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Approaches to the management of inbreeding and relationship in the German Holstein dairy cattle population

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Abstract

The aim of this study was to estimate the current level of inbreeding in the German cow population and for bull dams born in Germany, to find out sires most related to different subsets of their breed and to demonstrate the negative effect of homozygosity in the case of complex vertebral malformation (CVM). Further on, the application of optimum genetic contribution (OGC) theory for the selection of bull dams and bull sires in different breeding scenarios was investigated. Levels of inbreeding for the cow population were in a low range from 0.97% to 1.70% evaluating birth years from 1996 to 1999 in a total dataset of 244,427 registered Holstein cows. The inbreeding coefficient of 8030 bull dams was much higher, i.e. 3.71%, for the birth year 1999. Increases in inbreeding of 0.19% per year indicated an effective population size of only 52 animals. Individual sires like R.O.R.A. Elevation and Hannoverhill Starbuck were highly related to potential bull dams with coefficients of relationship of 13.4% and 12.9%, respectively, whereas P.F. Arlinda Chief (16.3%) and Carlin-M Ivanhoe Bell (16.1%) were highest related to the best available AI sires. Coefficients of relationship were calculated by classes of estimated breeding values (EBV) for production traits showing highest values above 7% in the two highest EBV-classes. The optimum genetic contribution theory using official EBVs and approximative, for zero inbreeding corrected EBVs, was applied for elite matings in a breeding program embracing 30 young bulls per year to find the optimal allocations of bull sires and bull dams. Compared with the actual breeding program applied in practice, OGC-theory has the potential to increase genetic gain under the same constraint for the increase of average relationship by 13.1%. A more relaxed constraint on increase in inbreeding allowed even higher expected genetic gain whereas a more severe constraint resulted in more equal contributions of selected bull sires. Contributions from 21 selected bull sires and 30 selected bull dams for a scenario at 5% constrained relationship were used to develop a specific mating plan to minimise inbreeding in the short term in the following generation applying a simulated annealing algorithm. The expected coefficient of inbreeding of progeny was 66.3% less then the one resulting from random mating. Mating programs can address inbreeding concerns on the farm, at least in the short term, but long-term control of inbreeding in a dairy population requires consideration of relationships between young bulls entering AI progeny test programs.

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Significantly better EBVs of CVM-free bulls compared with CVM-carriers for the paternal fertility justify the application of OGC for elite matings.

Keywords: Dairy cattle; Inbreeding; Relationship; Optimum genetic contributions

1. Introduction

Selection schemes in Holstein dairy cattle are characterized by the widespread use of genetically superior proven AI sires. Especially the bull sire path in all Holstein breeding programs around the world is dominated by only a few sires per year. Miglior (2000) evaluated the pedigrees of young bulls from birth years 1970 to 1990 in Europe, North America and Oceania. He found an increasing percentage of bulls born sired by the 5 bulls with most sons in the three continents. In Europe including France, Germany, Italy and The Netherlands, about 55% of sons were from 5 sires in 1990, whereas in 1970, this value was below 25%. Although this extreme selection has been responsible for rapid genetic progress over the short term, there is an increasing concern that the extensive use of a few outstanding bulls might result in detrimental effects in the long term. The selection of bull sires for generating test bulls is the most important tool in dairy cattle breeding programs and therefore mainly responsible for the status of inbreeding and relationships between animals in the whole population. If the parents are related, some of the alleles transmitted to the offspring by each parent will be copies of the same alleles found in the common ancestors which caused the parents to be related. As the genetic relationship between parents increases, the likelihood that pairs of alleles in offspring are copies of a single allele in an ancestor generations back increases. Such alleles are said to be identical by descent and the negative effects were summarized by Falconer (1989): loss in genetic variability, higher chance of appearance of detrimental recessive genes in the homozygous state and inbreeding depression. The upward trend of the inbreeding level in different dairy populations is carefully evaluated in several papers (Wiggans et al., 1995; Miglior, 2000; Thompson et al., 2000; Weigel, 2001; Kearney et al., 2004). Results on the effects of inbreeding on the animals' performance in terms of production, fertility and health are compiled in Table 1. Results for inbreeding depression are not so worrying at the moment, but could be of dramatic impact in the long term regarding the small sample of selected bull sires per year.

Apart from this, the accumulation of lethal recessive defect genes is of practical economical concern. Matings between highly related individuals increase the risk of appearance of lethal recessive genes in the homozygous state like the single recessive gene causing complex vertebral malformation (CVM). Besides from malformed dead born calves, abortion in the early stage of parity is another symptom in the homozygous state (Agerholm et al., 2001). Thus, CVM-carriers should have a reduced paternal fertility (Berglund and Persson, 2003). Since the detection of the gene causing CVM presumably originated from a mutation in the genome of P.I. Star and widely distributed by his son Carlin-M Ivanhoe Bell (Thomsen et al., 2004), a rigorous cleanup program against CVM-carrier was announced by the German Holstein Association, i.e. to restrict their inseminations or consequent cullings. Konersmann et al. (2003) found 13.2% CVM-carriers among the total pool of 3024 German Holstein test bulls from birth years 1997 to 2000. The economical loss as a consequence of a rigorous culling decision assuming 20,000? costs per progeny tested young bull would be about 8 Mio. € in total. In general, traditional selection schemes in dairy cattle in Germany attempted to increase genetic response without regarding aspects of inbreeding in the long term. Considering aspects like inbreeding depression, homozygosity and the maintenance of genetic variability, methods should be applied to find the optimal balance between long term relationships between animals and selection response. Since Robertson (1961), many papers dealt with these two problems. Caballero et al. (1996) compared several mating systems with respect to the status of inbreeding and selection response. Selection response was little affected by the mating strategy, because all mating schemes were characterized by the

Table 1
Regression of productive and functional traits on 1% increase in inbreeding

Reference	Breed	Country	Trait	Regression per 1% of inbreeding
Hodges et al., 1979	HOL	Canada	Calving interval	+0.2 days
Hudson and Van Vleck, 1984	HOL	USA	Calving interval	+0.1 days
Hoeschele, 1991	HOL	USA	Days open	+0.13 days
			Service period	+0.11 days
Miglior et al., 1992	JER	Canada	305-day milk yield	−26.7 kg
			305-day fat yield	−0.6 kg
			Fat-%	−0.0028%
Casanova et al., 1992	Brown S.	Switzerland	305-day milk yield	−28.0 kg
			305-day fat yield	−0.1 kg
			Fat-%	−0.0005%
Short et al., 1992	HOL	USA	305-day milk yield	−22.6 kg
			305-day fat yield	−0.8 kg
			305-day protein yield	−0.9 kg
Miglior et al., 1995	Canada	Canada	SCS	+0.0012
Wiggans et al., 1995	Brown S.	USA	305-day milk yield	−24.6 kg
			305-day fat yield	−1.1 kg
			305-day protein yield	−0.9 kg
	HOL	USA	305-day milk yield	−29.6 kg
			305-day fat yield	−1.1 kg
			305-day protein yield	−0.9 kg
	JER	USA	305-day milk yield	−21.3 kg
			305-day fat yield	−1.0 kg
			305-day protein yield	−0.8 kg
Smith et al., 1998	HOL	USA	305-day milk yield	−26.7 kg
			305-day fat yield	−0.9 kg
			305-day protein yield	−0.8 kg
			SCS	+0.002
			Productive life	−5.9 days
Thompson et al., 2000	HOL	USA	305-day milk yield	−52 kg
			SCS	0.0

selection of animals with highest performance. The best method to reduce inbreeding was the minimum coancestry mating strategy and the avoidance of sib matings. The Optimum Genetic Contribution (OGC) theory maximises the genetic gain while constraining the rate of inbreeding or the relationships among selection candidates (Wooliams and Meuwissen, 1993; Meuwissen, 1997; Grundy et al., 1998) and has been extended by Meuwissen and Sonesson (1998) for overlapping generations. These methods choose the selected parents and assign genetic contributions to the next generation for each selected candidate. Further on, Sonesson and Meuwissen (2000) developed an algorithm to combine OGC results with specific mating strategies. In dairy cattle, OGC was applied in the United Kingdom Holstein population (Kearney et al., 2004) and in different breeds in the United States (Weigel and Lin, 2002) for matings between bull sires and bull dams. They found increased genetic gain at the same rate of inbreeding compared to traditional selection schemes.

The aim of our study was to determine the rate of inbreeding in the German Holstein cow population and in German bull dams, to evaluate the relationships of influential sires to different subsets of animals and to apply the optimal contribution theory for the optimal allocation of bull sires to bull dams under different restrictions.

2. Materials and methods

For calculations of inbreeding coefficients, coefficients of relationship and the application of OGC, four different datasets were available. Dataset 1 comprised 244,427 registered Holstein cows in first parity from one region (=region 1) within the western part of Germany representing birth years 1993 to 1999. Highly selected elite cows, i.e. 8030 bull dams born in Germany from 1981 until 1999 were included in dataset 2. Sons of these bull dams were progeny tested in the national German Holstein breeding program. Dataset 3 was identical with the official German national breeding value database from February 2003 and included 7933 bulls from birth years 1993 to 1998. Pedigrees for all analyses were extracted from the German Holstein database traced back to base animals born in 1950 (dataset 4). To characterize the quality of the pedigree information and to make results as inbreeding coefficients more interpretable, the PEDIG software developed by Boichard (2002) for the analysis of large populations was used. Information criteria characterizing the pedigree quality were the percentage of known ancestors per generation and the equivalent number of known generations, defined as the sum over all generations of the proportion of known ancestors at each generation. Inbreeding coefficients were calculated using the algorithm of Tier (1991) for the cow population (dataset 1) and the bull dams of dataset 2. Sires most related to the cows in dataset 1 were revealed by calculating average relationships by the tabular method (Emik and Terrill, 1949). Computable feasibility was achieved by creating subsets of the whole data. 10 samples including 100 cows per sample were randomly chosen out of dataset 1 and in each sample, average relationships to the sires were calculated. The 10 sires most related to these cows in average over all samples were R.O.R.A. Elevation, Hannoverhill Starbuck, P.F. Arlinda Chief, S-W-D Valiant, R.T. Leadman, To-Mar Blackstar, Cal-Clark B. Chairman, Carlin-M Ivanhoe Bell, Penstate Ivanhoe Star and Whittier-Farms Ned Boy (Table 2). The average production index (RZM) of the cows in the drawn samples was 109. In the next step, relationships of the 10 sires to the 100 highest ranked cows for RZM from region 1 (dataset 1) were calculated. The average production index of the highest ranked cows was RZM 138. In an additional scenario, the best 100 and the worst 100 bulls according to their production index (RZM) and conformation index (RZE), respectively, were extracted out of the national breeding value database (dataset 3) and relationships to the 10 sires were calculated. The last scenario for calculating relationships considered 7933 Holstein bulls from birth years 1993 to 2001 available in dataset 3 and 45,234 cows in dataset 1 from birth year 1999. Relationships between males and females were calculated, stratified by RZM-classes in increments of 12 points.

Bulls included in dataset 3 were divided in different groups according to their CVM-status. Mean EBVs for the paternal non-return rate at day 90 and paternal stillbirth of CVM-carrier and CVM-free bulls were compared within birth years 1996, 1997, and 1998, respectively. Additionally, inbreeding coefficients and relationships to Carlin-M Ivanhoe Bell and Penstate Ivanhoe Star for each group were calculated.

The OGC-concept, implemented in the program GENCONT (Meuwissen, 2002), was applied to find the optimal mating frequencies of bull dams and bull sires to breed the next generation of young AI bulls.

Table 2
Influential sires in terms of average relationships (in %) to different subsets of members of their breed

Influential sire	Randomly chosen 100 cows	100 bull dams	Best 100 bulls for RZM	Worst 100 bulls for RZM	Best 100 bulls for RZE	Worst 100 bulls for RZE
R.O.R.A. Elevation	12.1	13.4	11.7	17.2	16.6	13.4
Hannoverhill Starbuck	11.2	12.9	8.7	21.2	15.9	13.1
P.F. Arlinda Chief	9.7	7.9	16.5	16.6	12.4	10.9
S-W-D Valiant	8.1	9.1	11.7	13.3	13.7	14.0
R.T. Leadman	8.1	10.1	10.0	12.3	11.2	12.9
To-Mar Blackstar	7.5	7.8	13.1	18.5	18.4	7.2
Cal-Clark B. Chairman	7.2	7.4	8.8	10.5	13.4	8.5
Carlin-M Ivanhoe Bell	5.5	8.0	16.3	1.9	6.8	6.0
Penstate Ivanhoe Star	4.7	5.5	7.3	4.6	5.2	5.1
Whittier-Farms Ned Boy	3.6	2.9	2.6	3.4	3.3	3.6

The method implies a maximization of the average genetic merit of the selection candidates, $c'u$, by constraining the average relationship $c'Ac$ within this group, where c is a vector of contributions of each selected animal, u is a vector of estimated breeding values of selection candidates and A is the numerator relationship matrix between selection candidates (Meuwissen, 2002). The data file of selection candidates comprised the best 1000 cows for RZM fulfilling some phenotypic conformation criteria from region 1 (dataset 1) and the best 100 available AI sires for RZM from dataset 3. A pedigree file is mandatory for the GENCONT-program and was used as described above for the calculations of inbreeding coefficients and coefficients of relationship. The parameter file for GENCONT describes the structure of the breeding program. The annual number of young bulls in region 1 was determined to a value of 30. Using modern biotechnologies like embryo transfer or ovum pick up, at least one male progeny per bull dam seemed to be a realistic approach and therefore, 30 different bull dams should be selected out of the pool of 1000 female candidates. This definition of the breeding design implies equal genetic contributions of 3.33% of the 30 selected bull dams to the following generation. The maximum genetic contribution of individual sires was restricted to 20% establishing that the maximum number of progeny from the same sire is limited to a value of 6 sons. In different scenarios, constraints on the average relationships among future progeny were varied from 0.04 to 0.10. The method developed by Meuwissen and implemented in GENCONT seemed to be suboptimal if EBVs are not adjusted for zero inbreeding. Published EBVs in Germany which were used for our analysis are in general not adjusted. This implies that the OGC-method double counts losses from inbreeding, because the fact that published EBVs already include average effects of inbreeding is ignored. E.g., bulls that are highly related to their mates have inbred daughters giving less milk, and thus the EBVs of these bulls already account to some extent for their higher inbreeding losses. An additional approximative calculation was done to derive the impact of inbreeding adjusted EBVs on suggested genetic contributions for bull sires. In the first step of the approximation, average coefficients of relationship ($\bar{R}_{ij}$) between each of the 100 bull sires and the pool of 1000 bull dams were calculated. Following Short et al. (1992) and Wiggans et al., (1995), the depression per 1% of inbreeding is roughly about 1 kg protein considering 305-day protein yield. Expected inbreeding of progeny ($\bar{F}_k$) is half the relationship of their parents ($\bar{R}_{ij}$) and their inbreeding depression would be $\frac{1}{2}\bar{R}_{ij} \times 1$ kg in protein yield. EBVs in protein yield for sires are twice the phenotypic superiority of their daughters and hence, the impact on inbreeding depression of daughters on EBVs of sires is $\left(\frac{1}{2}\bar{R}_{ij} \times 1\ \text{kg}\right) \times 2$. The regression of RZM on the EBV for protein yield is 0.68 RZM-points/kg. Finally, the approximative, for zero inbreeding adjusted RZM (RZM_ad) is: $\text{RZM\_ad} = \text{RZM} + \left(\frac{1}{2}\bar{R}_{ij} \times 1\ \text{kg}\right) \times 2 \times 0.69$. Utilizing GENCONT and inbreeding adjusted EBVs (RZM_ad) for derivation of optimum genetic contributions, the average relationships among future progeny were constrained at 0.04 and 0.10, respectively.

After the ‘global’ determination of genetic contributions of male and female parents using official EBVs in RZM, a simulated annealing algorithm (Sonesson and Meuwissen, 2000; Press et al., 1992) was applied to define the specific matings between bull dams and bull sires considering their frequencies in vector c at 5% constrained relationship. The ultimate goal in this mating tool is to reduce the average inbreeding coefficient in the short term in the following generation. Input parameters were all possible relationships between pairs of selected bull dams and selected bull sires. By using simulated annealing, it is avoided that this algorithm ends at a local optimum. The scheme with the lowest average inbreeding coefficient in the next generation should be considered as the optimal one.

3. Results

3.1. Inbreeding coefficients, relationships and homozygosity

Fig. 1 shows the trend in inbreeding for German Holstein cows within region one from birth years 1993 to 1999. The coefficient of inbreeding increased from 0.97% in birth year 1991 to 1.7% in birth year 1997. In recent birth years from 1994 to 1997 inbreeding has increased at a rate of 0.21% per year

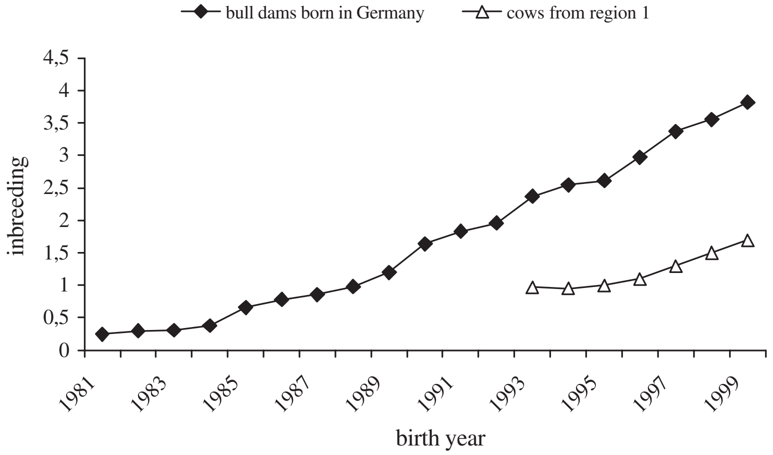

Fig. 1. Inbreeding coefficients (in %) for a subset of Holstein cows within one region of Germany and for bull dams of German young bulls by birth years.

whereas from birth years 1991 to 1993, the values of inbreeding were on a similar level. The same fact of faster inbreeding in younger birth years could be observed investigating bull dams stemming from Germany (Fig. 1). Before 1988, the average increase of inbreeding was less than 0.1%/year but in the following birth years greater than 0.2%/year. The average increase of inbreeding per year considering the whole period from 1981 to 1999 in the bull dam data set was 0.19%/year. Considering the generation interval of 5 years, the increase in inbreeding per generation was 0.95% ($\Delta F=0.0095$) and the effective population size will be $N_e=1/(2\times0.095)=52$ animals. This means that the same values in inbreeding will be obtained by random matings between 26 males and 26 females compared with the actual situation in Germany embracing over 1.5 Mio. registered Holstein cows, but a selective pool of outstanding sires. Pedigree quality information defined as the proportion of known ancestors per generation was 100% in generation 1, 99.2% in generation 2, 98.1% in generation 3, and 94.8% in generation 4, respectively, and dropped below 80% in generation 6. The number of complete generation equivalents, defined as the sum of the proportion of known ancestors over all generations traced was 6.15.

R.O.R.A. Elevation, Hanoverhill Starbuck, Pawnee Farm Arlinda Chief, S-W-D Valiant, R.T. Leadman and To-Mar Blackstar were the sires most related to the randomly chosen pool of cows with coefficients greater than 6% (Table 2). Apart from Whittier-Farms Ned Boy, the coefficients of relationship of these 10 outstanding sires to the best 100 elite cows for RZM from the same region slightly exceeded these initial results. Evaluating the relationships of the 10 influential sires to the best 100 and worst 100 bulls prevalent in the national German breeding value data base for production and conformation, the results can be summarised as follows (Table 2): Carlin-M Ivanhoe Bell is obviously extremely related (16.3%) to the best 100 RZM bulls, but less related (1.9%) to the worst 100 bulls for RZM. For Hannoverhill Starbuck, the opposite is true (8.7% vs. 21.2%). Cal-Clark B. Chairman and his son To-Mar Blackstar likewise R.O.R.A. Elevation and his son Starbuck have the highest coefficients of relationship to the best 100 bulls for RZE.

Bulls and cows having highest EBVs were in close relationship among each other (Fig. 2). The RZM-class from 142 to 154 points including genetically superior animals is characterised by a relatively high average coefficient of relationship of 7.35% between males and females compared to coefficients below 3% in the three lowest RZM-classes.

Mean EBVs for the paternal non-return rate and paternal stillbirth for CVM-carrier and CVM-free bulls of German origin stratified by birth years of bulls are given in Table 3. Differences in the EBVs between groups of bulls were in a range from 2.1 to 4.7 favouring CVM-free bulls in all subclasses.

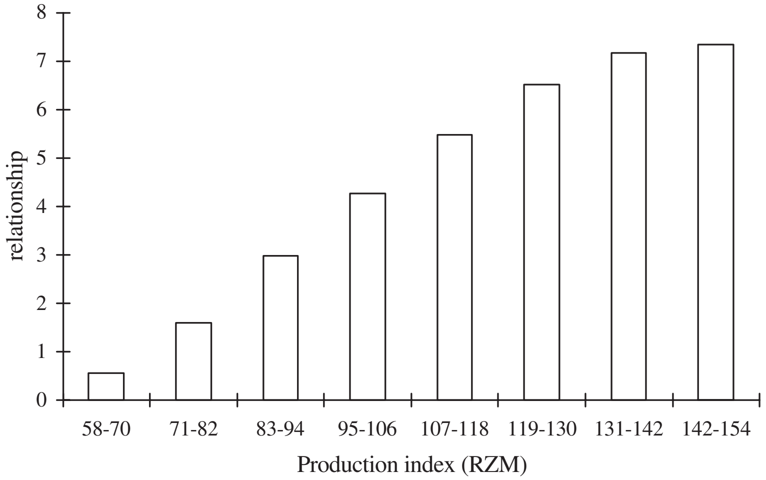

Fig. 2. Average relationship (in %) between AI bulls and cows from one region within Germany by RZM-classes for production traits.

CVM-carrier bulls showed a slightly higher inbreeding coefficient compared with CVM-free bulls, but all were closely related to Carlin-M Ivanhoe Bell (17.1–18.3%) and Penstate Invanhoe Star (12.2–13.3%) which were identified as ancestors for the CVM mutation.

3.2. Application of optimum genetic contribution theory and mating plan optimisation

Table 4 displays inbreeding coefficients and relationships of 100 potential bull sires, 1000 potential bull dams, the total pool of 1100 selection candidates and the coefficient of relationship between bull dams and bull sires. Coefficients were substantially higher for males than for females. The average inbreeding coefficient considering all candidates was 1.89% and the relationship between them 5.37%. For the sake of completeness of calculations, the average relationship of the population considering different numbers of sexes was calculated as $(\bar{R}_{ss}+2\bar{R}_{sd}+\bar{R}_{dd})/4=6.19\%$, whereas $\bar{R}_{ss}$ is the average relationship among males, $\bar{R}_{dd}$ among females and $\bar{R}_{sd}$ among both sexes. This value is higher than the relationship without correction (6.19% vs. 5.37%) due to less numbers and higher coefficients of relationship among bull sires. However, the crucial value considering the next generation is the coefficient of relationship between the group of 100 bull sires and the group of 1000 bull dams (5.93%).

If elite matings were at random between the selected bulls and dams, the inbreeding coefficient should roughly the half the average relationship of the elite animals of the parent generation. With ΔF per generation of 0.95% the expected inbreeding coefficient would be $(5.37\%-2*0.95\%)/2=1.735\%$. The

Table 3

EBVs for paternal non-return rate and paternal stillbirth, inbreeding coefficients and coefficients of relationship to C.-M I. Bell and P.I. Star by the CVM-status of bulls for birth years 1996, 1997 and 1998

	1996		1997		1998	
	CVM-carrier	CVM-free	CVM-carrier	CVM-free	CVM-carrier	CVM-free
No. of bulls	22	797	49	841	18	567
EBV paternal non-return	96.6	98.3	95.9a	100.6^{b}	94.6^{a}	99.4^{b}
EBV paternal stillbirth	96.3^{a}	99.1^{b}	99.2	101.3	99.3	101.5
Inbreeding coefficient	3.6%	2.9%	3.7%	3.3%	3.9%	3.4%
Relationship—C.M I. Bell	17.2%^{a}	4.8%^{b}	17.1%^{a}	5.2%^{b}	18.3%^{a}	4.3%
Relationship—P.I. Star	12.8%^{a}	3.6%^{b}	12.2%^{a}	3.7%^{b}	13.3%^{a}	3.1%^{b}

Different superscripts within traits and birth year indicate significant difference ($P<0.05$), *t*-test.

Table 4
Inbreeding coefficients and coefficients of relationship (in %) for selection candidates

Selection candidates	Inbreeding	Relationship
100 bull sires	2.93	7.65
1000 bull dams	1.78	5.28
1100 bull sires and bull dams	1.89	5.37
Relationship among 1100 bull sires and bull dams corrected for the number of animals in both sexes	–	6.19
100 bull sires–1000 bull dams	–	5.93

observed average inbreeding coefficient of the bull dams (1.78%) is very close to this value, demonstrating that elite mating decisions neither aim at avoiding inbreeding, nor deliberately use inbreeding in a systematic way. The optimal number of bull sires at each level of the relationship constraint and the corresponding expected genetic gain in production traits are shown in Fig. 3. For the lowest level of the average relationship at 4%, the optimal number of bull sires was 21 and the average RZM of the selected group was 133.2. At the highest relationship constraint (10%), the optimal number of bull sires decreased to 9 and the average RZM increased to 144.3. As it is common practice in German breeding programs, the number of bull dams in our study was fixed to a constant value of 30, but for different constraints of relationships different bull dams were selected. Fig. 4 illustrates in detail the mechanism of optimum genetic contribution theory for bull sires. Constraining the average relationship at 10%, 9 bull sires having high RZM-values within a range from 142 to 151 were selected. Different mating frequencies were suggested for the selected sires with a positive correlation of breeding value and contribution. The highest ranked bull was used for 20% of the matings, while the lowest ranked bull was only used for 6.2% of the matings. Applying a much more severe constraint at 4% for the average relationship resulted in a greater variety of 21 selected bull sires with almost uniform contributions and lower EBVs. The best bull sire (RZM = 151) was not considered in the selection decision any more. A practical constraint could be not to exceed the actual coefficient of relationship among selection candidates. Constraining the relationship at the actual value of 5.37% resulted in 19 selected females and in an average RZM of 139.3 which is slightly below the maximum of RZM = 144.3. The actual conventional mating scheme of the breeding organisation located in region 1 considered 8 bull sires and 30 bull dams. The average RZM of selected candidates was 124.1 and the average relationship among selected animals was 6.23%. Constraining the relationship at 6%, OGC application enabled an average RZM of 140.7 as indicated in Fig. 3. Thus, applying the OGC-concept allowed more genetic gain at the same rate of inbreeding when compared to the traditional selection scheme.

Contributions from 21 selected bull sires and 30 selected bull dams for a scenario at 5% constrained

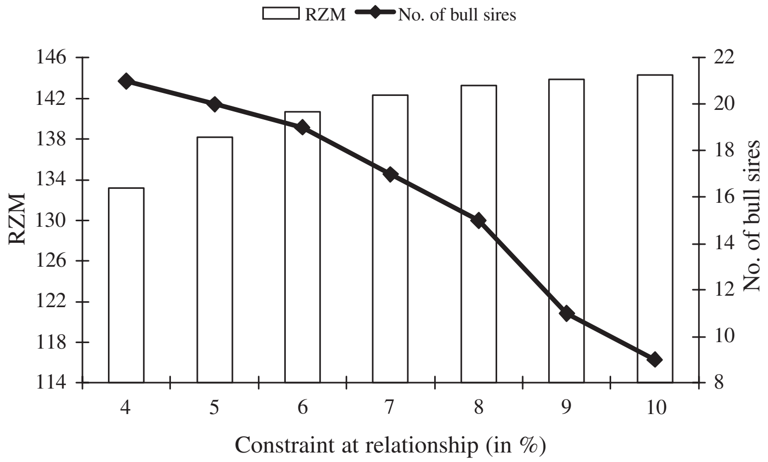

Fig. 3. Production index (RZM) of selected animals and number of bull sires at different constraints for average relationships.

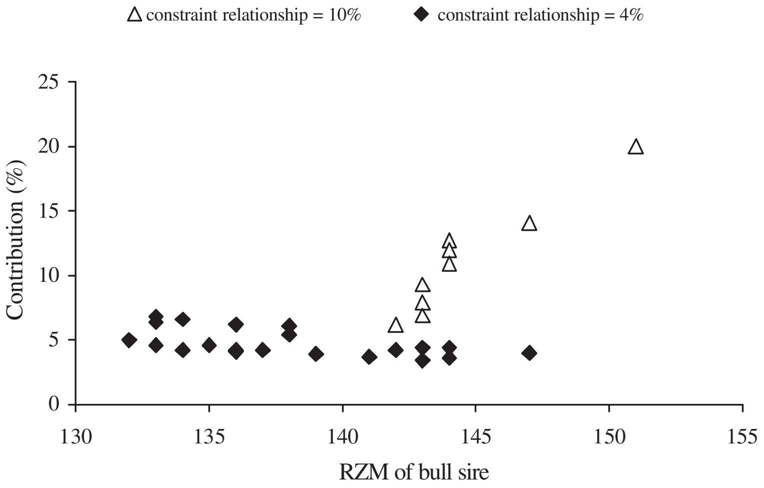

Fig. 4. Association between optimised contributions of bull sires and their production index (RZM) for two levels of constraint on average relationship.

relationship were used to develop a specific mating plan to minimise inbreeding in the short term in the following generation applying the simulated annealing algorithm (Sonesson and Meuwissen, 2000). The algorithm enabled a mating plan with an average inbreeding coefficient of only 0.46%. For comparison, 21 bull sires and 30 bull dams mated at random results in a much higher inbreeding coefficient of 1.38%.

The comparison of genetic contributions of individual bull sires applying OGC and including inbreeding adjusted EBVs and non-adjusted EBVs for 0.04 and 0.10 constraints on the average relationships among future progeny resulted in minor differences. At 4% constrained relationship, 19 common bull sires were selected and only 2 bull sires were different in both analysis. The average difference in genetic contributions of the common sires was only 0.02%. For the relaxed constraint at 10% relationship and utilizing inbreeding adjusted EBVs, 10 bull sires were selected compared with 9 selected bull sires in the

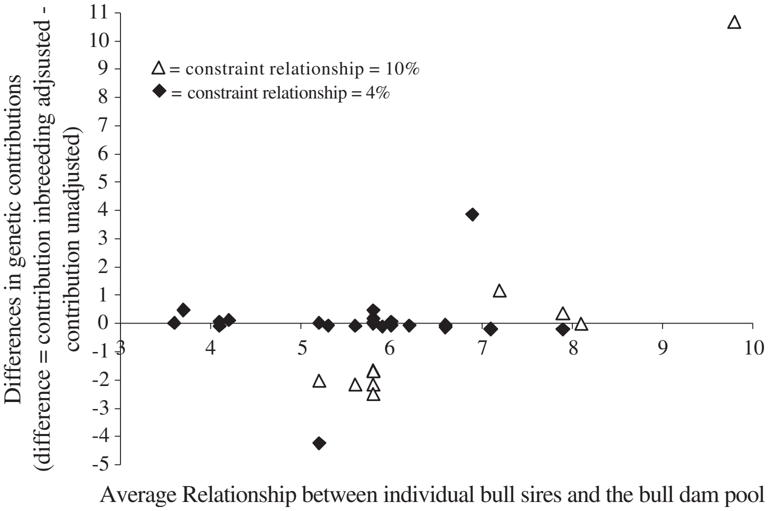

Fig. 5. Differences in genetic contributions for selected bull sires using inbreeding adjusted EBVs and non-adjusted EBVs for two levels of constraint on average relationship.

previous scenario including unadjusted EBVs. The average difference of theses same 9 sires in genetic contributions was −1.18% in a range from −2.48% to +1.15%. The tenth sire was selected for 10.6% of all matings using inbreeding adjusted EBVs. Differences in genetic contributions with and without adjustments of inbreeding in dependence of average relationships of individual sires to the group of 1000 bull dams are depicted in Fig. 5 and showing greater impact in differences for the more relaxed constraint at 10% relationship.

4. Discussion

4.1. Inbreeding, relationships and homozygosity

The actual inbreeding coefficient in the subset for Holstein cows was 1.7% and therefore in the range that was calculated recently by Swalve et al. (2003) for the cow population within the region of Lower Saxony and by Kearney et al. (2004) for the UK dairy population. Neglecting unknown pedigrees in the study of Swalve et al. (2003) only lead to marginal increases up to an inbreeding coefficient of 1.94%. These German and UK results for inbreeding are in contradiction to examinations conducted by Wiggans et al. (1995) or Miglior (2000) for Holsteins cows located in North America. They found inbreeding coefficients above a value of 4%. The main reasons for differences in the status of inbreeding of cows across countries could be explained in a longer period of breeding dual purpose cows in Germany (Mügge et al., 1999) and in the large number of cow sires used for AI as published in the annual statistics for inseminations (ADR, 2003). Miglior (2000) gave the recommendation to North American Holstein associations to change their breeding policies and to open their herd books to registration of non-North American germplasm, as it is common practise in Europe. But nevertheless, not the actual level of inbreeding is of much concern because such values depend on the depth of the recorded pedigree and results are unsuitable for comparisons across populations or regions. The increase of inbreeding per year or generation rather seems to be a more adequate measure. Weigel (2001) has shown that inbreeding rates within numerically small breeds such as Guernsey, were not substantially different from those in numerically large breeds such as the Holstein. He concluded that selection intensity is the most important predictor of the inbreeding rate. Miglior (2000) distinguished between different phases, before and after the 1980s. Before birth years 1989, he found slow increases in inbreeding varying from 0.02% to 0.09% per year in Holsteins from Europe and North America finally reaching increments up to 0.29 per year at the end of the 1990s. Values for the effective population size in the US-Holstein population were 39 (Weigel, 2001) and 70 in Danish Holstein (Sorensen et al., 2004) and therefore similar to our results. The importance of the variety of bull sires in the status of inbreeding was studied by Goddard and Smith (1990) applying a simulation. They reported an expected increase in inbreeding rates of 0.125%/year including 20 bull and 0.25%/year with 10 bull sires per generation.

The trend in inbreeding is undoubtedly the tool most frequently used to describe genetic variability. However, some drawbacks may arise utilizing this tool especially the fact that the computation of the individual coefficient of inbreeding is very sensitive to the completeness of pedigree information. If information is missing, large biases when estimating the rate of inbreeding could be expected (Boichard et al., 1997). Maignel et al. (1996) considered the number of complete generation equivalents, defined as the sum of the proportion of known ancestors over all generations traced, as the best criterion to characterize completeness of pedigree information. In addition, the known ancestors per generation could be another useful parameter to rigorously interpret and compare inbreeding coefficients (Boichard, 2002). The number of complete generation equivalent in our study was 6.15 and therefore above the value of 4.75 calculated by Maignel et al. (1996) for French Holstein. Maignel et al. (1996) included pedigrees for cows calving from 1975 to 1995 and found limited pedigree information for animals born before 1966. Considering generations 1 to 5, we found percentages of known ancestors above 85%, which is very similar to French Holstein or Normande (Maignel et al. 1996).

R.O.R.A. Elevation, Pawnee Farm Arlinda Chief, S-W-D Valiant and Hanoverhill Starbuck with coefficients of relationship to the cows of 11.7%, 9.5%, 8.5% and 5.4%, respectively, were also found as dominant sires in a study by Swalve et al. (2003) in another region of Germany. R.O.R.A. Elevation was announced as most related to the US-Holstein population (AIPL, 2003) with an expected inbreeding coefficient of 7.7% of future daughters and found in 91% of all cow pedigrees in the study from Swalve et al. (2003). In Danish Holstein (Sorensen et al., 2004), 8 ancestors contributed about 50% to the reference population and the most important sires were R.O.R.A. Elevation (13.5%), Pawnee Farm Arlinda Chief (10.7%) and Carlin-M Ivanhoe Bell (8.3%). Young and Seykora (1996) identified the two sires R.O.R.A. Elevation and Pawnee Farm Arlinda Chief that together accounted for nearly one-quarter of the genes of registered US Holstein animals born in 1990. Van Raden and Smith (1999) extracted a random sample of cows from birth year 1995 to find out the most related sires to this group. To-Mar Blackstar and R.O.R.A. Elevation were most related to the Holstein breed with expected inbreeding of 7.9% and 7.7%, respectively.

The effect of the autosomal recessive defect gene causing CVM on the paternal non-return rate was also investigated in Swedish Holstein cattle (Berglund and Persson, 2003). Analogous to our study, heterozygous CVM-carrier bulls were compared with CVM-free bulls. EBVs for 168 days non-return of non-carriers were significantly higher. Persson (2003) used the same data and additionally investigated non-return rates for 56 days and also found significant differences between CVM-carriers and non-carriers. Poor paternal fertility was also found in a large research project conducted in the Netherlands which comprised more than 500,000 inseminations of cows that were sired by CVM-carrier bulls (Olson, 2001). The service sires included 38 CVM-carrier bulls and 77 non-carrier bulls. The services to CVM-carrier bulls resulted in 5.38% fewer live calves than were produced by services to non-carrier bulls. Kuhn et al. (2005) used approximately 3 million records from about 1.7 million daughters of sires with known genotype for CVM to estimate the effect of the CVM allele on production traits like lactational milk, fat, and protein yield and somatic cell score. For all traits, effects were minor, i.e. milk yield was 160 kg higher for CVM-carriers. Such results justify a rigorous clean up program against CVM-carriers, because the impact on economically important production traits will be marginal.

4.2. Optimum genetic contributions

Because of high relationships between potential bull sires and bull dams as shown in Fig. 2, alternative mating designs should be developed to control inbreeding in the long term. The expected inbreeding coefficient of young bulls in AI programs is half the relationship of their parents. Some of these young bulls will reach the status of a proven sire and they will have a sustained impact on inbreeding coefficients of the complete German Holstein population. In cattle breeding, the extensive use of relatively few sires can generate very large families counting hundreds or even thousands of descendants. This inbreeding presents a major concern since recessive disease-causing alleles are rapidly transmitted to a large number of offspring as it was the case for CVM by the wide spread use of the influential bull sire Carlin-M. Ivanhoe Bell. In conclusion, to control relationships among animals on the bull dam and the bull sire path of selection seemed to be the best and easiest approach for implementation of new breeding designs. Meuwissen and Goddard (1997) considered the control of inbreeding during the selection of young bulls entering AI programs in terms of corrected EBVs according to the mean relationship among selected animals. The main relationship between selected bulls decreased from 0.393 to 0.308, but selection response was slightly lower (1.098 vs. 1.054). Weigel and Lin (2002) used the method of Meuwissen (1997) and constrained the level of inbreeding in the next generation and found that the optimal number of bull sires and bull dams decreased as the inbreeding constraint increased, particularly at low levels of inbreeding. Weigel and Lin (2000) compared the weighted mean lifetime net merit and the weighted mean adjusted lifetime net merit of the selected group. The weighted mean lifetime net merit after adjustment to zero using a cost factor of $23 per 1% inbreeding as proposed by Smith et al. (1998) was highest at an intermediate level of inbreeding. Colleau et al. (2004) applied optimal mating methods for the procreation of young bulls to be progeny-tested, for the use of service bulls on non-elite cows and in a third distinct step for selection of AI bulls among all progeny tested bulls. At each step, the objective was to minimize the average pairwise relationship coefficient applying dynamically rules in a single step. The method implies that selection of matings was directly targeted and selection and contribution of parents were post determined with and without an economical constraint. Similar to our results and similar to other studies utilizing the OGC-theory (i.e. Meuwissen, 1997; Kearney et al., 2004), a substantial decrease of the average relationship coefficient would have been possible at each selection step without penalizing the average EBV. Kearney et al. (2004) investigated the association between optimised contributions and index scores for three levels of constraints on inbreeding for selected males. As the constraint relaxed, fewer sires were required and the differences in contributions among selected sires increased. They also pointed out that at severe constraints, the males with highest EBVs do not necessarily have the highest contributions. These findings are in accordance with our results comparing scenarios at 4% and 10% constrained relationship. At the lower constraint, the number of selected males increased from 9 to 21 with relatively equal contributions per sire from 3.7% to 6.8% and eliminating one superior sire having a contribution of 20% in the less stringent scenario allowing 10% for the constrained relationship.

Differences in contributions of bull sires with and without a correction of EBVs on zero inbreeding were negligible considering the stringent restriction at 4% average relationship. There were only a few sires fulfilling this stringent requirement considering long term relationships and these sires were relatively equally suggested for the mating plan. A more relaxed constraint at 10% average relationship and utilizing inbreeding adjusted EBVs resulted in greater impact on genetic contribution of sires. Sires highly related to the pool of bull dams now will have a greater chance to contribute to the next generation. Apart from the optimum genetic contribution theory, the routine correction of EBVs on zero inbreeding should be taken into consideration for the official estimation of breeding values.

In conclusion, optimised selection theory seems to be a promising tool to achieve higher genetic gains at the same rate of inbreeding, or in lower rates of inbreeding at the same gain when compared to conventional selection schemes ignoring relationships. At the same level of relationship, the mean EBV of selected parents was 13.1% above the results from the conventional selection scheme applied in the practical breeding program. Simulation studies showed improvements in genetic gain greater than 20% over BLUP truncation selection at the same rate of inbreeding (Meuwissen, 1997; Grundy et al., 1998). Avenado et al. (2003) have demonstrated for a population of sheep and a population of beef cattle that the optimisation tools constitute a highly effective way of managing genetic gain and inbreeding. As found in our study, more relaxed constraints on increase in inbreeding allowed even higher expected genetic gain in both populations. The decision how much increase in inbreeding per generation should be allowed is really difficult to predefine. Wooliams et al. (2002) have described the rate of inbreeding as a measure of risk from the perspective of the breeding program justifying its management with arguments that go beyond avoiding inbreeding depression and loss of genetic variation in the selected trait.

5. Conclusion

Inbreeding coefficients of German Holstein cows were below 2% and for highly selected elite cows slightly below 4%. But nevertheless, the control of relationships between elite matings seemed to be an essential tool to manage the level of inbreeding in the population in the long term because particular famous bulls were highly related to their breed and relationships about 8% were found between potential bull dams and bull sires. Application of optimum genetic contribution theory was applied for a practical breeding program for matings between bull dams and bull sires and at the level of tolerated relationships between selected candidates, OGC showed about 13.1% higher genetic gain compared with the practical conventional selection scheme. In conclusion, the optimum genetic contribution theory in combination with specific mating plans seemed to be a promising tool to control relationships in the long and inbreeding in the short term in practical livestock populations. This work demonstrates that the application of dynamic optimisation tools allows the management of inbreeding without any concomitant loss in genetic gain. However, the approach seemed also to be valid for conservation purposes in which the aim may be to minimize the inbreeding rate while achieving a predefined level of genetic gain. A first attempt to manage inbreeding in the German Holstein population could be to publish the average relationships of each sire to the population as it is common practice in Canada or in the United States.

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