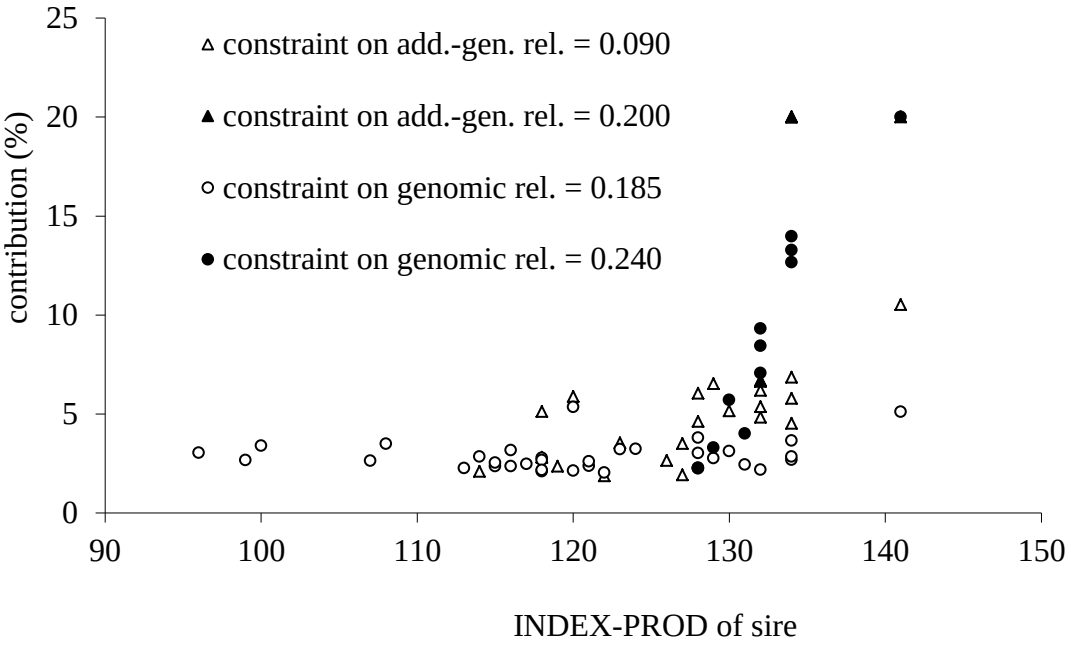

Figure 6. Association between optimized genetic contributions of bull sires and their production index (INDEX-PROD) for two levels of constraint on average additive genetic (constraint on add.-gen. rel.) and genomic relationship (constraint on genomic rel.).

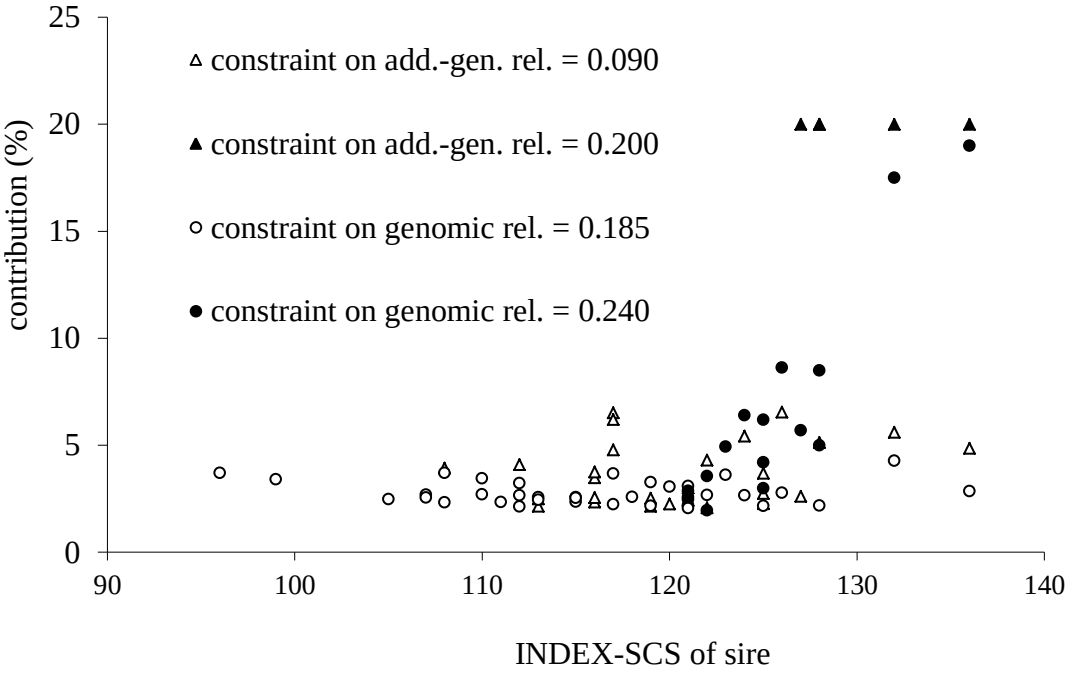

Figure 7. Association between optimized genetic contributions of bull sires and their somatic cell score index (INDEX-SCS) for two levels of constraint on average additive genetic (constraint on add.-gen. rel.) and genomic relationship (constraint on genomic rel.).

Specific mating designs

Average relationships of mating partners when combining results from the SDP algorithm with simulated annealing are shown in Figure 8 and Figure 9 for INDEX-PROD and INDEX-SCS, respectively. Following these results, a further reduction of coefficients for genomic and pedigree relationships is possible when only focussing on the minimization of relationships or inbreeding coefficients of individuals in the following generation by using an annealing algorithm as proposed by Sonesson and Meuwissen (2000). For example, with selection based on INDEX-PROD and restricting the maximal additive genetic relationship to a value of a_{ij} = 0.09, all possible sire-dam pairs suggested by the SDP algorithm had an average additive genetic relationship of a_{ij} = 0.068, and an average genomic relationship of f_{ij} = 0.179. Matings proposed by the annealing algorithm had an average additive

genetic relationship of a_{ij} = 0.048, and an average genomic relationship of f_{ij} = 0.164. A comparable scenario using SDP with a constraint on genomic relationship at f_{ij} = 0.185 led to an average additive genetic relationship of all possible sire-dam pairs of a_{ij} = 0.078, and an average genomic relationship of f_{ij} = 0.165. The average additive genetic relationship was a_{ij} = 0.06, and average genomic relationship was f_{ij} = 0.135 when subsequently applying the simulated annealing algorithm.

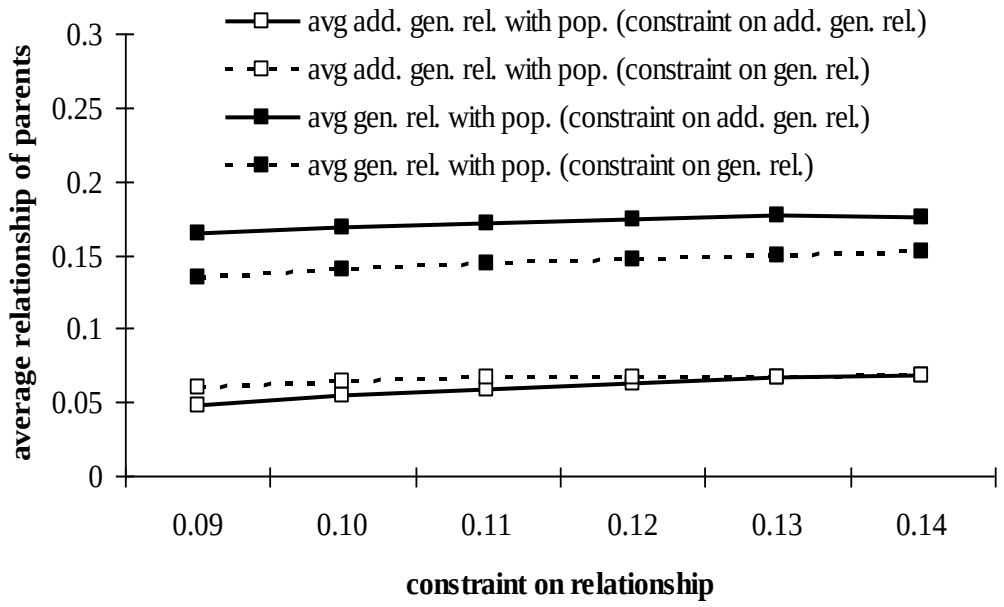

Figure 8. Average relationships of parents of the next generation when specifying matings with an annealing algorithm at different constraints for average additive genetic and genomic relationships (selection criteria: INDEX-PROD; solid lines = constraint on additive genetic relationships; dashed lines = constraint on genomic relationships; lines with white squares = realized additive genetic relationships; lines with black squares = realized genomic relationships)

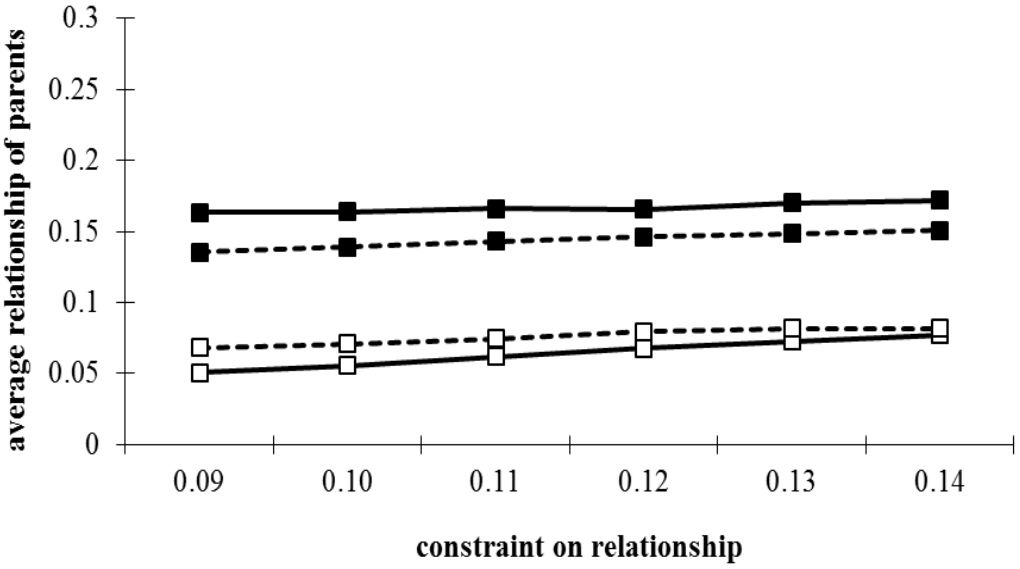

Figure 9. Average relationships of parents of the next generation when specifying matings with an annealing algorithm at different constraints for average additive genetic and genomic relationships (selection criteria: INDEX-SCS; solid lines = constraint on additive genetic relationships; dashed lines = constraint on genomic relationships; lines with white squares = realized additive genetic relationships; lines with black squares = realized genomic relationships)

The results from the simulated annealing algorithm were also in agreement with calculations conducted in another region of Germany for Holstein dairy cattle (König and Simianer, 2006). As one specific example from this study, 21 selected bulls and 30 selected cows were mated at random. The expected inbreeding coefficient for their progeny was 1.38 %. In contrast, the simulated annealing algorithm suggested a mating plan with an average inbreeding coefficient in the next generation of only 0.46 %.

Again, the mating design from the simulated annealing algorithm can be considered as a strategy for avoiding or minimizing inbreeding in the short term. Such a strategy could make sense for species or breeding plans characterized by long generation intervals, especially in dairy cattle or horse breeding programs (Niemann et al., 2009). For species with short generation intervals, e.g. pig or poultry breeding, the advantage from minimizing inbreeding in the short term will erode very quickly (König et al., 2010). But

also competitive future genomic dairy cattle breeding programs will be characterized by a substantial shortening in generation intervals, especially on the bull sire and cow sire pathway of selection (Schaeffer et al., 2006). From this point of view, the general OGC concept without the application of specific mating plans should be the major motivation.

General perspective

Daetwyler et al. (2007) pointed out that genomic selection will lead to lower inbreeding than traditional selection schemes, because the accuracies of estimated Mendelian sampling terms will be higher. This allows a higher differentiation within families, and a lower probability of co-selection of sibs. From the practical point of view (König et al., 2009; Hayes et al. 2009), a shorter generation interval in combination with high accuracies of GEBVs for young sires may lead to higher rates of inbreeding. Therefore, methods for optimizing long term genetic contributions as presented in this study are of major importance to avoid a future increase in inbreeding. Selection on bull sires and bull dams, as well as selection of cow sires is controlled by breeding organizations. Hence, the OGC concept as an additional so called 'controlling instrument' could easily be implemented in this step of selection (König et al., 2007).

Most of the trends in terms of genetic gain or realized relationships in our study were similar when comparing results from restrictions on pedigree or on genomic relationships, but minor differences could be of practical importance. Consequently, the more sophisticated and innovative approach is based on marker data and should be applied for scientific objectives as suggested by Pimentel et al. (2011b).

We applied the OGC concept for the selection of bull sires and bull dams within a framework of a genomic breeding program as suggested by Schaeffer (2006), and by König et al. (2009). The genomic era further allows for a change from the four-pathway selection strategy in dairy cattle as introduced by Rendel and Robertson (1950) to a two-pathway selection strategy (König and Swalve, 2009). Such a strategy implies that a multitude of male calves, being all selection candidates for AI, are genotyped. This would erode the traditional concept of mating designs and selection

strategies for bull sires and bull dams. Hence, further improvements for maximizing genetic gain and minimizing relationships should focus on SNP-patterns of male calves, e.g. the construction of a heterozygosity index. Our approach should be considered as a breeding tool in the transitional phase from the conventional towards the genomic era. However, we also assume that some form of pre-selection in terms of elite matings may still exist, and already at this early step of selection, minimizing relationships will contribute to ensure long term selection response. Without pre-selection, the proposed method might be challenging for extremely large datasets, but as stated by Sonesson et al. (2011), using genomic relationships will result in a more precise control of the genomic inbreeding.

Conclusion

Due to the continuous increase of inbreeding, the accumulation of defect genes, and the risk of inbreeding depressions, Holstein dairy cattle breeding programs should consider both aspects maximizing genetic gain and minimizing long term genetic relationships. In contrast to previous applications using GENCONT software and pedigree based relationships, we focused on semi-definite programming and relationships constructed from SNP data. For moderately as well as for lowly heritable traits, our approach can identify those mating partners that ensure a maximum genetic gain at specific constraints on maximum relationship. Our approach has been suggested to identify elite matings between pre-selected bull sires and bull dams using SNP data, but the flexibility of this concept, i.e. the combination of pedigree based and marker data, allows an application for a broad variety of aspects to maintain genetic diversity (e.g. Wang, 2001).

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