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EVALUATION OF GENETIC ANALYSES AND SELECTION STRATEGIES FOR THE IMPROVEMENT OF FUNCTIONAL TRAITS IN DAIRY CATTLE

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SUMMARY

The overall aim and content of this thesis is reflected by the title: "*Evaluation of genetic analyses and selection strategies for the improvement of functional traits in dairy cattle"*. The thesis is divided into eight chapters.

CHAPTER I starts with a general discussion summarizing the current status of functional traits in dairy cattle breeding programs, providing some theoretical background for the analysis of categorical data and repeated measurements, and finally suggesting some ideas for the implementation of sustainable breeding strategies.

In **CHAPTER II**, generalized linear mixed models (GLMMs) with a logit link function were applied for the genetic analysis of four different claw disorders. Estimates of heritabilities ranged between 7.3% and 11.5%, and all claw disorders were highly correlated among each other. Genetic correlations among disorders and test day milk yield ranged between 0.06 and 0.37, indicating a physiological antagonism between production and health. Claw disorders were genetically positively correlated with conformation traits related to feet and legs. However, as shown by selection index calculations, a substantial reduction of incidences for claw disorders is only possible when applying direct selection strategies.

The range of heritabilities of these claw disorders and genetic correlations with production traits were confirmed in **CHAPTER III** when applying threshold methodology in a Bayesian framework. Estimates from a linear model were relatively similar, but turned out to be inferior according to the BIC when compared to threshold models. A new perspective in the field of dairy cattle breeding is provided through the application of recursive models. Relationships between four different claw disorders and test day milk yield were analyzed in a Bayesian framework by fitting recursive linear and recursive threshold models to data from 5360 Holstein cows. A two-way causal path was postulated describing first the influence of test day milk yield on claw disorders and, secondly, the effect of the disorder on milk yield at the following test day. Heritabilities of disorders were slightly larger when applying recursive threshold models compared to linear recursive models. Posterior means of genetic correlations between level of milk yield at individual test days and disorders ranged between 0.16 and 0.43, suggesting that breeding strategies focussing on increased milk yield increase susceptibility to claw disorders. Structural coefficients in the model described recursiveness at the phenotypic level. The increase of disease probability per 1 kg increase of test day milk yield was between 0.003 and 0.024.

Structural coefficients ranging between –0.121 and –0.670 predict that one unit increase in the incidence of any disorder results in a reduction of milk yield by up to 0.67 kg per day.

Genetic analysis of fertility traits was the main subject in **CHAPTER IV**. GLMM-Possion models were applied for count traits related to embryo transfer (ET) in donor cows, and threshold methodology was used for the genetic analysis of pregnancy in recipients. Several theoretical investigations suggested the application of MOET breeding schemes, but their success often failed due to limited number of offspring per donor. Based on the estimates for heritabilities (e.g. 0.23 for flushed ova), it was suggested to include traits related to ET in a combined breeding goal for potential bull dams. In analogy to the claw disorders, a genetic antagonism was found between functional traits (e.g. transferable embryos) and production traits (305-d lactation milk yield). In a synergistic model considering several genotypes simultaneously, the impact of the genetic parents on pregnancy of recipients was investigated. The direct heritability for pregnancy in the recipient after ET was 0.056, whereas the relative genetic impact of maternal and paternal components on pregnancy of recipients describing a donor's and a sire's ability to produce viable embryos was below 1%. The genetic correlation between the direct effect of the recipient and the sire of embryos for pregnancy after ET was -0.32, and -0.14 between the donor cow and the recipient. These results suggest that sires which should be preferred in selection for the improvement in conception ability were not inevitably the best when considering pregnancy of recipients.

Inclusion of aspects of behavior and temperament in dairy cattle breeding programs can contribute to improve labor efficiency in dairy cattle farming. Especially the increasing use of automatic milking systems (AMS) in Germany demand such cows that go voluntary in the milking box. Fifteen farms located in Northwestern Germany with the same type of AMS were used in the study in **CHAPTER V** to estimate genetic parameters for the trait 'voluntary visits in the AMS = milking frequency per cow and day'. Repeated measurements were the average visits of cows on different test days in the milking box within different periods of days in milk (period 1 = calving to day 100, period 2 = day 101 to day 200, period 3 = day 201 to day 300). Genetic components were estimated defining different covariance structures for the repeated measurements. According to AIC, the autoregressive (AR(1)) covariance structure was superior to the compound symmetry (CS). Heritabilities for milking frequency per day applying the AR(1) structure for different periods for days in milk ranged between 0.16 and 0.22. This moderate heritability estimated from objective measurements indicates the general possibility for selection on behavior in dairy cattle.

Traditional dairy cattle breeding programs in Germany do not consider the status of inbreeding or relationship when selecting bull dams and bull sires, and when defining specific mating strategies among them. The increase of inbreeding as outlined in **CHAPTER VI** can contribute to increase the frequency of involuntary cullings (due to fertility, mastitis and claw disorders) of cows. Optimum genetic contribution (OGC) methodology was applied for the selection of bull dams and bull sires using data from one German Breeding organization. At the level of tolerated relationships among selection candidates, OGC revealed an additional 13.1% genetic gain compared to the current selection program. Applying a simulated annealing algorithm to develop specific mating schemes leads to a reduction of the inbreeding coefficient in the next generation of about 66.3% compared to the one resulting from random mating. Hence, the implementation of OGC in dairy cattle breeding programs is strongly recommended.

The development of controlling or monitoring instruments is of increasing concern in several fields of agriculture. In **CHAPTER VII**, a controlling value, defined as the ratio of realized and expected selection intensities for cow sires, was developed. The controlling value indicates the effectiveness of cow sire selection for different traits (estimated breeding values). Especially for functional traits such as longevity, somatic cell score, and the complex of fertility, a more intensive selection was suggested. More than 60% of artificial inseminations in the German Holstein dairy cattle population resulted from cows sires from the regional breeding program. Hence, the application of a more stringent selection of cow sires for functional traits will strongly influence the genetic level in the whole cow population in these functional traits.

A general discussion about the results and the applied statistical methodologies from the previous chapters, and some further prospects and concerns for dairy cattle breeding programs based on advances in moleculargenetics, are given in **CHAPTER VIII**. As shown in this thesis, there is potential for breeding towards functional traits in German Holstein dairy cattle. The basic requirement is to set up a suitable recording system, then to apply the best methodology for genetic evaluation, and finally to define the optimal breeding strategy including controlling tools. However, the genetic part only represents about 10% of the total phenotypic variation among animals. 95% of the total variation in fertility, 90% of the variation in health, or 80% of the variation in behavior is due to the environmental impact. The individual herd management predominantly describing husbandry and feeding strategies was the most important factor when analyzing claw disorders, pregnancy, or behavior as well.

CHAPTER I

INTRODUCTION

Functional traits: Importance and current status in breeding programs

Definition and importance

In a review by Mark (2004), functional traits are defined as those characters of an animal that increase farming efficiency not by higher outputs of products, but by reduced costs, which is the classical definition by Groen et al. (1997). As pointed out by Bishop et al. (2002), the economic burden only due to infection diseases amounts to nearly 20% of the total output value in animal production. Beyond theses economic reasons, concerns for animal welfare, directions of the law (e.g. § 1 German law for animal breeding; § 11b German law for animal protection) as well as demands of consumers enforce the implementation of functional traits in breeding goals (Simianer and König, 2002).

As shown by the annual statistics published by the German Cattle Breeders Federation, the average productuion level in lactation milk yield increased by an average of 100 kg per year and reached a current level of 8,524 kg (ADR, 2005). Fleischer et al. (2001) examined the realtionship between milk yield and incidence of certain disorders in German Holstein cows. An increase of milk yield was generally associated with an increased risk for the occurrence of any type of disease (Table 1). Results were verified by recently published trends for production traits and diseases in Norwegian dairy cattle obtained from a long-term selection experiment (Heringstad et al., 2007).

Table 1. Probability (in %) of appearance of some diseases dependent on 305-d milk yied (according to Fleischer et al., 2001)

	305-d milk yield (in kg)			
	6,000	8,000	10,000	12,000
Retained placenta	7.0	8.5	12.5	17.0
Metritis	18.5	19.5	22.5	25.5
Ovarian cysts	8.5	13.0	19.5	27.0
Mastitis	18.0	25.0	34.5	38.5
Claw disorders	16.5	21.0	26.0	32.0
Milk fever	2.0	3.0	4.0	5.0

Increased income based on higher milk yield per cow and year can be eroded due to increased costs. For example in the case of claw disorders, Esslemont (1996) calculated an economic loss due to to lameness of 615 € per cow and year: 65 € additional veterinary costs, 30 € for increased labour time, 240 € replacement costs, 205 € for the extended calving interval, 50 € for the decrease in milk yield, and 25 € for discarded milk. The negative impact of increased somatic cell count on dairy cow profitability for a 30 head dairy cow farm was given by Zeddies (1997). Results of his study are summarized in Table 2.

Table 2. Additional costs for different levels of somatic cell count for a German dairy cattle farm consisting of 30 Holstein cows according to Zeddis (1997).

	Somatic cell count			
	200,000	300,000	400,000	500,000
Cases of clinical mastitis / year	18	19	20	20.5
Involuntary cullings due to mastitis (cows / year)	2.10	2.22	2.30	2.33
Prohibition of milk delivery (€ / year)	0	0	665	997
Decrease in milk yield (in %)	6.6	8.6	10.0	11.0
Decrease in milk yield (kg / year)	12,870	16,770	19,500	21,450
Loss in marginal return due to the decrease in milk yield (€ / year)	2,025	2,572	2,991	3,290
Veterinary costs (€ / year)	460	485	511	524
Loss due to discarded milk (€ / year)	552	582	614	629
Increased labour (€ / year)	230	243	256	262
Replacement costs (€ / year)	357	378	392	397
Total loss in the dairy cattle herd (€ / year)	3,574	4,262	5,422	5,767
Total loss per diseased cow (€ / cow)	198	224	271	281

Functional traits in current breeding programs

In a recent study, Miglior et al. (2005) compared national selection indices for dairy cattle of 15 countries and the average relative emphasis on production, durability-health, and reproduction was 59.5%, 28%, and 12.5%, respectively. In Germany, the relative weights of the sub-indices

RZM (production), RZE (conformation), RZS (somatic cell score), RZZ (fertility) and RZN (longevity) in the overall index RZG are 50%, 15%, 5%, 5%, and 25%, respectively. There still is a high weight of nearly 60% on production suggesting antagonistic relationships between productivity and functionality. Examples of the antagonistic relationships between production and functional traits estimated in Scandinavian Holstein populations are given in Table 3.

Table 3. Examples of antagonistic genetic realtionships between production and functional traits

Trait	Genetic correlation	Author
Clinical mastitis	0.43	Heringstad et al., 2005
Clinical mastitis	0.45	Carlen et al., 2004
Interval from calving to first insemination	0.47	Andersen-Ranberg et al., 2005
Non-return 56 d	-0.18	Andersen-Ranberg et al., 2005
Somatic cell count	0.23	Carlen et al., 2004
Disease liability	0.57	Jakobsen et al., 2003

However, currently effort is made by various breeding organisations for the inclusion of additional functional traits in a combined breeding goal for dairy cattle. When comparing breeding goals over the last two decades, the emphasis of dairy cattle breeding objectives has gradually shifted from production traits towards functional traits such as fertility, longevity and calving traits (Mark, 2004). The main problem in the past for the inclusion of functional traits in the breeding goal was the lack of appropriate data, and in most cases, indirect measurements were used. In the case of udder health, RZS is used as an indicator for mastitis, but Heringstad et al. (2000) found an average estimated genetic correlation between somatic cell count and clinical mastitis of only 0.6 based on several values from the literature.

Considering longevity (RZN) in breeding programs is associated with another problem. Some of the daughters of a bull are still alive in the moment of genetic evaluation, and incomplete knowledge of their herd life does exist (Vucasinovic et al., 2002). These observations are defined as so called "censored data". Excluding these data from the genetic evaluation would bias estimated breeding values for longevity of bulls. Another possibility would be to wait until all daughters of a bull are culled. However, such a selection strategie for longevity is inefficient, because generation intervals substantially increase (Vucasinovic et al., 2002). This problem is solved in most genetic evaluations for functional longevity due to the application of survival analysis (Ducrocq, 1987). Survival analysis combines information of dead (uncensored) and alive (censored) animals. This method is implemented in the ‘Survial Kit’ (Ducrocq and Sölkner, 1998). The software 'Survival Kit' allows a combination of direct survival measurements and other indicator traits related to survival. Buenger et al. (2001) used the ‘Survial Kit’ for longevity analyses in the German Holstein dairy cattle population. Among all type traits, they identified udder and feet and leg traits as particularly valuable, early predictors for longevity.

Early prediction of longevity through type traits is associated with another problem. The question remains if the subjectively scored type traits are the best solution when evaluating longevity. Beside the subjective classification for type traits, several studies (e.g. Gengler et al., 2006) focused on the problem of heterogeneity of variance and covariance components. 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. The impact of heterogeneous variances on estimated breeding values for production traits in Germany is described in several studies (e.g. Gernand et al., 2007). However, for production traits, more daughters per bull, larger contemporary groups, and objectively measured traits can minimize this problem.

Selection for higher milk yield has led to a substantial decline in fertility due to the unfavorable genetic correlations or antagonistic relationship between production and reproduction traits (Price et al., 2004). Annual statistics published by the German Cattle Breeders Federation (ADR) showed that more than 25% of cow disposal reasons were attributed to reproductive failure. As a consequence, among all functional traits, fertility was the first to be included in the overall breeding goal in German Holstein dairy cattle, and it is officially evaluated since 1995. The reproduction sub-index (RZZ) is defined as an index combining the direct and maternal EBV for calving ease, stillbirth and non-return rate after 90 days. However, there is no selection pressure on these traits. When evaluating genetic trends in dairy cattle (Schmidtko et al., 2006), there still is a slight decrease or stagnation in EBVs for fertility traits. Additionally on the phenotypic scale, involuntary cullings due to fertility still increase. Further attempts to improve reproductive performance consider additional fertility traits in breeding programs such as age at first calving, interval from calving to first service, gestation length and calf size, and distinguish between heifer and cow fertility for genetic evaluation (Jamrozik et al., 2005). The main problem associated with genetic evaluation for fertility traits seemes to be associated with data quality. Traits describing pregnancy, e.g. non-return rates measured at 56 or 90d after a first insemination, do not account for cow cullings or matings done by natural service bulls. Results from statistical analysis related to fertility in dairy cattle are likely to be different when information of true pregnancy, e.g. rectal palpation done by veterinarians, is available (König et al., 2006). In addition, the impact of maternal and paternal components of inheritance increases the complexity of statistical models when evaluating fertility traits. Many studies have shown an antagonistic relationship between milk production and fertility. This is especially the case between milk yield measuring during the high yielding period, and cow (= female) fertility (Muir et al., 2004). Many different criteria have been used to estimate persistency (see e.g. Swalve and Gengler, 1999), but none are optimal or generally implemented into genetic evaluation systems. Through the application of random regression models for test day yields as applied in most countries, lactation curves for each parity of every cow can be estimated. Therefore, one specific measure of persistency within lactations could be based on the shape of the lactation curve after identified peaks as applied in some previous investigations (e.g. König et al., 2007). However, low genetic correlations for persistency across lactations (Jamrozik et al. 1997), even when using results from random regression test day models, complicate the interpretation and the application of EBVs for persistency in practical breeding programs.

Milking speed and temperament of dairy cows is strongly related to labour time in dairy cattle farming (Devir et al., 1993). Both traits are also classified as functional traits, and they have been inlcuded in the national German genetic evaluation since August 2004. Data for milking speed are a combination from time measurements of milk flow and subjective impression by the herdsman. In the Western regions of Germany, mainly subjective classification can be found, sometimes supported by measurements of milk flow. In large-scale farms in Eastern Germany, scoring and knowledge of individual cows is difficult, and mainly milk flow measurements are used. The owner or herdsman also provides information about temperament of cows during the procedure of linear scoring for conformation traits. Subjective scores are related to the following attributes: Very nervous, nervous, average, calm, or very calm. When Leitch (1994) reviewed world selection indices for dairy cattle, the main question she dealt with was the relative emphasis on production and type. As indicated above, within a few years, this has changed completely, and several functional traits are considered in dairy cattle breeding objectives. The focus today is the ratio of production and functionality. However, the weights of sub-indices for functional traits in the overall breeding goal are comparably low. The main problem is the lack of appropriate data for the genetic evaluation of functional traits wich are mainly based on indirect measurements. A substantial improvement for functionality in acceptable time can only be achieved via direct selection on various diseases as recently shown by König and Swalve (2006) when evaluating different selection strategies. Examples for some functional traits which have recently been, or will be analyzed in research projects, are summarized in Table 4.

Table 4. Examples for the direct recording of functional or health traits of the next generation. Adopted from Mark (2004) and modified to the German situation.

Trait	Value	Recording possibility
Body condition score	Positively correlated to health and fertility	Type classifiers
Locomotion	Correlated with claw disorders	Type classifiers
Claw disorders	Direct impact on costs (e.g. labor, discarded milk, treatment)	Claw trimmers
Temperament, activity	Direct impact on labor costs, indicator for oestrus	Online; requires high-tech parlors or AMS or pedometer
Clinical mastitis	Direct impact on costs (e.g. labor, discarded milk, treatment)	Veterinarians
Temperature of milk	Indicator for fever or oestrus	Online; requires high-tech parlors or AMS
All other diseases (ketosis, displaced abomasums, milk fever)	Direct impact on costs (e.g. labor, discarded milk, treatment)	Veterinarians
Feed intake (efficiency)	Direct effects on costs and health	Only in special herds (on station test for bull dams, cooperator herds for progeny testing)
Weight of calf	Correlated with calving ease	Cooperator herds for progeny testing

The direct, accurate recording of health traits is a prerequisite for genetic evaluation, and such a system is practiced in the Nordic countries for more than 30 years. Traditionally, the Scandinavian countries have a leading position in registration and collection of information about new health traits (Mark, 2004). Health data collected via veterinary systems are integrated in the national electronical database system. A detailed overview about the recording system for health traits and the procedure from data collection up to genetic evaluation is given by Heringstad et al. (2000), and most of genetic parameters related to diseases are from Scandinavian dairy cattle (Table 3). Simianer and König (2002) compared the success of several breeding programs across countries. They identified a substantial advantage in selection response for udder health for the Scandinavian countries due to the direct recording and selection on mastitis. Modern technology gives new recording opportunities for functional traits.

Estimation of genetic parameters for categorical traits

The general threshold concept

In animal breeding, the major tasks of data analysis are estimation of the breeding values of animals and of genetic (co)variance components. Luo et al. (2001) indicated that many studies have also used linear models for genetic analysis of traits that are recorded with discrete categories, although such data are not normally distributed. Most traits related to functionality or health (Table 2) are characterized by specific distributions which are not Gaussian. In the case of counting variables (e.g. counting the occurrence of disease within a specific time period), the distribution is Poisson. A categorical trait phenotypically shows distinct categories. For two categories, as mostly the case for diseases, the trait is a so-called "binary trait". The distribution of a binary trait is Binomial.

Also for categorical traits, many genes might be involved in an infenitesimal model (= polygenic model of inheritance; Schaeffer, 2006a). This implies that the underlying susceptibility to a disease trait is considered to be continuous and to follow a normal distribution. Schaeffer (2006a) explained the threshold concept: The underlying scale is defined as the liability scale. On this liability scale is a threshold point (for a binary trait), or several threshold points for a categorical trait phenotypically expressed in more than two classes. Assuming a binary disease, the animal expresses the disease phenotype above the threshold point. The only other possibility is the case that the animal does not express this disease (below the threshold point). This general concept for the analysis of categorical data using the "liablity concept" as introduced by Gianola and Foulley (1983) is of principal relevance for statistical applications and interpretations of results from quantitative genetic analyes of functional traits, and this basis is used for extensions in CHAPTERS II, III, and IV. Hence, due to the central relevance in the present thesis, the most important features of a threshold model are given in detail below. According to Schaeffer (2006a), these features and characteristics for settting up and solving the mixed model equations are:

The general linear model in matrix notation is

$$y = Xb + Zu + e$$

where y = vector of observations representing a variable on the unknown underlying, unobservable liability scale. This unknown y is affected by fixed effects (vector b), random animal effects (vector u), and the random residual component effects e. The incidence matrixes for fixed and random effects are X and Z, respectively. The analysis is a simultaneous estimation of the threshold points, fixed effects, and random effects from the data solved in a set of non-linear estimation equations. Starting values of the thresholds have to be chosen, and they are used to estimate y. In the ongoing process, estimates for y are then used to estimate new threshold points as well as effects in vectors b and u. The estimation procedure is finished until the threshold points are stable within a predefined convergence criterion.

According to Schaeffer (2006a), for solving the equations, several parameters based on the normal (Gaussian) distribution function need to be computed in repeated steps. The cumulative distribution function $\Phi(x)$ determines the area under the Gaussian curve up to the value of x, whereas x is a value ranging from minus infinity to plus infinity. The height of the standard Gaussian curve (mean = 0, variance = 1) at the point for x is determined by $\phi(x)$. The probability of x lying between two threshold points, or in the distinct category k, is given by $P(k)$. Iteration is applied to solve the following set of equations:

$$\begin{pmatrix} Q & L'X & L'Z \\ X'L & X'WX & X'WZ \\ Z'L & Z'WX & Z'WZ + G^{-1} \end{pmatrix} \begin{pmatrix} \Delta t \\ \Delta b \\ \Delta u \end{pmatrix} = \begin{pmatrix} p \\ X'v \\ Z'v - G^{-1}u \end{pmatrix}$$

where again matrix X = incidence matrix for fixed and matrix Z = incidence matrix for random effects, and t = vector of threshold points at the end of each iteration. The change in solutions for t, b, and u between iterations is indicated by Δ. Accordingly, also the values of the matrices X, L, W and vectors p and v change with each iteration. The solution of the equations starts by choosing threshold values for t from the data, i.e. through the knowledge of the distribution of animals in different categories. The different steps how to solve this set of equations are also clearly described by Schaeffer (2006a), especially the details how to calculate the elements in the matrices Q and W, and vector v and p. For the estimation of variance components, Schaeffer (2006a) pointed to Harville and Mee (1984), who suggested a procedure within a restriced maximum likelihood (REML) framework. In a threshold model, the residual variance is usually fixed, i.e. to a fix value of 1. Hence, estimation of variance components "only" includes the variances of the other random effects. The generalized inverse of the coefficient matrix in the equations is (Schaeffer, 2006a):

$$C = \begin{pmatrix} C_{tt} & C_{tx} & C_{xx} \\ C_{xt} & C_{xx} & C_{xz} \\ C_{zt} & C_{zx} & C_{zz} \end{pmatrix}.$$

REML expectation maximization (EM) can be applied in an iterative process until convergence is reached. The estimator of variance of the random effect u is:

$$\sigma_u^2 = (u'G^{-1}u + tr(G^{-1}C_{zz}))/d\,,$$

where d = number of levels in u and $G = I\sigma_s^2$ or $G = \sigma_u^2$ if a sire or an animal model is being fitted. The heritability is estimated on the liability scale, but can be transformed in a binary case to the observed scale by the following formula developed by Robertson and Lerner (1949):

$$h_{observed}^2 = h_{liability}^2 z^2 /(p(1-p))$$

where p and z are the paremters describing the Gaussian curve (percentage of observations in one categories, and height of the curve at the truncation point, respectively).

However, the whole problem in genetic evaluation for threshold characters as described above seems to be Bayesian in nature. Proper starting values for vectors b, u, and t, respectively, have to be chosen. Methods by Harville and Mee (1983) have been evaluated e.g. by Hoeschele and Gianola (1989). As an alternative, "real" Bayesian statistics can be used instead of REML. Luo et al. (2001) focused on procedures such as the Gibbs sampler (Geman and Geman, 1984). Similar methods were shown by Wang (1998) for a general application in animal breeding. Also Sorensen et al. (1995) showed that the Gibbs sampler is a suitable method in a threshold model.

The generalized linear model

When applying threshold methodology, the link between the liability and the observed scale is the cumulative normal distribution function. In a binary case, e.g. for a disorder and given the diseased incidence π for this disorder, the inverse relationship determines the relationship between the threshold and the overall mean μ as follows:

$$\mu = \Phi^{-1}(1-\pi)$$

Generalized linear models (GLMM) were introduced by Nelder and Wedderburn (1972). The GLMM is a furhter extension of the linear mixed model that has been applied in animal breeding over decades. A GLMM's main feature is a link function that relates the mean of a population to a linear predictor (as shown in the equation above). Hence, GLMMS can be applied to a wide range of data analysis problems of non-Gaussian traits. Examples might be data that are not normally distributed or such kind of data, where variances increase with the mean. The linear equation $\eta_i = x_i^{'}\beta$ of a GLMM is identical with traditional linear models. A link function g specifies the relationship between the expected value of the response variable y_i and the linear predictor η_i:

$$g(\mu_i) = x_i^{'}\beta$$

The distributions, link functions and corresponding variance functions for GLMMs as used in CHAPTERS II and IV are given in Table 3.

Table 3. List of distributions, link functions and associated variance functions used in CHAPTERS II and IV

Distribution	Link function	Variance function
Normal	Identity $\eta = \mu$	$V(\mu) = 1$
Binomial	Logit $\eta = \log\left(\frac{\mu}{1-\mu}\right)$ Probit $\eta = \Phi^{-1}(\mu)$	$V(\mu) = \mu(1-\mu)$
Poisson	Log $\eta = \log(\mu)$	$V(\mu) = \mu$

Statistical analysis of longitudinal data

In animal breeding, there are more and more traits of interest recorded repeatedly per animal. Those repeated measurements, e.g. measurements on a time scale, are known as longitudinal data

(Schaeffer, 2006b). Phenotypic expression of those traits may change as time changes. Classical examples for repeated measuremtens are test-day production records of dairy cows, with obvious differences in milk production at the beginning and the end of lactation (Meyer, 2003). At different points during lactation, not only the means but also the variances of the trait are different. Also diseases occur at several points during the lifetime or in the course of lactation; however, the disease incidences are different among animals. As an explanation on a biological basis, there could be different genes that are responsible for phenotypic expression of a trait at different time points (Schaeffer, 2006b).

Earlier analyses treated such data simply as repeated records assuming homogenous variances (Meyer, 2003), and modeling a permanent environmental effect. Such a repeatability model is the "simplest" version to analyse longitudinal data, in which observations of the same animal are considered to be the same trait. Alternatively, for data spanning larger periods of time with obvious changes in means and variances, measurements in different periods are treated as different traits, and multivariate analyses should be applied (Meyer, 2003). For example, for production traits, 305-d yields in different lactations were considered as different traits in a multivariate genetic analysis. In general, animals are of different ages at different dates for measurements, and a multiple trait model should include a function to account for this. Kirkpatrick et al. (1990) proposed the use of covariance functions for this type of longitudinal data or repeated measurements in order to estimate variances and covariances of a longitudinal trait at or between different time point. Such type of analyes points to random regressions, where random effects (genetic effects and permanent environmental effects) can be depicted as deviations from a fixed curve (Schaeffer, 2006b). Schaeffer (2006b) espcially referred to Meyer (2000) and Pool et al. (2000), who compared many random regression models with different orders of orthogonal polynomials for the genetic and permanent environment effects. Kirkpatrick et al. (1990) recommended orthogonal polynomials, and the easiest way seems to be the application of Legendre polynomials of in general order two to four as done in most official national genetic evaluations.

Several reviews on the application of random regression models have been given, e.g. by Swalve (1995) or by Schaeffer et al. (2000). Through the application of random regression coefficients, it is possible to calculate daily additive-genetic as well as permanent environmental variances. However, also the residual effect is defined as a temporary environmental effect that may change (Schaeffer, 2006). Therefore, also residual variance should not be assumed to be constant within the observed time period. Residual variances can be modelled with a function of time, or residuals can be grouped into intervals and assuming equal variances within these intervals (Schaeffer, 2006).

Possible covariance structures for longitudinal data analysis and evaluated in CHAPTER IV for measurements in dairy cow behaviour, are compound symmetry (CS), unstructured (UN), and autoregressive AR(1) as described in detail by Littel et al. (1997). The CS structure implies that observations of the same animal have homogenous (co)variances and consequently, the correlations between all combinations of measures at different time points are the same. A major disadvantage of the CS covariance structure is the fact, that this structure is often unrealistic when the repeated measures are serial measurements, i.e. when the same response is measured over time (Dallal, 2007). Usually, consecutive measurements will be correlated stronger than measurements made farther apart. The AR(1) structure can handle these difficulties with serial data when the measures are equally spaced over time and considers lower correlations for measurements farther apart. Dallal (2007) also pointed out that in some cases for longitudinal data, no standard covariance structure seems appropriate. The UN structure specifies no patterns in the (co)variance matrix, and is completely flexible (Littel et al., 2000). The flexibility is associated with the drawback of having a very large number of possible patterns related to the structure of the residual variance-covariance matrix, and maybe resulting in longer computing time to solve mixed model equations. A further associated drawback might be related to failures when settig strict convergence criteria.

Sustainable breeding strategies

In addition to the implementation of data recording systems for functional traits and the application of proper statistical models for genetic evaluation, sustainable breeding strategies should be developed to ensure genetic gain in the long term. Selection index theory was applied in some studies (e.g. de Haas et al., 2001; König and Swalve, 2006) to determine additional genetic gain per year or per generation when using direct measurements instead of indicator traits. However, these studies focused on the improvement of only one single disease trait in the breeding goal. The evaluated breeding strategies considered different sizes of progeny groups and the variety of index sources. For multiple traits in a breeding goal and when applying selection index calculations, economic weights for these traits have to be derived. Additionally, as indicated by Nielsen et al. (2006), the concept of sustainability in agricultural production has received increasingly attention. Hence, nonmarket values such as the value of improved animal welfare or increased acceptance in society, have an impact on animal production and should be taken into account when deriving economic weights. The most common methods used to derive economic weights with the objective of maximizing the profit of the farmer or maximzing the profit in a production system do not consider the concept of sustainability. The first idea of adding a nonmarket value in the overall breeding goal was introduced by Olesen et al. (2000). A good overview of the literature showing the methods how to derive nonmarket values for traits in a breeding goal is given by Nielsen et al. (2006).

However, scenarios for breeding strategies as well as the utilization of most appropriate weights for traits in animal breeding programs do not consider the effects of any specific mating system on long term selection response. Especially for Holstein dairy cattle, and due to the easy implementation of artificial insemination, selection schemes worldwide are characterized by the widespread use of the same, genetically superior sires. This led to a substantial increase of inbreeding in the most important Holstein populations (Miglior, 2000), and to a decrease in the effective population size. For example, Weigel (2001) calculated a value of N_e = 39 for the effective population size of Holstein dairy cattle in the United States. The increased probability of pairs of alleles being identical by descent will result in a higher risk that detrimental recessive genes appear in offspring in the homozygous state. Additional selection response for functional traits based on expensive recording systems, best available statistical methods, and on optimal weights in an overall breeding goal, will be eroded in the long term due to inbreeding depressions.

Mating programs to select cow sires with lowest inbreeding coefficients are available for farmers. The minimization of inbreeding on the farm level is less powerful, because bull dams and bull sires are highly genetically related among each other. The control of relationships among elite matings (bull dams and bull sires) determine inbreeding coefficients of future progeny and will be a crucial part in dairy cattle breeding programs to ensure selection response in the long term. New methods are available for an optimal strategy considering both the maximization of genetic gain and minimizing genetic relationships in the long term, and furthermore specifying individual matings. This is the methdological background of the optimum genetic contribution theory, which first was theoretically described by Wooliams and Meuwissen (1993). A possible application of the optimal contribution theory in German dairy cattle breeding programs is introduced in CHAPTER VI and will be yet more relevant, if the reproduction performance of bull dams can be increased (CHAPTER IV).

In dairy cattle breeding programs, competition for semen sales has expanded from the national to an international market. The implementation of an international genetic evaluation for dairy sires in the middle of the eighties has significantly contributed to this circumstance. Hence, the objective of breeding organizations is to generate proven bulls that are genetically superior to maintain or to expand the market share of semen sales in a global market (Dekkers and Shook, 1990). Several strategies to increase the number of bulls over a fixed market threshold were discussed by Dekkers et al. (1996) for conventional breeding programs. Further tools or strategies offered by molecular genetics and new reproduction technologies in alternative breeding programs are summarized by Swalve and König (2007). Also within their national area, the first objective of breeding organizations should always be to improve the economic efficiency of dairy production by providing genetically superior semen at a low price to producers. The requirement for such an objective is a strong selection of proven bulls out of the pool of selection candidates after progeny testing according to their total net merit index. Due to the quantity of proven sires offered as cow sires for artificial insemination, Leisen (1999) assumed additional potential for the improvement of genetic gain in the whole population when reducing the numbers of cow sires. Efficient selection strategies, also for cow sires, require controlling tools, which can be easily implemented in the daily work routine of a dairy cattle breeding organization. In CHAPTER VII, a new method for the application of such a controlling instrument is suggested and evaluated.

Scope of the thesis

The scope of this thesis comprises several topics related to functional traits, from the evaluation of recording systems up to the application of controlling instruments in practical dairy cattle breeding programs. The different objectives of the complete thesis are outlined in the following 6 topics:

1.) The estimation of genetic co(variance) components for a magnitude of functional traits obtained from recently established recording systems, which are not considered in current dairy cattle breeding programs. Traits of interest were different claw and foot disorders

(CHAPTER II and CHAPTER III), traits related to embryo transfer in donor cows and fertility of recipients and its interactions (CHAPTER IV), and behavior measurements in automatic milking systems (CHAPTER V). Genetic correlations among these functional traits and other production as well as conformation traits were estimated to set up the most appropriate combined breeding goal.

2.) The application and evaluation of modern statistical methods for the evaluation of these traits, which are characterized by specific, non-Gaussian distributions. Generalized linear mixed model (GLMM) technique with a logit as well as probit link function was applied for the analysis of categorical traits, i.e. claw disorders (Chapter II) and pregnancy after embryo transfer (CHAPTER IV). Traits related to embryo transfer, such as the number of fushed ova, are count variables following a Poisson distribution. In this case, a GLMM with a poission distribution and a log link was applied (CHAPTER IV). In a second dataset of various claw disorders, genetic parameters were estimated via linear and threshold models in a Bayesian Framework (CHAPTER III).

3.) High milk yield may increase liability to any diseases and, in turn, the disease may affect milk yield adversely. These types of direct effects between phenotypes have not been considered in classical mixed model approaches, but can be inferred using the simultaneous and recursive models described in a quantitative genetics context by Gianola and Sorensen (2004). A simultaneous and recursive (SIR) model is one of the many members included in the general concept of "structural equation models", where the main objective is to introduce causal pathways. Recursive models in a Bayesian framework were studied using linear and threshold models for of test day milk yield and claw disorders (CHAPTER III).

4.) For the analysis of repeated measurements (longitudinal data), i.e. the voluntary entries of a cow in an automatic milking system (AMS) per day, different covariance structures were investigated (CHAPTER V). Selection of the most appropriate model was done comparing different information criteria.

5.) In addition to the application of selection index theory for finding the optimal combination of index sources in various scenarios (CHAPTER II) or the comparison of direct versus indirect selection response (CHAPTER II, CHAPTER III, CHAPTER IV), optimum genetic contribution (OGC) theory was applied to ensure selection response in the long term (CHAPTER VI). OCG balance selection response and relationship in the long term. Hence, the actual status of inbreeding in the German Holstein population as well as in the highly selected group of bull dams was evaluated, and detrimental effects of inbreeding on functional traits were also summarized (CHAPTER VI). Finally, a simulated annealing algorithm was applied to suggest specific matings between bull dams and bull sires in the case of one selection program (= breeding organization in Germany).

6.) Current selection strategies for proven bulls among the pool of test bulls for functional as well as for production traits were compared for the 14 different German dairy cattle breeding organizations (CHAPTER VII). A so-called controlling value was developed for practical applications in dairy cattle breeding programs to evaluate selection strategies as soon as possible. This method is flexible and also allows the implementation of controlling values for functional traits.

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CHAPTER II

GENETIC PARAMETERS OF CLAW AND FOOT DISORDERS ESTMATED WITH LOGISTIC MODELS

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ABSTRACT

The primary aim of this study was to estimate heritabilities for different types of claw and foot disorders and the genetic relationship of disorders with milk yield and selected conformation traits applying logistic models in Holstein dairy cattle. The study is based on data of 5634 Holstein cows kept in large-scale dairy farms in Eastern Germany. Dichotomous response variables were the presence or absence of the disorder in 2003. Cows that were less than six weeks in 2003 present in herds were excluded from the analysis. Incidences disregarding repeated measurements for digital dermatitis (DD), sole ulceration (SU), wall disorder (WD) and interdigital hyperplasia (IH) in rear legs were 13.2%, 16.1%, 9.6% and 6.3%, respectively. The herd effect was highly significant for all disorders. Incidences increased with increasing parities for SU and WD, but were highest among heifers for DD. High milk yield at the first two test days after calving was associated with a greater risk for claw and foot disorders in the same lactation. Estimates of heritability were 0.073 for DD, 0.086 for SU, 0.104 for WD and 0.115 for IH. Genetically, health problems appear to occur in clusters, i.e. a cow showing one disease has an increased genetic risk to show another claw disease. This phenomenon was also observed between claw and foot disorders and the somatic cell score. Genetic correlations between milk yield in early lactation and disorders were 0.240 for DD, 0.057 for SU, 0.270 for WD, and 0.336 for IH indicating a physiological antagonism. Correlations between breeding values for claw and foot disorders of bulls and official breeding values for functional type traits were mostly favorable. Routine recording of claw data will be a new chance to improve claw health within the population as was elaborated by different scenarios applying selection index procedures.

(**Key words:** Generalized Linear Mixed Models, claw and foot disorders, genetic parameters)

Abbreviation key: DD = digital dermatitis, **IH** = interdigital hyperplasia, **SU =** sole ulceration, **WD** = wall disorder, **EBVs** = estimated breeding values, **SCS** = somatic cell score

INTRODUCTION

As the level of milk production in dairy cattle increases, correlated increase of health problems need to be studied in more detail. Health problems result in higher culling rates, increased veterinary costs, and economic losses due to lower production and discarded milk. In recent years, research on health traits has focused on fertility and mastitis. In the Nordic countries for example, clinical mastitis has been included in dairy cattle breeding objectives since the late 1970s. Genetic evaluation is based on defining the trait as a binary response in a linear model (Heringstad et al., 2000). In Germany, inclusion of health traits in selection programs has been limited because of a lack of reliable data on disease events. In addition, the discrete nature of most disease observations makes their statistical analysis and interpretation more difficult (Mäntisaary et al., 1991).

In the last ten years, involuntary culling due to feet and leg disorders is of increasing relevance. As stated by Fatehi et al. (2003), results of a survey by the National Animal Health Monitoring System (APHIS, 1996) in the US reported that 15% of all cullings were directly due to lameness or leg injury. In Germany, disposals because of feet and leg disorders among all disposals were reported to be 3.2% in 1980 and 9.1% in 2000 as shown in annual statistics published by the German Cattle Breeders Federation (ADR, 1980; ADR, 2000). Enting et al. (1997) concluded that clinical lameness is one of the most costly diseases in dairy cattle. The economical loss due to feet and leg disorders in a one hundred cow herd in Great Britain was 8000 Euro per year on average (Esslemont et al., 2000). Much of the variability in feet and leg health is associated with environmental effects, but a few studies have revealed a genetic impact on such traits. An overview of published heritability estimates for different types of claw and foot disorders and related traits in different dairy breeds since 1990 is given in Table 1. Several papers have focused their investigations on locomotion or overall feet and leg problems. Detailed research on different claw and foot disorders including relatively large datasets comparable to our study was only done by Huang and Shanks (1995). Effective selection strategies require estimates of genetic parameters of claw and foot disorders. Correlations with other variables of economic importance are also required to allow the development of a combined breeding value for production and functional traits.

The intent of this work was to estimate heritabilities of some clinical claw and foot diseases of Holstein dairy cows kept in large-scale dairy farms in Eastern Germany and to measure genetic and environmental correlations between diseases and production traits. Milk production in dairy cows demands high energy input, and this input is missing to maintain e.g. the reproductive cycle (Fleischer et al., 2001). To assess the impact of physiological stress, much attention was given to the impact of milk yield at the beginning of lactation on claw and foot disorders in the following stage of lactation. Furthermore, estimated breeding values (**EBVs**) for claw and foot disorders of widely used sires were correlated with the official breeding values of these sires for some type traits. Results revealed to what extent claw and foot disorders are sufficiently covered by the type recording schemes implemented today in Germany.

Table 1. Heritability estimates for different types of claw and foot disorders and related traits in dairy cattle.

author	breed[1)]	No. of cows	model	trait	h^2
Boettcher et al., 1998	HOL	1342	Linear animal model	Clinical lameness	.10
			Threshold animal model	Clinical lameness	.22
Fatehi et al., 2003	HOL	53,736	Linear animal model	Claw uniformity	.03
Huang and Shanks, 1995	[2)]	1239	Linear animal model	Heel erosion	.13
				Sole ulcers	.03
				Interdigital dermatitis	.07
				Laminitis	.14
				Corkscrew claw	.05
				White line separation	.08
Lyons et al., 1990	HOL	9187	Linear animal model	Trimmed feet	.08
				Foot problems	.11
				Crampy	.11
				Locomotion	.11
Paget et al., 2004	JER	6590	Linear animal model	Locomotion	.22
	GUE	3838	Linear animal model	Locomotion	.17
Sander-Nielsen et al., 1996	DF	163,361	Linear sire model	Feet and leg diseases[3)]	.01
	RD	58,259	Linear sire model	Feet and leg diseases[3)]	.01
	DJ	31,559	Linear sire model	Feet and leg diseases[3)]	.001
Uribe et al., 1994	HOL	5217	Threshold sire model	Culling for leg problems	.15
Van Dorp et al., 1998	HOL	3190	Linear animal model	Lameness	.16
Van Dorp et al., 2004	HOL	3298	Linear animal model	Locomotion	.06

[1)] HOL = Holstein Friesian, JER = Jersey, GUE = Guernsey, DF = Danish Friesian, RD = Red Danish, DJ = Danish Jersey

[2)] 1239 cows of five breeds: Ayrshire, Brown Swiss, Guernsey, Holstein and Jersey

[3)] Feet and leg diseases include heel erosion, interdigital dermatitis, interdigital necrobacillosis, interdigital skin hyperplasia, laminits, arthritis, sole ulcer, pressure injuries and tenosynovitis of hoofs

MATERIALS AND METHODS

Materials

The data set comprised test day production records and claw and foot disorders recorded in 2003 from 5634 Holstein cows in 9 large-scale dairy farms from one region in Eastern Germany collected by 9 different hoof trimmers. The guideline for classification of individual claw and foot disorders was developed by the German Agricultural Society and all trimmers were trained for uniform identification of traits. Claw and foot diseases were divided into four different categories digital dermatitis (**DD**), sole ulcer (**SU**), wall disorder (**WD**) and interdigital hyperplasia (**IH**) (Figure 1) and analysed separately.

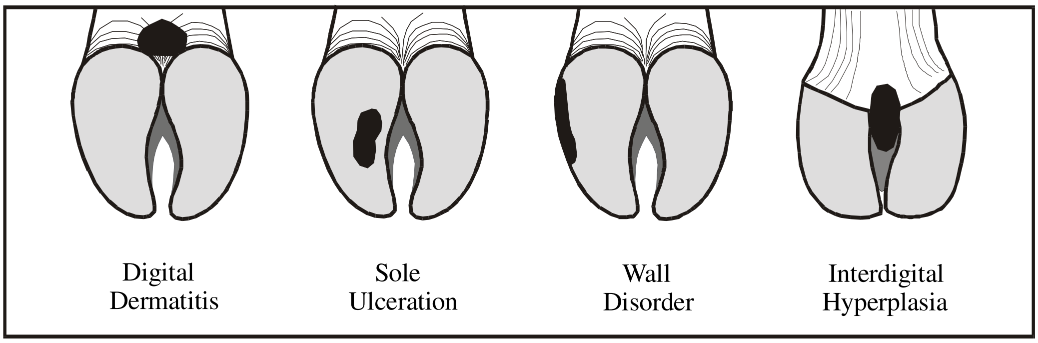

Figure 1. Localisation of investigated claw and foot disorders as defined for this study

IH and to a large degree, DD, are foot disorders that do not directly affect the medial or distal claw on each foot, whereas SU and WD belong to classical claw disorders. Wall disorder mainly describes the different types of white-line-disease and further lesions along the wall of the claw. A few specific cases of heel erosion were considered together with digital dermatitis, because both disorders are caused by bacteria. Disorders were scored on an all or none basis. If a cow had the health problem in one or both rear legs, she was given a score of 1, otherwise she was given a score 0. Repeated measurements of same claw and foot diseases were not taken into account and hence, no effects of lactation stage were considered in the model. Cows that were less than six weeks in 2003 present in herds were excluded from the analysis. Therefore, each cow was given a 6-week opportunity in 2003 to exhibit claw or feet disorders. Production traits were averaged from the first two test days of cows calving in 2003. This was done to define the production level in early lactation. The interval between two test days in the official German milk recording system is generally four weeks. Analogous to milk yield, somatic cell count (SCC) was averaged from first two test days after calving. The monthly test-day SCC was log-transformed into monthly test-day somatic cell score (SCS) to achieve normality and homogeneity of variances as: SCS = $\log_2$(SCC/100,000)+3 (Ali and Shook, 1980).

For 41 sires with at least 40 daughters in the claw database, correlations between EBVs of linear type traits (official national German EBVs from 02/2004) and breeding values of claw or foot disorders were calculated. Because the simple correlation between estimated breeding values for disorders and estimated breeding values for type traits does not fully reflect the genetic relationship between the traits, adjustments were made to approximate the genetic correlations.

Statistical Models

Because disorders were treated as binary traits, the residuals cannot be normally distributed. The best function to describe the relationship between the dependent and independent variables is not linear, but rather S-shaped. This is the primary reason why a linear logistic model with mixed effects was used. As described by Rodriguez-Zas et al. (1997) the probability of observing the event of interest (e.g., claw and foot disorder) was

$$\pi_i = \text{Prob}\,(Y_i = 1|\theta)$$

where θ is a parameter vector including fixed and random effects. The logit of the observation Y_i was

$$\log\left[\frac{\pi_i}{1-\pi_i}\right] = \eta_i$$

Since π is the probability of Y = 1, it follows that 1 - π is the probability of Y = 0 and so $\frac{\pi}{1-\pi}$ is the ratio of the two probabilities, which, when stated in the form of odds, gives the odds of having Y = 1. Any factor that increased η_i led to a concomitant increase in π_i. A linear model can be imposed on the vector of logits such that

$$\eta = X\beta + Zu$$

η = N x 1 vector of logits (N = number of observations)
X = N x p incidence matrix (p = number of levels of fixed effects)
β = p x 1 vector of fixed effects
Z = N x C incidence matrix (C = number of animals)
u = C x 1 vector of random effects

First analysis of variance of the measurements was carried out using logistic models implemented in the SAS glimmix macro (Wolfinger and O'Connell, 1993) that included the fixed effects of the herd and lactation number as well as a regression on milk yield up to the third polynomial degree in order to fit regression curves. Interaction between lactation number and milk yield in linear and exponential terms was also considered in model statements. Non-significant regression coefficients of different polynomial structure were removed from the model by using sum of square type I tests (Wald-type tests) and F-statistics at $P < 0.05$ rather than likelihood ratio tests. Sum of square type I tests provide a sequential analysis approach which is appropriate for polynomial formulated models. The F-ratios used in the analysis of variance are identical to the Wald/rank(K) F-statistics as defined by Littell et al. (1999). Wald-type tests were also used to identify significant fixed effects on claw and foot disorders (type III tests of fixed effects).

The final generalized linear model used to determine the impact of environmental effects and covariates on the incidence of disorders for WD and IH was:

$$\text{logit}\,(\pi_{rst}) = \log\left[\frac{\pi_{rst}}{1-\pi_{rst}}\right] = \eta_{rst} = \varphi + \gamma_r + \lambda_s + b_1 Y_{rst} + b_2 Y^2_{rst} + b_3 Y^3_{rst}$$

π_{rst} = probability of occurrence for claw and foot disorder of cow t in parity r and herd s

φ = overall mean effect

γ_r = fixed effect of parity

λ_s = fixed herd effect

Y_{rst} = average milk yield of test day 1 and test day 2 of cow t in parity r and herd s

b_1, b_2, b_3 = linear, quadratic and cubic regression of claw and foot disorder on milk yield

For SU, the linear regression gave the best fit, whereas for DD, the effect of milk yield was not significant at all.

The inverse link function is defined as $h(\eta) = \mu$. The inverse link was used to obtain predicted values of μ from the estimated β vector in $\eta_i = X\beta$. For the normal distribution, $h(X\beta) = X\beta$. For the binomial, $\eta=\log[(\pi/1-\pi)]$ and hence $\pi=h(X\beta)=\exp(X\beta)/\ [1+\exp(X\beta)]$.

Estimation of variance components was done using univariate animal models for REML and applying the package ASReml (Gilmour et al., 1998) including logistic link functions. The model for genetic analysis is extended to:

$$\text{logit}\ (\pi_{rst}) = \log\left[\frac{\pi_{rst}}{1-\pi_{rst}}\right] = \eta_{rst} = \varphi + \gamma_r + \lambda_s + \tau_t$$

π_{rst} = probability of occurrence for claw and foot disorder of cow t in parity r and herd s

φ = overall mean effect

γ_r = fixed effect of parity

λ_s = fixed herd effect

τ_t = random animal effect

Heritabilities were calculated using the variance of the logit link function. This implies a correction of the residual variance by factor $\pi^2/3$ (Southey et al., 2003). Estimates of random effects of animals (EBVs) were also calculated in a univariate model. The data set of EBVs of sires was subsequently edited such that each sire in the data set had at least 40 daughters. This editing for progeny group size of sires was to ensure that estimated breeding values of sires from this part of the analysis were sufficiently reliable. Bivariate analyses were carried out to estimate correlations between disorders and production traits, using a combined logistic and linear model. Fixed effects for the logistic and linear model were the same as for the univariate analysis. Genetic correlations between binomially distributed traits (claw and foot disorders) were also estimated via ASReml using the logit link function. Genetic correlations between normally distributed traits (milk yield, SCS) were estimated using the identity link function.

Approximate transformations of correlations between EBVs for disorders and EBVs for type traits into genetic correlations between traits was done as suggested by Calo et al. (1973) and Blanchard et al. (1983):

$$\tilde{r}_{g_{1,2}} = \frac{\sqrt{(\sum_i R_{i_1})*(\sum_i R_{i_2})}}{\sum_i (R_{i_1} * R_{i_2})} * r(EBV_1, EBV_2),$$

where R_{i_j} is the reliability of the EBV of bull i in trait j. Reliabilities for individual sires and different claw and foot disorders were calculated applying selection index procedures. Only progeny records of bulls were considered as information sources in approximate index calculations. For the interpretation of correlations between breeding values it is essential to know that higher values for official EBVs of type traits are generally favourable. For claw and foot disorders, low values of EBVs indicate genetically favorable bulls having fewer diseased daughters.

Utilized heritabilities for claw and foot disorders in index procedures were from results in the present study. Reliabilities for individual sires and different traits were in a range between 0.43 and 0.92, indicating the variation in the number of daughters per sire from 41 up to 637.

RESULTS AND DISCUSSION

Mean incidence

Table 2 gives an overview of mean incidences of claw and foot disorders in the complete data and in herds with highest and lowest incidences for each trait. Mean incidences of observed claw and foot disorders of Holstein cows on large-scale dairy farms were in a wide range as reported in the literature, mainly in veterinarian studies. Prevalences for lameness associated with SU or WD of 8 to 15% in US studies (Warnick et al., 1995; Wells et al., 1993) and an average prevalence of 20.6% in Britain (Clarkson et al., 1996) were reported. In our study, we found an incidence for SU of 16.1% and 22.1% of the cows were diagnosed for SU and/or WD. For DD, observed incidences (13.2%) were lower than found by Somers et al. (2003) in Holstein cows in the Netherlands. All investigated herds in the Netherlands were infected by DD, resulting in an average cow level prevalence of 30%. This indicates that the level of DD infection has increased considerably over the last 10 years in The Netherlands. The frequency of cows with at least one treatment because of feet and leg diseases was 6% in Danish Holsteins in a period from 0 to 4 month after calving and is therefore at a low level (Hansen et al., 2001). Smits et al. (1992) surveyed the prevalence of IH from 34 purebred and crossbred Holstein-Friesian and Dutch-Friesian herds. Incidences about 8.8% were slightly higher than found in our study. Huang and Shanks (2001) investigated claw and foot disorders on 4722 records of 1239 cows in five dairy breeds. The incidence of defect on any claw over a lifetime was 4.2% for IH.

Table 2. Incidences of different types of claw and foot disorders on large-scale dairy farms.

	Digital dermatitis	Sole ulcer	Wall disorder	Interdigital hyperplasia
Best herd	0.018	0.019	0.005	0.007
Average	0.132	0.161	0.096	0.063
Worst herd	0.418	0.324	0.185	0.167

As shown in Table 2, differences in claw and foot disorders between herds were remarkable. We have tried to explain such differences by information collected in herd management programs. This attempt was not successful. For example, the best and the worst herd for SU used identical management strategies: feeding total mixed rations, two hours pasture a day for lactating cows and the same husbandry system and floor surfaces. But nevertheless, manifold other risk factors and their interactions causing feet and leg disorders within strata can be assumed. Total mixed rations for example are varying with their ratios of roughage to concentrate, their protein supply or their supply of minerals, histamine and amino acids (cystine, methionine). Analysing these factors clearly was beyond the scope of this study. Herd's hoof care practices such as the frequency of trimming were identical in all farms.

Fixed effects and covariates

In the first analysis, fixed logistic models were used to determine the environmental effects on claw and foot diseases. Herd effect significantly ($P < 0.001$) affected all disorders, whereas parity was only significant on WD and SU ($P < 0.05$). As expected, incidences of these diseases increased with increasing parities (Table 3). Enevoldsen et al. (1990) found similar results when analysing sole ulcer occurrence in 23 Danish herds composed of 3328 Danish Black and White cows, which are comparable with Holstein Friesian. They reported SU-occurrence in one foot in 20.0% of cows in lactation 1 and in 23.5% of cows in lactation 2 to 9. Incidences of IH found by Smits et al. (1992) increased by parities and were 3.4%, 9.4% and 11.6 in parity one, two, and three or above, respectively. We found that heifers liability to DD was slightly above the incidence of adult cows, i.e. 13.9% in parity one and 12.5% in parity three and above. Also, an effect of selection is anticipated. Healthy cows have fewer disease problems and have a greater opportunity to reach the subsequent parity. Especially on large-scale farms in Eastern Germany selection pressure is high and replacement rates are increasing steadily (Bergfeld, 2004).

Table 3. Least-Square-Means for incidences of different claw and foot disorders stratified by parities.

	Digital dermatitis	Sole ulcer	Wall disorder	Interdigital hyperplasia
Parity 1	0.139	0.139^{a}	0.059^{a}	0.058
Parity 2	0.133	0.147^{a}	0.094^{b}	0.066
Parity >2	0.125	0.185^{b}	0.167^{c}	0.070

^{a,b,c} Different superscripts within column indicate significant differences (*P < 0.05).*

High milk yield in early lactation stratified for different parities was associated with higher incidences in SU, WD and IH as illustrated in Figures 2,3 and 4.

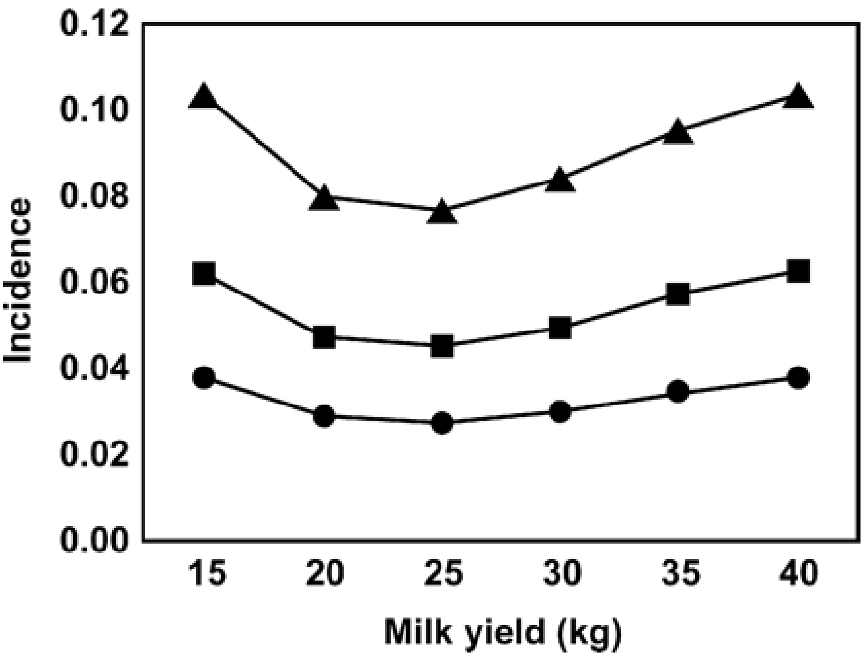

Figure 2. Incidences (Least-Square-Means) of wall disorders in parity 1(●), 2 (■), and 3 or later (▲) dependent on average milk yield (kg) of test day 1 and 2 after calving.

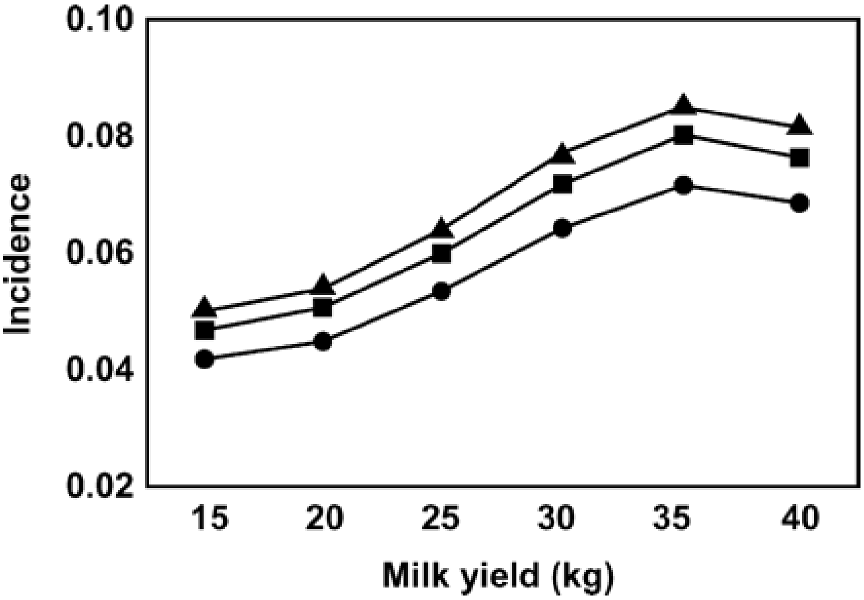

Figure 3. Incidences (Least-Square-Means) of interdigital hyperplasia in parity 1(●), 2 (■), and 3 or later (▲) dependent on average milk yield (kg) of test day 1 and 2 after calving.

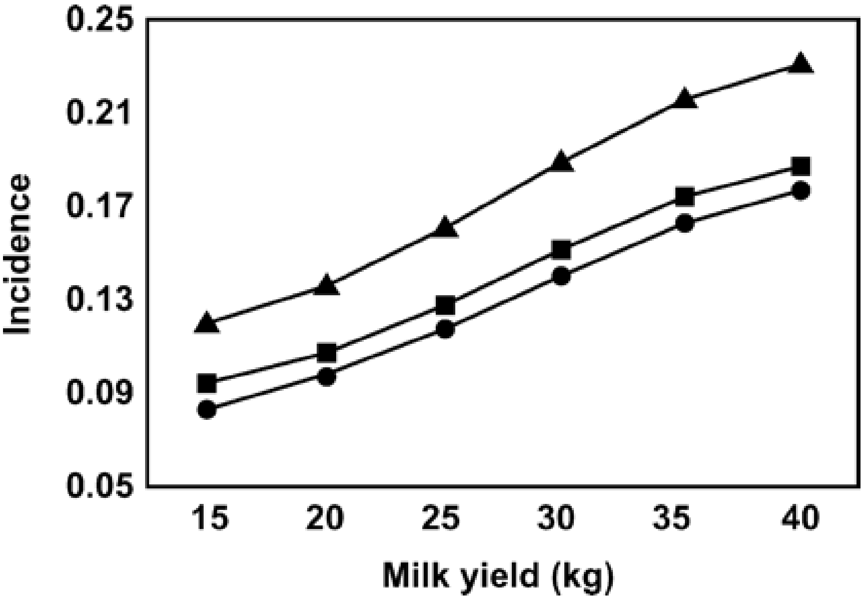

Figure 4. Incidences (Least-Square-Means) of sole ulceration in parity 1(●), 2 (■), and 3 or later (▲) dependent on average milk yield (kg) of test day 1 and 2 after calving.

The interaction between milk yield and parity was not significant on SU, WD, IH, and DD, respectively. Collard et al. (1999) have shown that high milk yield within the first third of lactation increases a cow’s risk to be affected with health problems. They concluded that metabolic stress occurs when the cow’s energy intake does not match its requirement and the cow is unable to compensate and mobilizes its body reserves too quickly. In their study, increased digestive and locomotive problems were associated with longer and more extreme periods of negative energy balance. In early lactation, cows are fed high energy diets with relatively low ratios of roughage to concentrate. Such a ration increases the risk of rumen acidosis and related disorders, which are expected to predispose the cow to laminitis. High body weight in combination with high milk yield have been postulated by Enevoldsen et al. (1990) as dominant risk factors for sole ulcers. In their study, fat-corrected milk at the first test day was used because it was expected to be high for those cows that were fed a high amount of concentrate relative to roughage immediately after calving. In the study of Fleischer et al. (2001), the 305-d yield from the previous and current lactations were used as the standard for milk yield. A higher estimated probability of appearance of claw diseases with increasing lactation yields in the current lactation was observed. On the other hand, severe lameness reduces a cow's ability for daily milk production. Warnick et al. (2001) investigated the effect of lameness on milk production in two New York dairy farms. In both herds, milk production decreased significantly for cows diagnosed lame. The decrease was largest for cows in second or higher lactation and when the degree of lameness was judged by farm employees to be more severe. In our data, 85% of diseased cows were first observed 60 days or more after calving. Therefore, the amount of milk yield from test day 1 and test day 2 after calving was less affected by actual claw and foot disorders.

Heritability estimates

Table 4 displays results of genetic analysis with respect to heritabilities and genetic correlations. Heritabilities for claw and foot disorders were in a range from 0.073 (DD) to 0.115 (IH). Maximum Likelihood procedures, which can be applied to estimate genetic parameters in logistic models were used in several investigations to analyze categorical mastitis data in dairy cattle (e.g. Rodriguez-Zas et al., 1997; De Haas et al., 2003). In general, heritabilities were slightly above estimates from linear models. As shown in Table 1, Huang and Shanks (1995) estimated heritabilities for different claw and foot disorders in linear and threshold models. Results of both models were similar.

Table 4. Heritabilities (diagonal) and genetic correlations (above diagonal) among disease and production traits. Standard errors of estimates in brackets.

	Digital dermatitis	Sole ulcer	Wall disorder	Interdigital hyperplasia	Milk yield	SCS
Digital dermatitis	0.073 (±0.009)	0.561 (±0.073)	0.337 (±0.139)	0.391 (±0.099)	0.240 (±0.145)	0.151 (±0.176)
Sole ulcer		0.086 (±0.006)	0.443 (±0.115)	0.498 (±0.112)	0.057 (±0.122)	0.276 (±0.159)
Wall disorder			0.104 (±0.0014)	0.668 (±0.111)	0.270 (±0.127)	0.187 (±0.173)
Interdigital hyperplasia				0.115 (±0.021)	0.336 (±0.140)	0.149 (±0.173)
Milk yield					0.277 (±0.031)	0.198 (±0.110)
SCS						0.093 (±0.019)

Heritabilities for sole ulcer, interdigital dermatitis and white line separation estimated in threshold models were 0.024, 0.013, and 0.150, respectively. White line separation is an avulsion or separation of the wall of the hoof from the sole and comparable with wall disorder in our study. In contrast, heritabilies for the individual diseases interdigital dermatitis (0.01) , interdigital necrobacillosis (0.00), laminitis (0.01) and sole ulcer (0.01) in Danish Holstein were low (Sander-Nielsen et al., 1996). Uribe et al. (1995) defined culling that is due to leg problems as a binomial trait, assuming an underlying threshold model that included fixed and random effects. Sire and residual components of variance were estimated by restricted maximum likelihood resulting in an estimated heritability of 0.14. To evaluate clinical lameness in 24 herds in Minnesota, Wisconsin and Virginia (Boettcher et al., 1997), cows were observed walking and were assigned a score between 0 and 4, where 4 = inability to walk. Estimates of heritability were 0.10 and 0.22 from the linear and threshold models, respectively. Paget et al. (2004) classified the linear type traits locomotion and feet and legs on a scale of 1 (poor) to 9 (very good). Heritabilities found in this study were 0.17 for locomotion in Guernsey and 0.22 in Jersey breeds. Heritability estimation for clinical lameness conducted by Van Dorp et al. (1998) in a total of 4368 first lactation records of Holstein cows from 30 herds was 0.16 and thus similar to results found by Distl et al. (1990). In the study of Lyons et al. (1991), heritabilities for individual locomotion traits using producer data supplied by dairy farmers from Wisconsin, Minnesota and Iowa were 0.14, 0.09, 0.20 and 0.09 for trimmed feet, leg problems, foot problems, and crampy, respectively. Heritability estimate of the health category locomotive was 0.16. Fatehi et al. (2003) estimated genetic parameters for claw traits in Canadian Holstein stratified by housing systems. Heritabilities for claw uniformity were 0.03 in a tie stall and 0.04 in a free-stall barn. Claw uniformity described the relative size of the outer and inner claws of the rear feet. High scores were associated with a uniform size of both claws and fewer disorders. Reported heritability estimates for IH were 0.31 in Simmental dual purpose cows (Baumgartner, 1988). In contrast, Greenough (1991) found no evidence for a genetic background of this disease in Holsteins.

Genetic correlations between disorders and production traits

In our study, most genetic correlations between disorders were large and positive (Table 4). Genetically, health problems appear to occur in clusters. The genetic correlations suggest that cows genetically susceptible to some type of health problems are likely to be susceptible to other health problems as well. In the analysis of Lyons et al. (1990), genetic correlations between health traits were positive except for reproduction with mammary and respiratory traits. In their study, the genetic correlation between locomotion and mastitis was 0.09. We found genetic correlations between SCS and individual claw and foot diseases in a range from 0.15 to 0.24 (Table 4).

Selection in dairy cattle has generally focused on increased milk yield, which can have an unfavorable effect on the occurrence of disease. Estimates of phenotypic and genetic correlations between 305-d milk yield and lameness of first lactation cows were 0.04 and 0.24 in a study conducted by Van Dorp et al. (1998), indicating an antagonism. Our estimates for genetic correlations between milk yield of the first two test days after calving and the susceptibility to claw and foot disorders ranged between 0.056 for SU and 0.336 for IH. However, standard errors were substantial. The positive genetic correlations indicate that selection or breeding on increased milk yield in the first stage of lactation increases the susceptibility to claw and foot disorders in the following lactation stage. Lyons et al. (1991) reported that the genetic correlations between 305-d milk yield and the susceptibility to all categories of health traits except reproductive disorders were positive. In detail, genetic correlations to milk yield were 0.48 for trimmed feet, 0.32 for leg problems, 0.31 for foot problems and 0.37 for crampy. Uribe et al. (1995) found that genetic correlations between culling for leg problems and production of milk, fat and protein were positive and moderate indicating that long-term selection for these traits might increase culling for impaired legs. Environmental correlations were negative. In our study, correlations between residuals were near zero. Sander-Nielsen et al. (1996) reported a high genetic correlation between digestive diseases and claw diseases in a range from 0.85-0.95. This might be due to the fact that the most common diseases in feet are caused by physiological problems.

Correlations with type traits

Correlations between estimated breeding values for claw and foot disorders and official breeding values for type traits of bulls are presented in Table 5. However, correlations between breeding values are not identical with genetic correlations unless accuracies of estimated breeding values are close to one. Therefore, results should only be interpreted as general trends, keeping in mind that correlations between breeding values are always an underestimation of genetic correlations. Using the approximation of Calo et al. (1973), approximate genetic correlations were calculated and are also given in Table 5. Genetically, favorable animals are characterized by less disorders or the absence of disorders and high scores for type traits. Not surprisingly, genetic correlations were mostly negative between conformation traits describing the structure of feet and legs and individual claw or foot disorders. For example, the genetic correlation between foot angle and sole ulcer is -0.29 and suggests that animals with steeper angles are less susceptible for sole ulcer. For practical breeding decisions, results of correlations are favorable. Wells et al. (1993) found a similar relationship between foot angle and clinical lameness on the phenotypic scale. They reported an odds ratio of 2.4 for a decrease of 10° in the angle of the rear lateral claw. Rear leg rear view is a trait with an intermediate optimum. Values less than 100 indicate steep legs which seemed to be favorable. We found that bulls that transmitted straighter legs viewed from the rear side had fewer daughters with claw and foot disorders. Phenotypic estimates from some studies indicate that cows slightly straighter than mid-ranged for rear legs side view might be most desirable (McDaniel, 1995). Cows with a higher feet and leg score, steeper foot angle, and straighter legs showed a genetically significantly better locomotion in an analysis conducted by Van Dorp et al. (2004). Applying linear and threshold models Boettcher et al. (1997) found that low foot angle, hocking in and wide rumps were mostly associated with clinical lameness.

Table 5. Correlations between disorders and conformation traits: Correlations between the percentage of healthy daughters and breeding values of conformation traits, correlations between breeding values (r_{EBV}), and approximate genetic correlations ($\tilde{r}_g$).

	Digital dermatitis			Sole ulcer			Wall disorder			Interdigital hyperplasia		
Linear scored type trait	% healthy daughters	r_{EBV}	$\tilde{r}_g$	% healthy daughters	r_{EBV}	$\tilde{r}_g$	% healthy daughters	r_{EBV}	$\tilde{r}_g$	% healthy daughters	r_{EBV}	$\tilde{r}_g$
Feet & leg score	0.39	-0.42	-0.55	0.41	-0.34	-0.45	0.59	-0.61	-0.81	0.58	-0.54	-0.72
Rear leg side view	-0.34	0.38	0.50	-0.46	0.37	0.48	-0.50	0.53	0.67	-0.49	0.36	0.44
Foot angle	0.44	-0.46	-0.61	0.26	-0.22	-0.29	0.29	-0.22	-0.28	0.37	-0.18	-0.22
Hocks	-0.03	0.02	0.03	0.23	-0.17	-0.22	0.44	-0.45	-0.57	0.21	-0.51	-0.63
Rear leg rear view	0.41	-0.37	-0.49	0.25	-0.24	-0.31	0.42	-0.54	-0.68	0.55	-0.40	-0.50
Stature	0.09	-0.16	-0.21	-0.13	0.17	0.22	0.03	0.08	0.10	-0.01	0.21	0.26
Dairy character	-0.03	-0.05	-0.07	0.07	0.08	0.10	0.25	-0.05	-0.06	0.09	-0.02	-0.03
Body depth	0.05	-0.06	-0.08	-0.08	0.18	0.23	0.06	0.03	0.04	-0.06	0.27	0.33
Strength	0.07	-0.05	-0.07	-0.24	0.25	0.32	-0.17	0.20	0.25	-0.11	0.27	0.33

Genetic correlation between clinical lameness and rear legs side view was essentially zero, indicating that neither posty nor sickled hocks were strongly associated with clinical lameness. Boelling et al. (2001) estimated genetic correlations between hoof measurements and claw diseases in future AI bulls and body conformation traits in their daughters of the breeds Danish Red, Danish Friesian and Jersey. The correlations between claw diseases of bulls and linear type scores of daughters for foot angle, rear leg side view, rear leg rear view and quality of hocks were either negligible or inconclusive. In our study, among the other type traits like stature, dairy character or body depth correlations were not significantly different from zero, but strong cows seemed to be at higher risk concerning SD, WD and IH. Boettcher et al. (1997) reported that genetic correlations between clinical lameness and body depth, strength, and rump width were moderate and positive, but correlations were close to 0 for stature. We found a correlation near zero between all types of claw and foot diseases and dairy character. Other studies (e.g. Hansen et al., 2001) reported antagonistic relationships between dairy character and other diseases except mastitis. They suggested that dairy character should be given a negative rather than a positive weight in the breeding goal.

Utilizing the phenotypic and genetic parameters obtained in the first part of the current study for sole ulcer and genetic parameters estimated by Bünger (1999) for foot angle, two different breeding scenarios were developed. This was done in order to combine type traits (foot angle) and claw disorders (sole ulcer) in selection index procedures. The alternatives included selection based on foot angle alone, which is common practice at the moment, sole ulcer, and a combination of both. The general breeding goal is to improve claw health within the Holstein population. Therefore, the only trait defined in the aggregate genotype was sole ulcer. Applying the selection index procedure using the SIP computer program (Wagenaar et al., 1995) and assuming 50 daughter records per sire, the correlation between the index and the aggregate genotype was calculated and compared for the three different scenarios. Assuming a standardized selection intensity equal to 1.0, selection response for the trait in the aggregate genotype was calculated. Phenotypic and genetic correlations between sole ulcer and foot angle for selection index calculations were -0.02 and –0.29. As shown in Table 6, inclusion of claw disorders in index sources will increase reliabilities of estimated breeding values and expected selection response for foot health substantially. Because of the moderate correlations between sole ulcer and foot angle, inclusion of foot angle in selection decisions will lead to marginal additional benefits in estimated reliabilities and genetic gains for sole ulcer. Genetic progress towards foot health can be tripled by recording and using detailed foot disease records for selection.

Table 6. Correlation between index and aggregate genotype (r_{TI}) and selection response from one round of selection for different breeding scenarios (section intensity = 1).

Index sources	Breeding goal	r_{TI}	Selection response (reduction of incidences per generation)
Foot angle	Sole ulcer	0.239	0.041
Sole ulcer	Sole ulcer	0.723	0.122
Foot angle + Sole ulcer	Sole ulcer	0.731	0.124

CONCLUSION

The individual herd management prevalently describing husbandry and feeding strategies was the most important factor affecting incidences of all claw and foot disorders significantly. The number of parities was only significant for SU and WD, but not for IH and DD. Heritability estimates for claw and foot disorders were low to moderate using logit link-functions in evaluation models. Nevertheless, heritability estimates are large enough to make selection for reduced health problems feasible. Furthermore, a strong relationship was observed between milk yield in the first stage of lactation and disorders. Continued selection for high production may increase the proportion of cows in extreme negative energy balance during early lactation causing health problems. Most claw and foot diseases occurred together genetically, this was also the case for claw and foot diseases and increased SCS. Correlations between breeding values of claw and foot disorders and functional type traits describing the conformation of feet and legs were generally favorable. High scores for stature, strength and body weight seemed to be negatively associated with incidences of sole ulcer. The results of our study underline the importance of accurate and complete data recording of individual disorders. At the moment, selection for improved feet and leg health is practised indirectly bases on conformation traits, but direct selection on individual disorders will be a new opportunity to improve selection response towards functional health in dairy cows. The establishment of an identical guideline for classification of individual claw and foot disorders within al regions of Germany as developed by the German Agricultural Society will allow such detailed recording systems.

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CHAPTER III

EXPLORATION OF RELATIONSHIPS BETWEEN CLAW DISORDERS AND MILK YIELD IN HOLSTEIN COWS VIA RECURSIVE LINEAR AND THRESHOLD MODELS

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ABSTRACT

Relationships between claw and foot disorders and test day milk yield recorded in 2005 on 5360 Holstein cows, daughters of 511 sires, kept in 11 large-scale dairy farms in Eastern Germany, were analyzed in a Bayesian framework with each of standard linear and threshold models, and recursive linear and threshold models. A two-way causal path was postulated describing first the influence of test day milk yield on claw disorders and, secondly, the effect of the disorder on milk production level at the following test day. Four different claw and foot disorders, i.e. digital dermatitis (DD), sole ulcer (SU), wall disorder (WD) and inter-digital hyperplasia (IH), were scored as binary traits within a period of 200 days after calving, and analyzed separately. Incidences of disorders were 13.6% for DD, 16.5% for SU, 9.8% for WD, and 6.7% for IH. Heritabilities of disorders were generally higher when applying threshold models or recursive threshold models than with linear or linear recursive models. Posterior means of genetic correlations between test days milk production levels and disorders were in the range from 0.16 to 0.43. This suggests that breeding strategies focusing on increased milk yield lead to an increase in incidence of claw disorders as a correlated response. Structural coefficients λ describe recursiveness at the phenotypic level. The increase of disease incidence (trait 2) per 1 kg increase of test day milk yield (trait 1) ranged from $\lambda_{21}= 0.004$ to $\lambda_{21}= 0.024$ when applying recursive linear and recursive threshold models to the four different claw disorders. Structural coefficients in the range from -0.12 to -0.67 predict that one unit increase in the incidence of any disorder reduces milk yield at the following test day by up to 0.67 kg. The rank correlation between sire posterior means for claw disorders from the different models was above 0.84, but some substantial changes in rank of individual sires in distinct top-10 lists were observed. Hence, the choice of statistical model has an impact on the estimation and interpretation of genetic parameters, and on practical selection decisions when comparing predicted breeding values of sires or assessing selection response. The Bayesian Information Criterion (BIC) favored the recursive threshold model as the best fitting model, and differences in BIC values between different models were largest for interdigital hyperplasia.

Key words: Claw disorders, milk yield, recursive threshold models, Bayesian methods

INTRODUCTION

In most dairy cattle breeding programs, selection has focused mainly on increasing milk production traits. Miglior et al. (2005) compared national selection indices of fifteen countries and the average relative emphasis on production, durability-health, and reproduction was 59.5%, 28%, and 12.5%, respectively. In the last decade, there has been a growing interest in including functional or health traits in total net merit indexes. In theory, the future development of disease incidence in dairy cattle mainly depends on the genetic correlations between susceptibility to diseases and milk yield. Reliable estimates of phenotypic and genetic correlations between disorders and other traits of economic importance are required to define a combined breeding value in dairy cattle in the near future, as it has been the case for decades for several health traits in Nordic dairy cattle populations (Heringstad et al., 2000).

Due to their economic impact (e.g., Enting et al., 1997; Kossaibati and Esslemont, 2000), claw disorders in German Holsteins are receiving as much attention as fertility or mastitis. To cope with this problem, the German association for claw hygiene and trimming developed a computer supported documentation and analysis system, as described by Landmann et al. (2006). Data from this recording system was used recently for estimating heritability of various claw disorders via logistic models (König et al., 2005a). Results agreed with those from other similar studies applying threshold animal models (Swalve et al., 2005) or threshold sire models (Van der Waaij et al., 2005). However, genetic correlations between claw disorders and production traits have varied markedly among different studies, due to different definitions of production traits, e.g., average of single test day production (König et al. 2005a) versus whole lactation milk yield (Swalve et al., 2005). Difficulties in evaluating diseases and their correlations with other traits of interest, that arise from the discrete nature of observations, have been overcome by applying generalized linear mixed models (Wolfinger and O'Connell, 1993).

Recently, Gianola and Sorensen (2004) proposed an extension of the multivariate mixed linear model to account for possible feedback and recursiveness among response variables assuming an infinitesimal, additive model of inheritance. These feedback models for biological systems were discussed by Haldane and Priesley (1905), Turner and Stevens (1959) and Wright (1960), and have a long tradition in econometrics (Haavelmo, 1943). In dairy cattle and goats, de los Campos et al. (2006a, 2006b) found an increased risk of infection in the udder with increasing milk yield acting, probably, as a stress factor. On the other hand, an increase of infection or somatic cells could affect milk yield adversely, which defines a feedback situation. These simultaneous and recursive relationships can not be modeled in standard linear models, at least explicitly.

Application of recursive models in animal breeding has been limited. In a recursive relationship, one variable affects another, but without a reciprocal effect. Sorensen and Varona (2006) used data from two breeds of pigs, and postulated a one-way causal path describing the influence of litter size on pig birth weight. This specification defines a recursive two-trait system. Legarra and Robert-Granié (2006) conducted a simulation study to investigate the impact of recursiveness of phenotypes for fertility and milk yield on estimates of genetic correlations between these traits. Lopez de Maturana et al. (2007) investigated relationships between fertility and dystocia in Holsteins, accommodating censored and discrete outcomes.

In the case of claw disorders and milk production in dairy cows, it seems sensible to postulate a two-way causal path. One path would describe the influence test day milk yield has on claw disorders, and the second path would pertain to the effect of the disorder on milk production level at the following test date. The main objective of this study was to apply recursive linear and threshold models to investigate relationships between different claw disorders and test day milk yield; to assess competing models using statistical criteria, and to infer the respective model parameters.

MATERIALS AND METHODS

Data

Data was from a new electronic recording system for claw disorders as described by Landmann et al. (2006) and collected by 5 different claw trimmers. The guideline for classification of individual claw disorders was developed by the German Agricultural Society, and all trimmers were trained form uniform identification of traits. The electronic recording system allows a combination with data form herd management programs and with information on test day records. The data set used here comprised test day production records and claw and foot disorders collected in 2005 from 5360 Holstein daughters of 511 sires kept in 11 large-scale dairy farms within one region in Eastern Germany. Cows of all parities were included. Claw and foot disorders were divided into four different categories: digital dermatitis (**DD**), sole ulcer (**SU**), wall disorder (**WD**) and interdigital hyperplasia (**IH**), and scored as “all or none” traits . A detailed description of the individual disorders is given by König et al. (2005a). The period of observation spanned 200 days, starting at calving. If a cow had the foot problem within this period in one or both rear legs, she was given a score of 1; otherwise she was scored 0. For each cow having a disorder, the nearest test day observation before and after the occurrence of the specific disease was identified. This definition involved 3 different traits: test day milk yield before occurrence of the disorder (**MY1** = trait 1); the disorder itself (trait 2), and test day milk yield after occurrence of the disorder (**MY2** = trait 3). Repeated episodes of a disease were not taken into account. If a cow had several entries of the same disorder within the 200-d period, the first observation with complete information, i.e., a test day record before the occurrence date of the specific disease, was stored. Cows without disorders were assigned a value of 0 for trait 2 at a general dummy date of day 100 within their lactation. The nearest test day observation for healthy cows before day 100 was defined as MY1 and the nearest test day observation after day 100 was MY2. Table 1 gives mean incidence of claw and foot disorders within the respective period and the average milk yield of cows before and after the occurrence of each specific disease.

Table 1. Incidencs of four types of claw and foot disorders within 200 days after calving, and average test day milk yield before (MY1) and after (MY2) diagnosis of the disorder. Test day milk yields of healthy cows are presented by disorder.

Disorder	Mean incidence (%)	Mean day of diagnosis of disorder	MY1 (kg)	MY2 (kg)	MY2 -MY1 (in % of MY1)
Dermatitis digitalis	13.67	95	32.61	30.14	-7.57
Healthy			31.31	30.01	-4.15
Sole ulcer	16.51	88	32.94	29.97	-9.02
Healthy			31.73	29.54	-6.90
Wall disorder	9.78	86	33.18	30.04	-9.45
Healthy			32.21	30.09	-6.58
Interdigital hyperplasia	6.72	101	32.30	30.08	-9.52
Healthy			31.18	29.41	-5.68

Statistical Methods

Four different sire models were used. Model M1 was a standard 3-trait linear mixed model. Model M2 was a threshold-linear model treating the claw disorder (i.e., the second trait) as a binary trait. In the threshold-liability model (Gianola, 1982; Gianola and Foulley, 1983), it is assumed that an underlying continuous variable, liability (l_{i2}), exists such that the observed binary variable y_{i2} takes a value of 1 if l_{i2} is larger than a fixed threshold $\kappa = 0$.

M3 was a recursive model assuming a multivariate Gaussian distribution for the three traits, and model M4 was a recursive threshold-linear model with two Gaussian traits and one binary trait. In recursive models M3 and M4, the structural coefficient λ_{21} is the gradient of disease with respect to MY1 for a model with fully recursive effect of trait 1 on trait 2. The rate of change in production level in MY2 with respect to the previous claw disorder is given by λ_{32} for a model with a fully recursive effect from trait 2 to trait 3. The recursive models can be written as follows:

$$\begin{pmatrix} \mathbf{\Lambda y}_1 \\ \mathbf{\Lambda y}_2 \\ \cdots \\ \mathbf{\Lambda y}_n \end{pmatrix} = \begin{pmatrix} \mathbf{X}_1 \\ \mathbf{X}_2 \\ \cdots \\ \mathbf{X}_n \end{pmatrix} \boldsymbol{\beta} + \begin{pmatrix} \mathbf{Z}_1 \\ \mathbf{Z}_2 \\ \cdots \\ \mathbf{Z}_n \end{pmatrix} \mathbf{u} + \begin{pmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \cdots \\ \mathbf{e}_n \end{pmatrix} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Zu} + \mathbf{e}$$

with $i = 1,2,...,n$ indexing the animals, each measured for the 3 traits. Above, $\mathbf{y}_i = (y_{i1} \quad y_{i2} \quad y_{i3})'$ in model M3 and $\mathbf{y}_i = (y_{i1} \quad l_{i2} \quad y_{i3})'$ in model M4; $\boldsymbol{\beta}$ is a vector of "fixed" effects (in a Bayesian context, these are location parameters with vague prior information) of order $f^* = \sum_{j=1}^{m} f_j$ and f_j is the number of fixed effects affecting trait j *(j=1,2,3).* Fixed factors included the effects of herd (11 levels), calving season (January – March, April – June, July – September, October – December) and of parity of the cow (3 levels: 1, 2, and > 2). Further, $\mathbf{X}_i$ is a $m \times f^*$ known incidence matrix linking phenotypic measurements in $\mathbf{y}_i$ (or a rotation thereof, via the matrix $\mathbf{\Lambda}$ explained later) to the fixed effects. Vector $\mathbf{u}$, of order $q^* = m\,x\,q$, represented sire effects, where q is the number of sires. $\mathbf{Z}_i$ is an $m\,x\,q^*$ incidence matrix linking $\mathbf{y}_i$ or $\mathbf{\Lambda y}_i$ to $\mathbf{u}$ and $\mathbf{e}_i$ is a vector of residual effects of order *m.* It is assumed that $\mathbf{u} \mid \mathbf{G}_0 \sim N(\mathbf{0}, \mathbf{A} \otimes \mathbf{G}_0)$ and $\mathbf{e} \mid \mathbf{R}_0 \sim N(\mathbf{0}, \mathbf{I} \otimes \mathbf{R}_0)$, where $\mathbf{G}_0$ is a genetic covariance matrix, $\mathbf{R}_0$

is a residual covariance matrix, $\mathbf{A}$ is an additive relationship matrix, and $\otimes$ indicates Kronecker product. It is also assumed that **u** and **e** are mutually independent.

A remarkable difference between a recursive model and a standard mixed model is that, in the former, each observation vector $\mathbf{y}_{i\cdot}$ is pre-multiplied by an unknown $m \times m$ matrix $\mathbf{\Lambda}$, whose elements need to be estimated. This matrix $\mathbf{\Lambda}$ contains the structural coefficients $\lambda_{ij'}$ describing the rate of change of trait i with respect to trait j' (Gianola and Sorensen, 2004). The form of $\mathbf{\Lambda}$ in this study was

$$\mathbf{\Lambda} = \begin{bmatrix} 1 & 0 & 0 \\ -\lambda_{21} & 1 & 0 \\ 0 & -\lambda_{32} & 1 \end{bmatrix}$$

In standard linear (M1) and threshold (M2) models $\mathbf{\Lambda}$ is an identity matrix, since traits do not affect each other.

Bayesian inference via Markov chain Monte Carlo (MCMC) methods was used to infer unknown parameters of interest. Bayesian analysis of linear model M1 was conducted as suggested by Sorensen and Gianola (2002), with location parameters sampled from a multivariate distribution and covariance matrices $\mathbf{G}_0$ and $\mathbf{R}_0$ (the 3 x 3 covariance matrices between sire and residual effects, respectively) sampled from inverse Wishart distributions. When extending a standard mixed model to include one binary trait in a threshold model, such as M2 and M4, one needs to sample the residual covariance matrix from a conditional inverse Wishart distribution, given that the variance of liability is fixed to 1 (Korsgaard et al., 2003). Further, in the recursive models M3 and M4, structural coefficients ($\boldsymbol{\lambda}$) were sampled using a Gibbs sampler (Gianola and Sorensen, 2004). Bayesian modeling and MCMC sampling procedures for simultaneous or recursive (**SIR**) models (e.g., M3 and M4) are described in detail in the users' manual of the SIR-BAYES software package (https://mywebspace.wisc.
edu/xwu8/programs/sir-bayes).

The MCMC sampling procedure consists of successive iterative updating of each parameter or group of parameters. Length of burn-in and of the sampling period were assessed by the method of Raftery and Lewis (1992), as implemented in the BOA software package (Smith, 2005), and using the first 10,000 iterations of a Gibbs chain of coefficients λ_{ij}. The structural coefficients mix more slowly than other parameters, so this assessment was deemed conservative. Based on the diagnostics and visual inspections of trace plots, chain lengths of between 180,000 and 230,000 iterations were run for different models and trait combinations; burn-in period was 10,000 rounds for all models.

Parameters from recursive models (M3 and M4) differ from those obtained using a standard mixed model and they should be viewed as “system parameters”. Gianola and Sorensen (2004) described how parameters of a recursive model can be transformed into parameters of a standard mixed model. Estimates of genetic, residual and phenotypic covariance matrices were obtained by applying the following matrix operations to the posterior samples of “system parameters”

$$\mathbf{G}_0^* = \mathbf{\Lambda}^{-1}\mathbf{G}_0\mathbf{\Lambda}^{'-1}$$

$$\mathbf{R}_0^* = \mathbf{\Lambda}^{-1}\mathbf{R}_0\mathbf{\Lambda}^{'-1}$$

$$\mathbf{P}_0^* = \mathbf{G}_0^* + \mathbf{R}_0^*,$$

where $\mathbf{G}_0$ and $\mathbf{R}_0$ are the “system covariance matrices” for the and sire and residual effects, and $\mathbf{G}_0^*$, $\mathbf{R}_0^*$, and $\mathbf{P}_0^*$ are the sire, residual and phenotypic variance-covariance matrices, respectively. Also the solution for the sire effects (posterior mean) from the recursive models were recalculated by

$$S^*_{0i} = \Lambda^{-1}S_{0i}$$

where S_0 is the “vector of system sire effects” for the *ith*-sire and S^*_{0i} is the regular effect of sire i.

Comparison of models was done using the Bayesian Information Criterion (**BIC**), (Schwarz, 1978). The standard mixed model (M1) was used as baseline, because when several models are to be compared, it is useful to compare each of them with a baseline model as done by Wu et al. (2007). To illustrate, the BIC for M4 was calculated as:

$$BIC_{M4} = 2(\bar{l}_{M1} - \bar{l}_{M4}) - (d_{M1} - d_{M4})\log n$$

where $\bar{l}$ is the average of sampled log-likelihoods, d is the dimension of the parameter vector θ and n is the sample size. Finally, the comparison of e.g. M3 with M4, is the difference $BIC_{M4} - BIC_{M3}$.

RESULTS AND DISCUSSION

Mean incidences of observed claw disorders in the first 200 days of lactation (Table 1) were in the range reported by König et al. (2005a) when considering the entire lactation of a cow, and nearly identical to those found in other studies (Somers et al., 2003; Van der Waaij et al., 2005).

In this study, the mean incidences of DD, SU, WD, and IH were 0.137, 0.165, 0.098, and 0.067, respectively. On phenotypic scale, it was observed (Table 1) that cows affected by any of the claw disorders had a larger decrease in test day milk yield (MY2-MY1) than healthy cows. The average day of occurrence of disorders was close to100, which was the fixed dummy date used for healthy cows to define the "before" and "after" test days. Healthy cows had a lower level of MY1 than diseased cows. Collard et al. (1999) found that high milk yield within the first third of lactation increases a cow's risk to experience health problems. An explanation could be that potential resource intake is insufficient to express further production potential. Additional resources of energy are drawn away from fitness traits such as fertility and health (Van der Waaij, 2004).

Posterior means of selected parameters from the standard linear mixed model (M1, $\lambda = 0$), standard threshold-linear mixed model (M2, $\lambda = 0$), recursive mixed linear model (M3) and the recursive mixed threshold model (M4) are shown in tables 2 (DD,) 3 (SU), 4 (WD), and 5 (IH). Heritability estimates of DD were in the range from 0.049 to 0.088; for SU between 0.097 and 0.124; for WD between 0.088 and 0.136, and for IH from 0.120 to 0.186. Threshold models (M2 and M4) lead to generally higher heritabilities on the liability scale than linear models (M1 and M3). For all disorders, the largest point-estimates of heritability were from the threshold model (M2). Varona et al. (1999) analyzed calving ease and birth weight applying linear-linear and linear-threshold models. They found that threshold-linear models accounted for the probabilistic structure of the binary trait, i.e. calving ease, are better than linear models; also, heritability of the binary trait was larger from threshold-linear models. This is what theory for analysis of categorical traits leads one to expect (Dempster and Lerner, 1950), and is in agreement with studies analyzing categorical data with different models (e.g. Weller and Ron, 1992; Andersen-Ranberg et al., 2005). For traits or disorders characterized by low incidences, e.g., IH, differences in heritabilities between linear-linear and threshold-linear models were substantial. Freund und Walpole (1980) argued that estimates of parameters for categorical traits when assuming an underlying Gaussian would be unbiased when $n\pi$ is greater than 5; with π is being the incidence of a disorder, and n the size of the smallest subclass in the statistical model. However, Huang and Shanks (1995) estimated heritabilities of SU and IH applying threshold and linear models, and results were very similar.

The estimated genetic correlation between MY1 and all claw disorders was typically positive, in the range from 0.15 to 0.43 over models (tables 2-5). The positive genetic correlations indicate that selection for increased milk yield in the early stage of lactation increases the susceptibility to claw disorders. In a previous study using logistic models, König et al. (2005a) averaged the amount of milk yield of the first two test days after calving and correlated this value with the estimated probability that a claw disorder occurred at any point of time in the same lactation. Despite differences in the definition of milk yield and in the observed time span, their results were nearly identical to those in the present study. König et al. (2006) showed that the market price of Holstein heifers sold in auction is mainly determined by their production measured at their first test day. In view of the estimates of genetic and of phenotypic correlations between MY1 and claw disorders, the most expensive heifers would have the greatest risk of being affected by any claw disorder.

Vinson and Kliewer (1976) compared linear and threshold models, and showed that genetic correlations from these models (at least for a simple specification) are expected to be the same. Genetic correlations from recursive models M3 and M4 were generally closer to zero than those estimated from models M1 and M2. Sorensen and Varona (2006) compared genetic correlations between litter size and litter weight using a standard mixed model and a recursive mixed model in two swine breeds. In Yorkshires, they found a sizable influence (λ coefficient) of litter size on birth weight; the genetic correlation in the recursive model was near zero, but it was –0.25 in the standard model. In the Landrace breed, the structural coefficient λ was negligible, and estimates of genetic correlations from the standard mixed model and the recursive mixed model were nearly the same. In our study, the posterior distribution of λ was different from zero (Table 6), which could explain differences in genetic correlations from standard linear or standard threshold models and recursive models. In a simulation study, Legarra and Robert-Granié (2006) concluded that ignoring a recursive relationship leads to overestimation of the genetic correlation. On the other hand, the genetic correlation would be underestimated when fitting a recursive model, if recursiveness does not exist.

Genetic correlations between all claw disorders investigated and MY2 were positive in a range from 0.074 to 0.168 for DD (Table 2), 0.317 to 0.441 for SU (Table 3), 0.164 to 0.279 for WD (Table 4), and 0.172 to 0.383 for IH (Table 5) for the various models. As shown in tables 2 through 5, estimates of phenotypic correlations between MY1 (or MY2) and claw disorders were also positive, but generally lower than genetic correlations. Incidence of any disorder is associated with a substantial decrease of test day milk yield on the phenotypic scale (Table 1); however, affected cows still produce more milk at the following test date than healthy cows. A higher susceptibility to disorders is also associated with higher production at the genetic level. Sizable positive genetic and phenotypic correlations between MY1 and MY2 were found, which is consistent with estimates from several studies dealing with test day models (e.g., Jamrozik and Schaeffer, 1997). This means that genetically superior cows for milk production at an early stage of lactation are also superior at a later stage but, nevertheless, these cows have a greater risk of being affected by any claw disorder. Heritability estimates of MY1 and MY2 at individual test days were identical to values found by König et al. (2005b) when analyzing genetic parameters of individual test-day production in large-scale dairy farms in Eastern Germany.

Table 2. Posterior means and standard deviations (in brackets) of heritabilities (h^2), genetic correlations (r_g), and phenotypic correlations (r_p) for dermatitis digitalis (DD) and test day milk yield before (MY1) and after (MY2) after diagnosis of disorder applying four different models[1]

	Model[1]			
	M1	M2	M3	M4
h^2_{MY1}	0.168 (0.05)	0.170 (0.05)	0.159 (0.04)	0.149 (0.05)
h^2_{DD}	0.070 (0.05)	0.088 (0.06)	0.049 (0.03)	0.056 (0.06)
h^2_{MY2}	0.178 (0.06)	0.179 (0.06)	0.167 (0.06)	0.156 (0.07)
$r_{g(MY1:DD)}$	0.351 (0.06)	0.331 (0.07)	0.265 (0.06)	0.279 (0.08)
$r_{g(MY1:MY2)}$	0.882 (0.07)	0.902 (0.05)	0.895 (0.05)	0.901 (0.04)
$r_{g(DD:MY2)}$	0.178 (0.06)	0.168 (0.07)	0.074 (0.06)	0.089 (0.08)
$r_{p(MY1:DD)}$	0.217 (0.10)	0.198 (0.09)	0.082 (0.10)	0.092 (0.11)
$r_{p(MY1:MY2)}$	0.762 (0.16)	0.702 (0.15)	0.779 (0.18)	0.800 (0.18)
$r_{p(DD:MY2)}$	0.195 (0.10)	0.189 (0.10)	0.153 (0.11)	0.144 (0.09)

[1] M1 = standard linear mixed model, M2 = threshold mixed model, M3 = recursive linear mixed model, M4 = recursive threshold mixed model

Table 3. Posterior means and standard deviations)in brackets) of heritabilities (h^2), genetic correlations (r_g), and phenotypic correlations (r_p) for sole ulcer (SU) and test day milk yield before (MY1) and after (MY2) after diagnosis of disorder applying four different models[1]

	Model[1]			
	M1	M2	M3	M4
h^2_{MY1}	0.159 (0.05)	0.159 (0.05)	0.152 (0.04)	0.160 (0.05)
h^2_{SU}	0.100 (0.07)	0.134 (0.08)	0.097 (0.07)	0.131 (0.06)
h^2_{MY2}	0.165 (0.08)	0.169 (0.07)	0.155 (0.08)	0.163 (0.08)
$r_{g(MY1:SU)}$	0.252 (0.11)	0.269 (0.12)	0.197 (0.10)	0.216 (0.11)
$r_{g(MY1:MY2)}$	0.927 (0.12)	0.900 (0.09)	0.915 (0.12)	0.896 (0.10)
$r_{g(SU:MY2)}$	0.409 (0.18)	0.441 (0.15)	0.365 (0.16)	0.317 (0.17)
$r_{p(MY1:SU)}$	0.186 (0.13)	0.201 (0.12)	0.125 (0.15)	0.163 (0.14)
$r_{p(MY1:MY2)}$	0.803 (0.18)	0.811 (0.17)	0.691 (0.19)	0.722 (0.18)
$r_{p(SU:MY2)}$	0.233 (0.14)	0.255 (0.13)	0.167 (0.12)	0.188 (0.13)

Table 4. Posterior means and standard deviations (in brackets) of heritabilities (h^2), genetic correlations (r_g), and phenotypic correlations (r_p) for wall disorders (WD) and test day milk yield before (MY1) and after (MY2) after diagnosis of disorder applying four different models[1]

	Model[1]			
	M1	M2	M3	M4
h^2_{MY1}	0.155 (0.05)	0.158 (0.05)	0.157 (0.04)	0.159 (0.04)
h^2_{WD}	0.101 (0.05)	0.136 (0.06)	0.088 (0.05)	0.128 (0.06)
h^2_{MY2}	0.178 (0.07)	0.186 (0.06)	0.177 (0.04)	0.180 (0.05)
$r_{g(MY1:WD)}$	0.416 (0.07)	0.436 (0.06)	0.313 (0.07)	0.303 (0.07)
$r_{g(MY1:MY2)}$	0.883 (0.07)	0.895 (0.05)	0.871 (0.05)	0.888 (0.05)
$r_{g(WD:MY2)}$	0.259 (0.08)	0.279 (0.08)	0.169 (0.10)	0.164 (0.09)
$r_{p(MY1:WD)}$	0.120 (0.08)	0.121 (0.07)	0.075 (0.12)	0.067 (0.11)
$r_{p(MY1:MY2)}$	0.722 (0.14)	0.736 (0.15)	0.709 (0.16)	0.691 (0.15)
$r_{p(WD:MY2)}$	0.193 (0.15)	0.199 (0.13)	0.097 (0.13)	0.089 (0.12)

[1] M1 = standard linear mixed model, M2 = threshold mixed model, M3 = recursive linear mixed model, M4 = recursive threshold mixed model

Table 5. Posterior means and standard deviations (in brackets) of heritabilities (h^2), genetic correlations (r_g), and phenotypic correlations (r_p) for interdigital hyperplasia (IH) and test day milk yield before (MY1) and after (MY2) after diagnosis of disorder applying four different models[1]

	Model[1]			
	M1	M2	M3	M4
h^2_{MY1}	0.159 (0.05)	0.171 (0.05)	0.164 (0.04)	0.149 (0.05)
h^2_{IH}	0.112 (0.05)	0.186 (0.04)	0.120 (0.06)	0.155 (0.06)
h^2_{MY2}	0.160 (0.06)	0.177 (0.06)	0.166 (0.09)	0.180 (0.10)
$r_{g(MY1:IH)}$	0.352 (0.04)	0.347 (0.07)	0.153 (0.11)	0.178 (0.10)
$r_{g(MY1:MY2)}$	0.832 (0.08)	0.900 (0.05)	0.896 (0.05)	0.897 (0.04)
$r_{g(IH:MY2)}$	0.395 (0.11)	0.383 (0.11)	0.172 (0.11)	0.201 (0.12)
$r_{p(MY1:IH)}$	0.123 (0.12)	0.193 (0.14)	0.062 (0.12)	0.075 (0.13)
$r_{p(MY1:MY2)}$	0.741 (0.16)	0.844 (0.18)	0.690 (0.17)	0.766 (0.18)
$r_{p(IH:MY2)}$	0.287 (0.13)	0.215 (0.12)	0.117 (0.12)	0.109 (0.14)

[1] M1 = standard linear mixed model, M2 = threshold mixed model, M3 = recursive linear mixed model, M4 = recursive threshold mixed model

The analysis of milk yield at test days before and after the occurrence of a disorder plus, the application of recursive models allows a better understanding of the interplay between production and disorders than in previous studies (König et al., 2005a; Swalve et al., 2005). Structural coefficients λ describe recursiveness at the phenotypic level (Gianola and Sorensen, 2004), and λ_{21}-values describing the effect of MY1 on claw disorders were in the range from 0.0034 to 0.0242 when applying models M3 and M4 (Table 6). Applying model M4, the structural coefficient λ_{21} is the gradient of the liability of the respective disease in dependency of MY1, and for Model M3 on the observed scale. For instance, a structural coefficient λ_{21} of 0.0242 for DD in model M3 leads to the prediction that one kg increase in MY1 results in an increase of incidence of DD of 2.42%. Structural coefficients for MY1 and other 3 disorders were below 1% when applying model M3. A structural coefficient λ_{32} of –0.672 (Table 6) for DD and MY2 predicts that one unit increase in the incidence of DD on the liability scale results in a reduction of 0.67 kg in MY2. Comparing structural coefficients λ_{21} for different claw disorders, the highest effect was found for DD (Table 6). One kg increase in milk yield (MY1) increases the incidence of DD by nearly 2.5%. In contrast to the other disorders, DD is caused by a specific bacteria and it can be anticipated that a high level in milk yield is associated with a low defense mechanism against the pathogen. Among all disorders, DD is of most concern when comparing mean incidences in recent years. E.g. Somers et al. (2003) studied Holstein cows in the Netherlands, and all herds investigated had cows infected by DD, resulting in an average cow level prevalence of 30%.

Table 6. Posterior means and standard deviations (in brackets) of structural coefficients λ for four claw disorders and milk yield applying recursive linear mixed model (M3) or recursive threshold mixed model (M4)

	Dermatitis digitalis		Sole ulcer		Wall disorder		Interdigital hyperplasia	
Parameter[1]	M3	M4	M3	M4	M3	M4	M3	M4
λ_{21}	0.0242	0.0160	0.0054	0.0042	0.0042	0.0039	0.0189	0.0034
	(0.0018)	(0.0008)	(0.0019)	(0.0047)	(0.0076)	(0.0066)	(0.0019)	(0.0010)
λ_{32}	-0.6724	-0.4420	-0.4467	-0.3971	-0.1250	-0.1199	-0.5622	-0.4551
	(0.1925)	(0.2162)	(0.1571)	(0.1552)	(0.1267)	(0.1203)	(0.1832)	(0.1473)

[1] λ_{21} = gradient of disease with respect to milk yield measured on the test day before the diagnosis of the disorder, λ_{32} = rate of change in production level in test day milk yield with respect to the previous claw disorder

A rational breeding program requires accurate estimates of genetic parameters. Different models used in this study lead to different genetic and phenotypic parameters, so it is essential to evaluate the support that evidence confers to these models. Table 7 gives BIC differences between models M2, M3, and M4, respectively. According to Raftery (1995), a difference of 6 or more points in BIC provides strong evidence in favor of the model with the smaller BIC, and differences of more than 10 points indicate pronounced evidence. There was very strong evidence in favor the recursive threshold model M4 compared with a standard threshold model M2 or a linear recursive model M3 for all claw disorders. The recursive model M3 gave a better fit to the data than the standard threshold-linear model M2, but there was only weak evidence in favor of model M3 compared with model M2 for SU. The model describing recursiveness and considering the binary structure of the data, i.e., model M4, was the most appropriate when analyzing the relationships between claw disorders and milk yield. The linear model M1 was defined as a baseline model for goodness of fit comparisons of models M2, M3, and M4, respectively. M1 was the least favored one, illustrating the pitfalls of treating binary data as Gaussian.

Table 7. Bayesian information criterion (BIC) pairwise differences for comparing threshold model (M2), recursive linear model (M3) and recursive threshold model (M4) for 4 claw disorders

	Dermatitis digitalis	Sole ulcer	Wall disorder	Interdigital hyperplasia
M2-M3	7	2	10	9
M2-M4	31	36	33	46
M3-M4	24	34	23	37

Analysis of claw disorders and milk yield utilizing the model found to be most supported has consequences on prediction of response to selection. For the direct comparison of results, heritabilities on the liability scale obtained from models M2 and M4 were transformed to the observed scale using the formula of Robertson and Lerner (1949). As an illustration, consider selection on MY1 and the correlated selection response in IH for models M1 and M4. Applying model M1, the predicted direct response per generation for MY1 is $\Delta G_{(MY1)} = ih_{(MY1)}\sigma_{A(MY1)} = i(0.106)$ and the predicted correlated response for IH when selecting on MY1 is $\Delta G_{(IH,MY1)} = ih^2_{(MY1)}\sigma_{A(MY1)}r_{g(IH,\ MY1)} = i(0.0037)$. In comparison, for the better model M4, the correlated selection response in IH would be equal to i(0.0016). For the same selection intensity, model M1 leads to an overstatement of correlated selection response of 1.1% per generation in incidence of IH, relative to what is expected from model M4. This simple scenario illustrated the impact of model assessment and selection on estimates of genetic parameters and on predicted selection response.

Rank correlations (Table 8) between sire posterior means within disorders applying models M1, M2, M3, and M4 were above 0.84 for all pairs of models, but there were substantial changes in rank for top-ranked sires (Table 9). For example, for IH, the best sire when applying model M1 was ranked as number 20 when using model M4. The rank correlations between sire posterior means were highest between recursive models M3 and M4, and lowest between the standard linear model M1 and the recursive threshold model M4 (Table 8). In the global market of Holstein dairy cattle breeding, only the top ranked sires are competitive, even if differences in predicted breeding values with lower ranked bulls are minor (Dekkers et al., 1996). Again, this underlines the importance of model choice in breeding value estimation.

Table 8. Rank correlation between sire posterior means estimated with 4 different models[1] for 4 claw disorders

Model[1]	Dermatitis digitalis	Sole ulcer	Wall disorder	Interdigital hyperplasia
M1:M2	0.93	0.91	0.94	0.93
M1:M3	0.91	0.90	0.89	0.92
M1:M4	0.85	0.86	0.88	0.84
M2:M3	0.85	0.86	0.87	0.85
M2:M4	0.93	0.92	0.93	0.94
M3:M4	0.95	0.98	0.98	0.97

[1]M1 = standard linear mixed model, M2 = threshold mixed model, M3 = recursive linear mixed model, M4 = recursive threshold mixed model

Table 9. The top 10 sires based on sire posterior mean for 4 claw disorders estimated with model M1 and their ranking applying models[1] M2, M3, and M4.

Dermatitis digitalis				Sole ulcer				Wall disorder				Interdigital hyperplasia			
M1	M2	M3	M4	M1	M2	M3	M4	M1	M2	M3	M4	M1	M2	M3	M4
1	7	10	19	1	9	2	14	1	11	10	16	1	17	6	20
2	12	2	17	2	7	12	18	2	4	15	8	2	7	12	18
3	20	8	21	3	13	6	8	3	1	9	11	3	8	1	9
4	1	9	3	4	2	13	1	4	16	8	21	4	12	6	11
5	6	14	5	5	23	16	21	5	2	1	7	5	1	13	8
6	23	7	20	6	8	15	6	6	13	5	18	6	20	9	28
7	11	1	13	7	4	20	17	7	3	11	1	7	4	14	6
8	4	22	2	8	5	1	5	8	23	26	24	8	3	7	12
9	10	18	9	9	15	20	31	9	6	16	10	9	9	22	18
10	8	15	4	10	3	14	1	10	8	20	2	10	23	17	29

[1]M1 = standard linear mixed model, M2 = threshold mixed model, M3 = recursive linear mixed model, M4 = recursive threshold mixed model

The question of how the impact of mutual effects between distinct traits on prediction of breeding values should be handled is of increasing interest in animal breeding. In the case of production and fertility, several authors (e.g., Bormann et al., 2002; Olori et al., 1997) observed a significant impact of pregnancy status on test day milk yield, depending on lactation stage. An analysis of Bohmanova et al. (2006) considered the effect of days open as well as state of pregnancy, i.e., traits describing fertility, on the prediction of breeding values for milk yield with a random regression test day model. Recursive models constitute an appealing alternative for dealing with this problem. If needed, the model can be expanded into one with simultaneous or feedback (even time lagged) relationships.

CONCLUSIONS

Claw disorders are of increasing concern within the German Holstein dairy cattle population and suitable data recording systems are just becoming available. Therefore, appropriate models for estimation of genetic parameters should be developed to make selection as effective as possible. In the case of disorders and production traits, recursiveness between traits as discussed by Gianola and Sorensen (2004) should be investigated further. The present study showed that ignoring recursive relationships between traits can lead to overestimation of the genetic correlation between claw disorders and test day milk yield. Differences in values of genetic parameters among different models have consequences on predicted responses to selection, as illustrated for interdigital hyperplasia, and on the ranking of top sires based on predicted breeding values. As shown in this study, the methodology can also be applied to categorical traits. Especially for claw disorders with a low incidence, such as interdigital hyperplasia, the recursive threshold model was superior when the BIC information criterion was used. Recursive threshold models in a Bayesian framework are useful tools for investigating similar questions in the whole field of animal breeding. Dairy cattle breeding schemes are moving towards the use of more complex breeding goals involving a multiplicity of binary coded health related traits. Hence, evaluation of recursive or even simultaneous threshold models is an important area of research.

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CHAPTER IV

GENETIC ANALYSIS OF TRAITS AFFECTING THE SUCCESS OF EMBRO TRANSFER IN DAIRY CATTLE

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ABSTRACT

The primary aim of this study was to estimate variance components for traits related to embryo transfer (ET) by applying generalized linear mixed models (GLMM) for different distributions of traits (Normal, Binomial, and Poisson) in a synergistic context. Synergistic models were originally developed for traits affected by several genotypes, denoted as maternal, paternal and direct effects. In the case of ET, the number of flushed ova (FO) only depends on a donor's maternal genetic effect, whereas paternal fertility must be considered for other embryo survival traits, such as the number of transferable embryos (TE), the number of degenerated embryos (DE), the number of unfertilized oocytes (UO), and the percentage of transferable embryos (PTE). Data for these traits were obtained from 4196 flushes of 2489 Holstein cows within four different regions of North-West-Germany from January 1998 through October 2004. Estimates of maternal heritability were 0.231 for FO, 0.096 for TE, 0.021 for DE, 0.135 for UO, and 0.099 for PTE, whereas the relative genetic impact of the paternal component was near zero. Estimates of the genetic correlations between the maternal and the paternal component were slightly negative indicating a genetic antagonism. For the analysis of pregnancy after ET, 8239 transfers to 6819 different Holstein-Friesian recipients were considered by applying threshold methodology. The direct heritability for pregnancy in the recipient after ET was 0.056. The relative genetic impact of maternal and paternal components on pregnancy of recipients describing a donor's and a sire's ability to produce viable embryos was below 1%. The genetic correlations of the direct effect of the recipient with the sire of embryos (paternal effect) and the donor cow (maternal effect) for pregnancy after ET were -0.32, and -0.14, respectively. With the exception of FO and PTE (-0.17), estimates of genetic correlations among traits for the maternal site were distinctly positive, especially between FO and TE (0.74). Based on this high genetic correlation and due the higher heritability for FO, indirect selection on FO will increase selection response in TE about 22% compared to direct selection on TE. The negative genetic correlation of -0.27 between TE and lactation milk yield indicates development of an index for bull dams in multiple ovulation and embryo transfer (MOET) breeding schemes combining production as well as traits related to ET.

Key words: Embryo transfer, synergistic groups, generalized linear mixed models, genetic parameters

INTRODUCTION

Nicholas and Smith (1983) introduced the application of a nucleus herd program based on multiple ovulation and embryo transfer (**MOET**) for increased genetic response to selection in dairy cattle. Subsequent studies in the 1980s and 1990s (e.g. Colleau, 1991) have followed; and the results revealed a potential of 10 to 20% additional genetic gain compared to traditional breeding programs. Gains are mainly due to the reduction of generation intervals. As a consequence, several dairy cattle breeding programs for the Holstein-Friesian breed in Germany as summarized by König and Swalve (2003) have included the ideas of Nicholas and Smith (1983) and established MOET breeding schemes to produce as many offspring of elite cows as possible. This was mainly accomplished in combination with an expensive centralized test on-station for potential bull dams to avoid biases in estimated breeding values due to preferential treatment (Kuhn et al., 1994) and due to the impact of heterogeneous variances in different environments on estimated breeding values of cows (e.g. Garrick and Van Vleck, 1987). However, the goal to produce at least 5 full sisters and 5 full brothers through the application of embryo transfer (**ET**) with the intention of replacing progeny testing and reducing generation intervals often failed.

As pointed out by König and Swalve (2003) and König et al. (2006), the superiority of MOET breeding programs will mainly depend on the number of progeny of superior cows and, therefore, depend on the success rate of ET. In addition to the improvement of technical methods associated with the ET biotechnology (e.g. Hasler, 1992) or the improvement of environmental conditions for donors and recipients (e.g. Kafi and McGowan, 1997), selection for characteristics related to ET can also contribute to more offspring per donor.

Genetic evaluations require accurate estimates of parameters. However, for traits related to ET, appropriate data are rare, and previous genetic studies were based on breeds other than Holstein (Liboriussen et al., 1995), accomplished in different populations (Benyei et al., 2004), or are somewhat out-dated (Preisinger et al., 1990). Furthermore, recent developments in statistical methods allowing application of a generalized linear mixed model (**GLMM**) technique (Schall, 1991) can be used to analyze ET data with appropriate distributions, such as Normal, Binomial, and Poisson. Also, in the case of ET, the complexity of several traits as well as of several genotypes has to be taken into account, and knowledge about their variance and covariance components for maternal and paternal effects is of basic concern and was not fully considered in previous studies. From the genetic point of view, the number of flushed ova describes a cow's own performance and only depends on the donor's genetic effect, whereas for traits describing embryonic survival, the paternal effect has to be taken into account too. The final pregnancy rate of embryos is affected by the genotype of the recipient, the genotype of the donor, and the genotype of the sire of embryos as well. Willham (1963) defined these traits depending on groups of animals representing direct, maternal, and paternal effects, as synergistic traits. The theoretical background of statistical models for evaluating synergistic traits in the case of fertility was carefully evaluated by Haussmann and Heinkel (1989). The increase of inbreeding in the German Holstein population and therefore the close additive genetic relationships among animals and especially between bull dams and bull sires (König and Simianer, 2006) enable reliable estimates of the covariances among genetic groups involved in a synergistic model for ET.

The objective of this study was to estimate variance and covariance components for the ovulation rate, traits describing embryonic survival as well as pregnancy after ET in a synergistic context and to apply generalized linear mixed models with appropriate link functions for various distributions of the traits studied. Results give detailed information on the interaction of different genotypes for different traits describing fertility in dairy cattle. As a further extension of this analysis, traits related to ET were correlated with other production traits of superovulated cows. Knowledge of variance and covariance components of all these traits can be used to develop an index or a complex breeding goal for potential bull dams and ultimately contribute to more success of existing MOET breeding schemes.

MATERIALS AND METHODS

Data

Data related to ET were obtained from 4196 flushings of 2489 Holstein cows within four different regions corresponding to four different breeding organizations A, B, C, and D of North-West-Germany from January 1998 through October 2004. Traits of interest were the number of flushed ova (**FO**), the number of transferable embryos (**TE**), the number of degenerated embryos (**DE**), the number of unfertilized oocytes (**UO**), and the percentage of transferable embryos (**PTE**) defined as PTE = TE * 100 / FO. Production traits were 305-d lactation yields for milk kg, fat %, protein %, and somatic cell count of all donor cows for the respective flushing year.

Somatic cell count was log-transformed into somatic cell score (**SCS**) to achieve normality and homogeneity of variances applying the formula by Ali and Shook (1980).

Table 1. Descriptive statistics of analyzed traits of embryo donor cows.

Trait	Mean	SD	Minimum	Maximum
No. of flushed ova	8.52	6.91	0	52
No. of transferable embryos	4.84	5.00	0	33
No. of degenerated embryos	0.81	2.25	0	29
No. of unfertilized oocytes	2.64	4.61	0	34
PTE (in %)	48.43	10.62	0	100
305-d milk yield (in kg)	9962.78	1507.60	8705.19	14831.77
Fat-%	4.16	0.48	3.51	5.59
Protein-%	3.44	0.19	2.63	4.14
Somatic cell score	2.39	1.11	0.04	7.28

[1]PTE = percentage of transferable embryos = no. of transferable embryos / no. of flushed ova

Donor cows were generally intensively selected elite cows for production (Table 1) and conformation traits and are heavily used as bull dams. Hence, the main intention of ET was to ensure at least one male offspring as a young sire for the progeny testing program, but also female progeny were preferred when selecting the next generation of future donor cows. Breeding organization A has implemented these ideas of an open MOET breeding scheme for nearly 20 years (Kandzi, 1988). The cycle of this breeding program is explained in Figure 1. On-station, bull dams were selected primarily for protein yield, type classification, and SCC, but currently there is no selection pressure on traits related to ET.

A total of 8239 embryos were transferred to 6819 different purebred Holstein-Friesian recipients kept in herds contracted by the respective breeding organization. Binary coded status of pregnancy of recipients eight weeks after ET was based on information from rectal palpation done by veterinarians. Phenotypic means, standard deviations, minima and maxima for all traits are in Table 1. Pedigrees of donor cows, service sires and recipients were available back to base animals born in 1940.

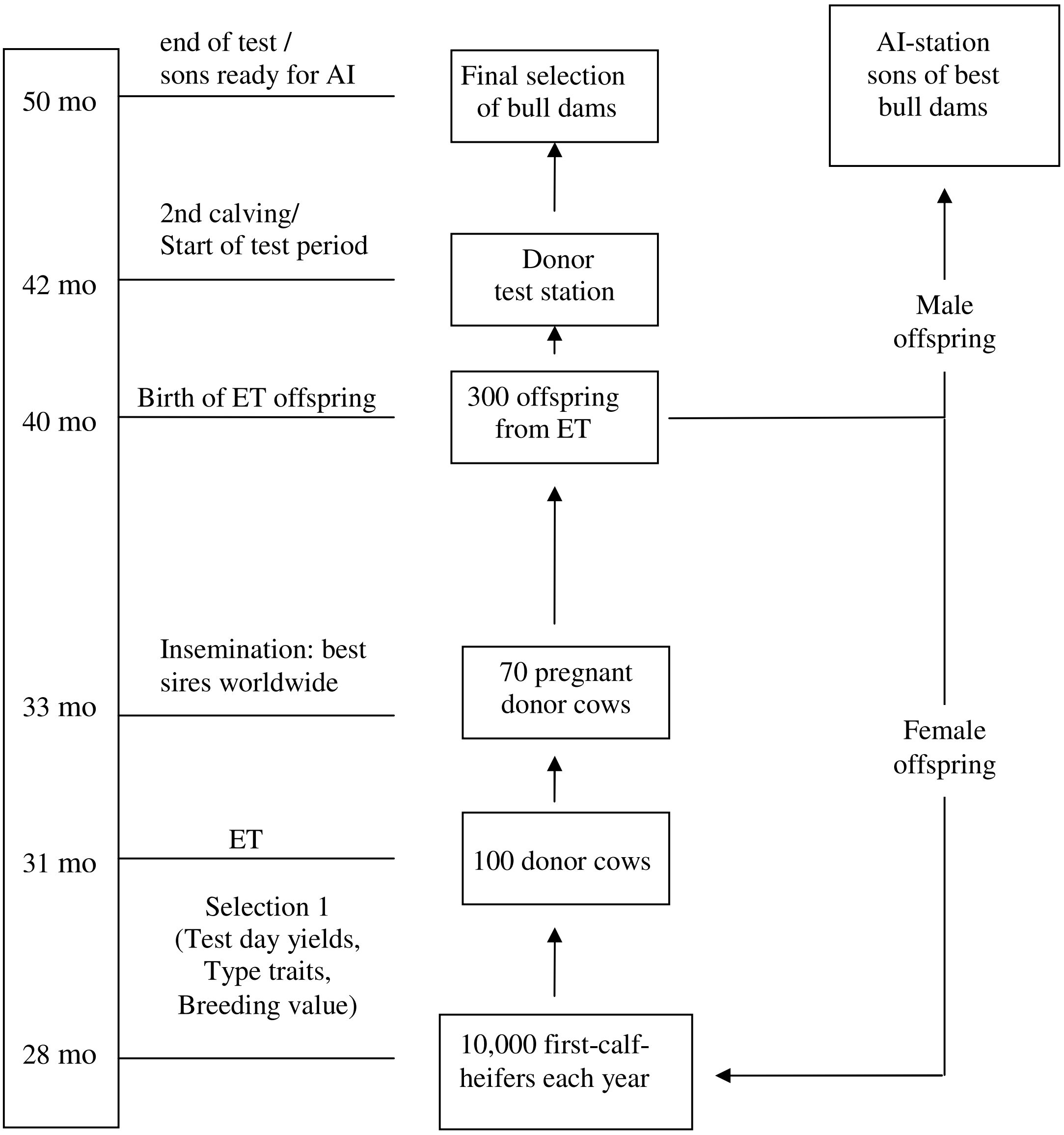

Figure 1. Structure of a MOET breeding program for one German breeding organization as developed by Kandzi (1988).

Statistical Models

The general terminology used in this paper in the context of synergistic models is depicted in Figure 2. Maternal effect is the impact of the genetic mother (donor) of ova or embryos, and the paternal effect is the impact of the genetic father (sire) of the embryos. When evaluating genetic components, the number of FO only depends on a donor's maternal genetic effect, whereas for traits describing embryonic survival, in this study TE, DE, UO, and PTE, the paternal effect has to be taken into account. Hence, for TE, DE, UO, and PTE, genetic covariances between maternal and paternal effects can be estimated. The term 'direct effect' is only used in this paper with regard to pregnancy after ET, and it describes the genetic ability of recipients to become pregnant. The maternal and paternal component in the case of pregnancy is the donor's and a sire's contribution, respectively, to produce viable embryos. The genetic covariance among direct effects and paternal as well as maternal effects indicates, if preferred sires for selection for improvement of conception ability of recipients are also the best sires to improve vitality of embryos.

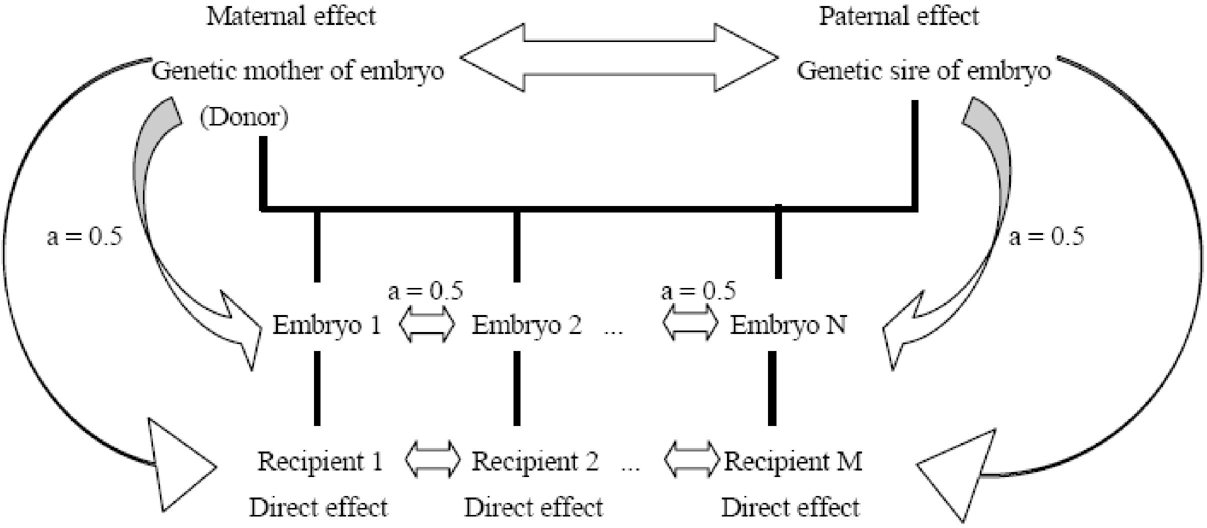

Figure 2. Structure for a synergistic model in the case of embryo transfer. (Arrows indicate possible or certain coefficients of relationship = a).

Maternal variance component for FO as well as the estimation of maternal and paternal variance and covariance components for TE, DE, UO, and PTE were estimated using univariate animal models for REML and applying the package ASReml (Gilmour et al., 1998). The genetic correlations for all possible combinations of these traits were estimated for the maternal component of FO, TE, DE, UO, and PTE, and the various production traits using bivariate animal models. In a bivariate analysis for estimating genetic correlations between two categorical traits, ASReml treats one of these traits in the linear sense. However, Vinson and Kluwer (1976) have shown that the genetic correlation computed from multi- or binomial phenotypes of related animals is equal to normally distributed variables, and vice versa. This was also recently shown by Mielenz et al. (2005) when analyzing genetic parameters for mortality in laying hens.

For pregnancy of recipients after ET, a univariate animal model was used to estimate the covariance among involved genetic groups for maternal, paternal, and direct genetic effects.

The program, ASReml, allows specification of both the distribution of the traits, and the application of a GLMM analysis through a link function. The traits FO, TE, DE, and UO, are count variables following a Poisson distribution (Figure 3).

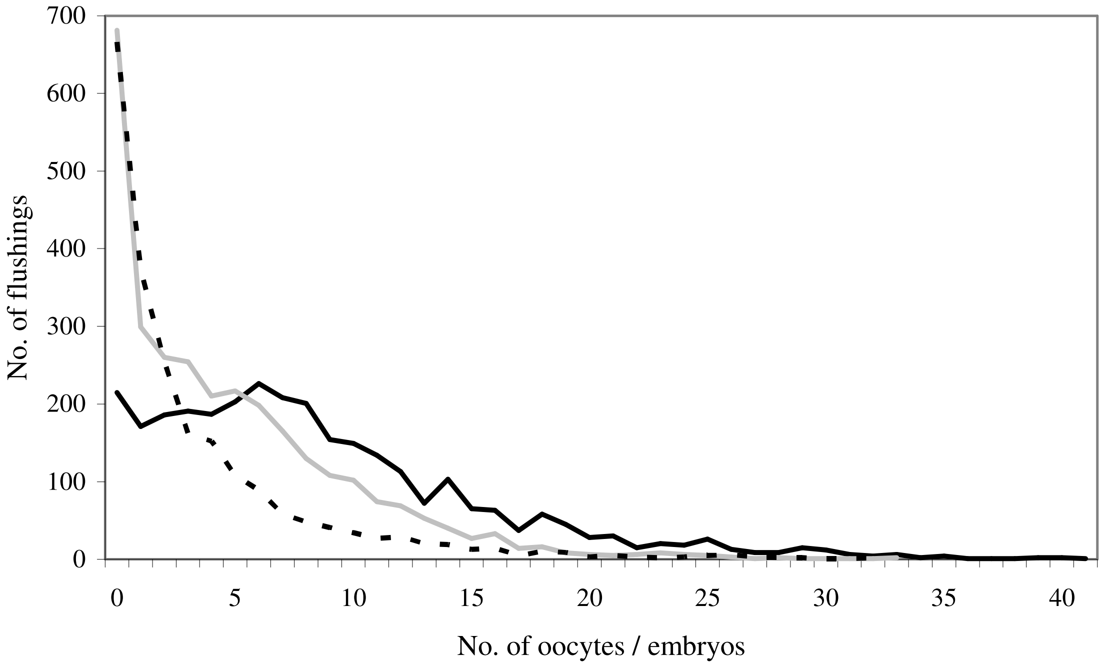

Figure 3. Distribution for flushed ova (black solid line), transferable embryos (grey solid line), and degenerated embryos (dotted line).

The link function f_i between the linear predictor η_i and the observations y_i used for these count data was a log link defined as $f_i = \log_e(\eta_i)$. Data measured on the percentage scale (PTE) were transformed by the arc-sine transformation (Sokal and Rohlf, 1995) to achieve homogeneity of error variance and then analyzed in a GLMM applying an identity link function. The probit link, modeling the probability [P(y = 1)] that a recipient has been pregnant after ET is given by $f_i = \Phi^{-1}[\eta_i]$ where Φ^{-1} is the inverse normal cumulative density function. This probit model is identical to a threshold liability model (Gianola, 1982; Gianola and Foulley, 1983). For calculating heritabilities in the GLMM Poisson-log model and in the threshold model, the residual variance was fixed to a value of 1.

Due to the different genetic groups involved in the phenotypic expression of the traits, different structures of the (co)variance matrices for random effects have to be applied. For FO, the model 1 for univariate analyses in matrix notation was:

$$y = Xb + Zd + Spd + e \ , \qquad [1]$$

where $y =$ vector of observations, $b =$ vector of the fixed breeding organization-year-season effect, $d =$ vector of random genetic effects of the donor, $pd =$ vector of permanent environmental effects of the donor, $e =$ vector of random residual effects, and $X, Z,$ and $S,$ are the incidence matrices relating records to fixed and random effect. It is assumed that

$$\text{var}\begin{bmatrix} u \\ pd \\ e \end{bmatrix} = \begin{bmatrix} gA & 0 & 0 \\ 0 & I\sigma^2_{pd} & 0 \\ 0 & 0 & I\sigma^2_e \end{bmatrix} \ ,$$

where g is the additive genetic variance for the maternal effect of the donor, A is the numerator relationship matrix, σ^2_{pd} is the variance due to permanent environmental effects of the donor, σ^2_e is the residual error variance and I represents the identity matrix. Model 2 for TE, DE, UO, and PTE was:

$$y = Xb + Zd + Spd + Ws + Vps + e \ , \qquad [2]$$

where s and ps are the vectors of random genetic and random permanent environmental effects of the sire and other effects are the same as in model 1. The corresponding matrix of variances and covariances for random effects, similar to an animal model for a maternal trait (Quaas and Pollak, 1980), was:

$$\text{var}\begin{bmatrix} d \\ s \\ pd \\ ps \\ e \end{bmatrix} = \begin{bmatrix} g_{11}A & g_{12}A & 0 & 0 & 0 \\ g_{21}A & g_{22}A & 0 & 0 & 0 \\ 0 & 0 & I\sigma^2_{pd} & 0 & 0 \\ 0 & 0 & 0 & I\sigma^2_{ps} & 0 \\ 0 & 0 & 0 & 0 & I\sigma^2_e \end{bmatrix},$$

where g_{11} is the additive genetic variance for the maternal effect of the donor, g_{22} is the additive genetic variance for the paternal effect of the sire, and g_{12} is the additive genetic covariance between maternal and paternal effects. The variances due to permanent environmental effects of the donor and the sire are σ^2_{pd} and σ^2_{ps}, respectively.

For pregnancy after ET, the statistical model was extended to the direct genetic effects of the recipient. The model 3a was as follows:

$$y = Xb + Mr + Npr + Zd + Ws + e \,, \qquad [3a]$$

where *r* and *pr* are the vectors of random genetic and random permanent environmental effects of the recipient, and *M* and *N* are the corresponding incidence matrices. The additive genetic effects of the donor, vector *d*, as well as the additive genetic effects of the sire of embryos, vector *s*, describe the genetic component of embryo vitality. All genetic effects can be linked based on the relationship matrix which allows the estimation of genetic covariances between the genetic groups involved. In the case of pregnancy after ET, the vector *b* included the fixed breeding organization-year-season effect, the status of transferred embryos (58.3% fresh, 41.7% frozen), quality classes 1 to 3 of embryos according to guidelines of the International Embryo Transfer Society (**IETS**, Stringfellow and Seidel, 1998), and embryo development according to IETS (3 different classes of embryo development).

Another, and even more straightforward alternative, is to simplify model 3a and to replace the sire and donor genetic terms by the genetic effect of the embryo. The model 3b was:

$$y = Xb + Mr + Npr + Qu + e \,, \quad [3b]$$

Vector *u* includes the additive genetic effect of the embryo and *Q* is the corresponding incidence matrix. All other effects are identical to those in model 3a.

RESULTS AND DISCUSSION

Variance components for genetic groups within traits

Most investigations dealing with genetic effects on traits related to ET, such as FO or TE, have focused on breed differences (e.g. Estrada et al., 1998; Herrler et al., 1991). Differences between breeds of donor cows were generally significant. However, estimates of genetic parameters for these traits within breeds and utilizing relatively large datasets including more than 1000 donor cows are restricted to a few publications. Heritabilities for maternal, paternal, and direct effects as well as the relative impact of the permanent environmental components for different traits affecting the success of ET found in the present study are summarized in Table 2. Maternal heritabilities were 0.231 for FO, 0.096 for TE, 0.021 for DE, 0.135 for UO, and 0.099 for PTE. Variance component estimation for FO and TE was done in some previous investigations (Liboriussen et al., 1995; Tonhati et al., 1999), and results were in the same range despite major differences in statistical models. A substantially higher maternal heritability of 0.59 for TE was only found by Piexoto et al. (2004) for ET results in Nellore cattle.

Table 2. Relative genetic impact of the donor (h^2_d), the service sire (h^2_s), the recipient (h^2_r), and the embryo (h^2_e) for various traits related to embryo transfer and relative impact of respective permanent environmental components σ^2_{pd}, σ^2_{ps}, and, σ^2_{pr} for analyzed traits.

Trait	Heritabilities				Permanent environment		
	h^2_d ± SE	h^2_s ± SE	h^2_e ± SE	h^2_r ± SE	$\sigma^2_{pd} / \sigma^2_p$ ± SE	$\sigma^2_{ps} / \sigma^2_p$ ± SE	$\sigma^2_{pr} / \sigma^2_p$ ± SE
No. of flushed ova	0.231 ± 0.091	_	_	_	0.114 ± 0.043	_	_
No. of transferable embryos	0.096 ± 0.087	0.012 ± 0.075	_	_	0.153 ± 0.048	0.002 ± 0.049	_
No. of degenerated embryos	0.021 ± 0.081	0.017 ± 0.077	_	_	0.060 ± 0.047	0.001 ± 0.040	_
No. of unfertilized oocytes	0.135 ± 0.090	0.027 ± 0.082	_	_	0.067 ± 0.044	0.001 ± 0.041	_
PTE[1]	0.099 ± 0.086	0.014 ± 0.075	_	_	0.161 ± 0.055	0.002 ± 0.048	_
Pregnancy after ET (Model 3a)[2]	0.008 ± 0.007	0.006 ± 0.002	_	0.056 ± 0.026	_	_	0.017 ± 0.014
Pregnancy after ET (Model 3b)[2]	_	_	0.015 ± 0.002	0.058 ± 0.025	_	_	0.018 ± 0.013

[1] PTE = percentage of transferable embryos = no. of transferable embryos / no. of flushed ova

[2] Model 3b versus model 3a: Genetic effects of sire and dam are replaced by the genetic effect of the embryo

The relative impact of the permanent environmental component of the donor was substantial and in the range of 0.06 to 0.16 for the investigated traits resulting in repeatabilities of 0.35 and 0.25 for FO and TE, respectively. Similar to the moderate maternal genetic impact of the donor on the number of FO, TE, and PTE, permanent environmental effects of the same magnitude due to special feeding or management strategies or due to a cow's individual reaction to hormone supplies can be anticipated when considering the ultimate success in ET. In contrast, the paternal heritability describing a sire's ability to fertilize flushed ova was quite low. The relative genetic impact of the paternal component was 0.012, 0.017, 0.027, and 0.014 for TE, DE, UO and PTE, respectively and is therefore similar compared to results of previous studies (e.g. Preisinger, 1990). The paternal permanent environmental component for these traits was also near zero. An explanation could be that, in general, high-quality semen is used for inseminations during ET. However, Bosselmann et al. (2005) found pronounced differences in the number of TE on the phenotypic scale for different service sires within flushing years, but these differences seemed to be associated with non-genetic effects.

The direct heritability for the recipient to become pregnant after ET was 0.056 (Table 2) and is therefore in the general range for non-return rates in dairy cattle reported in the literature (e.g. Jamrozik et al., 2005). A small fraction (17.2%) of all recipients was used for repeated embryo transfers and the permanent environmental component was small (1.7%). Interpreting this result, the pre-selection of recipients by veterinarians according to a recipient's fertility status must be taken into account. The relative genetic impact of maternal and paternal components on pregnancy of recipients describing a donor's and a sire's ability to produce viable embryos was less than 1%. The relative impact at the total variance for pregnancy was only 0.8% for the maternal component, and 0.6% for the paternal component. However, in general, poorest embryos were discarded before the transfer, explaining the minor importance of genetic parents of embryos when discussing fertility of recipients. The alternative model 3b revealed a similar heritability for the recipient (0.058), and the relative importance of embryo vitality for pregnancy after ET was 1.5%. The more robust model 3b led to higher additive genetic variances for the embryo effect, and even standard errors for genetic correlations between synergistic groups were less than results obtained from model 3a (Figure 4).

Genetic correlations between the maternal and paternal component within traits were negative, but near zero. Estimates for genetic correlations were –0.11 (± 0.139) for TE, -0.04 (± 0.127) for DE, -0.10 (± 0.132) for UO, and -0.08 (± 0.130) for PTE. Thus selection for the maternal component for TE will tend to leave sire fertility unaffected. According to the literature, genetic correlations between maternal and paternal effects for most fertility traits (e.g. the non-return rate measured at 90 d) are reported to be negative and assumed to be -0.05 for the official breeding value estimation in Germany (Pasman and Reinhardt, 1998). Studies revealing the physiological mechanisms for the phenomenon of slightly negative correlations between maternal and paternal effects for traits related to ET ought to be carried out in the future.

The genetic correlation between the direct effect of the recipient and the sire of embryos applying model 3a for pregnancy after ET was -0.32, and -0.14 between the donor cow and the recipient (Figure 4). These results suggest that sires which should be preferred in selection for the improvement in conception ability of recipients were not necessarily best when considering vitality of transferred embryos.

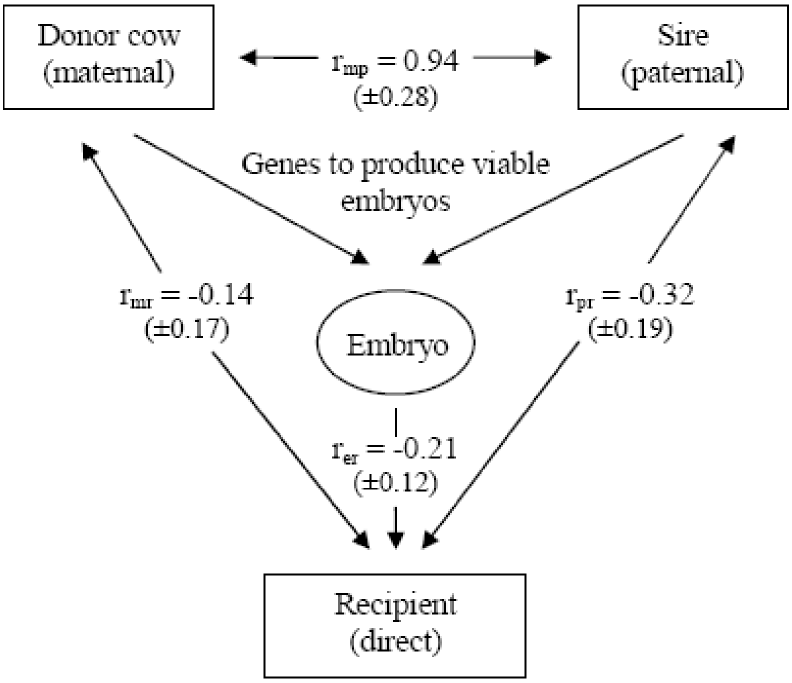

Figure 4. Genetic correlations in the synergistic model for the trait pregnancy after embryo transfer for the involved genetic groups (r_{mp} = genetic correlation between the donor cow and the sire of the embryo, r_{pr} = genetic correlation between the sire of the embryo and the recipient, r_{er} = genetic correlation between the embryo and the recipient, r_{mr} = genetic correlation between the donor cow and the recipient).

These results are in agreement with the genetic correlation of -0.21 (Figure 4) between the embryo effect and the effect of the recipient, where a simplification of the model was achieved due to the direct fit of the genetic effect of the embryo. The embryo genetic effects consist of half of the genes of the genetic mother, half of the genes of the genetic father plus the Mendelian sampling component, and, hence these correlations were expected to be similar.

Following the results for pregnancy after ET, it can also be anticipated that fertility after artificial insemination is determined by a complexity of different components. This could be the vitality of the embryo itself as well as the metabolism and intrauterine environment of the cow, which are not necessarily positively correlated among each other. Results encourage the general attempt of Haussmann and Heinkel (1989) to develop synergistic models for fertility in dairy cattle. The genetic correlation between the effects of the donor cow and the sire of the embryo was 0.94 indicating no differences for embryo vitality whether genes are transmitted from the paternal or from the maternal side.

Genetic correlations between different traits

Due to the minor impact of the paternal component, only the maternal path was considered when estimating phenotypic and genetic correlations between different traits (Table 3). The ultimate breeding goal is to increase the number of TE, but correlations to other traits are important to find the most suitable breeding strategy, e.g. direct selection on TE or via indirect selection on FO as suggested by Bosselmann et al. (2005). The number of FO has a positive correlation with the numbers of TE (r_g = 0.74), despite the positive genetic correlation between FO and DE (r_g = 0.89), or between FO and UO (r_g = 0.76). The genetic correlation between FO and TE in the study by Preisinger et al. (1993) was 0.63. A higher number of FO resulted in increased embryonic losses due to infertility and degeneration, as also indicated by the negative genetic correlation between FO and PTE (r_g = -0.17). Hence, breeding for increased FO also increases DE and UO, but cows selected for a high number of FO are still the best when regarding the number of TE. Indirect selection on FO will increase selection response in TE by about 22% compared with direct selection on TE, due to the higher heritabilities for FO found in the present study. Because of the pronounced genetic correlations associated among FO and TE, DE, and UO, the genetic correlations between TE and DE (r_g = 0.52) and TE and UO (r_g = 0.21) were also positive. A greater number of DE was genetically associated with a higher number of UO (r_g =

0.57). Phenotypic correlations between all these traits were in the same range as genetic correlations (Table 3).

Table 3. Estimates of genetic correlations (above diagonal; ± standard errors) and phenotypic correlations (below diagonal) for flushed ova (FO), transferable embryos (FE), degenerated embryos (DE), unfertilized oocytes (UO), the percentage of transferable embryos (PTE)[1] and 305-d lactation yields for milk kg, fat %, protein %, and SCS for the maternal path (donor cow).

Trait	FO	TE	DE	UO	PTE	Milk kg	Fat %	Protein %	SCS
FO		0.741 ± 0.080	0.898 ± 0.149	0.755 ± 0.092	-0.173 ± 0.100	-0.239 ± 0.087	-0.002 ± 0.055	0.003 ± 0.059	-0.347 ± 0.079
TE	0.677		0.722 ± 0.138	0.211 ± 0.142	0.562 ± 0.131	-0.272 ± 0.090	-0.004 ± 0.061	0.005 ± 0.060	-0.407 ± 0.088
DE	0.310	0.160		0.566 ± 0.168	-0.193 ± 0.158	-0.199 ± 0.095	0.211 ± 0.101	0.247 ± 0.104	0.181 ± 0.109
UO	0.513	-0.001	-0.018		-0.840 ± 0.111	-0.148 ± 0.091	-0.005 ± 0.099	0.001 ± 0.105	-0.125 ± 0.102
PTE	-0.072	0.684	-0.210	-0.663		-0.036 ± 0.105	-0.003 ± 0.109	0.011 ± 0.110	-0.391 ± 0.112
Milk kg	-0.211	-0.308	-0.187	-0.111	-0.082		-0.566 ± 0.051	-0.440 ± 0.053	0.013 ± 0.075
Fat %	-0.010	0.012	0.233	0.027	-0.091	-0.679		0.810 ± 0.068	-0.192 ± 0.097
Protein %	-0.044	0.001	0.199	-0.082	-0.074	-0.550	0.771		-0.130 ± 0.099
SCS	-0.591	-0.603	0.220	-0.008	-0.381	0.172	-0.344	-0.143	

[1]PTE = percentage of transferable embryos = no. of transferable embryos / no. of flushed ova

As recently shown by Miglior et al. (2005), in most conventional dairy cattle breeding programs, selection is mainly focused on milk yield or production traits. Due to the high selection pressure on production, the success in other traits will largely depend on the genetic correlations between these traits and milk yield. Donor cows are highly pre-selected for milk yield and characterized by a high production level in milk yield greater than 9962 kg per lactation (Table 1), but the success of ET often failed. As shown in Figure 3, 22.6% of all flushes failed completely resulting in zero TE. This could be due mainly to the negative phenotypic as well as negative genetic correlations between milk yield and TE found in the present study. The genetic correlation between 305-d lactation milk yield and TE was -0.27 and -0.21 on the phenotypic scale. The phenotypic relationship between the production level and traits related to ET was analyzed in several previous studies (e.g. Wichmann, 2000; Manciaux et al., 2005). Manciaux et al. (2005) grouped donor cows according to their 305-d production level for milk yield. The average number of TE of cows producing more than 11,000 kg milk was 4.9 compared to 7.5 TE of donor cows ranging between 9000 kg and 11,000 kg of milk per year. Glatzel et al. (1999) focused their investigations on test day records when discussing phenotypic relationships between milk yield and TE. High levels of test day milk yield were generally associated with fewer TE. An explanation could be that potential energy intake is insufficient to express further production potential. Additional resources are drawn away from fitness related traits such as fertility and health (Van der Waaij, 2004) and therefore result in fewer TE.

Despite the optimization of ET when considering the amount of test day milk yield, mainly to find the optimal point during a cow’s lactation for flushing, breeding strategies can contribute to ensure more success of MOET breeding programs. Based on genetic parameters found in the present study, an index for potential bull dams including production traits as well as traits related to ET can be developed. Further studies in this field of research, also across country borders, can contribute to increase the amount of data and to ensure more reliable estimates for genetic variance and covariance components.

Genetic and phenotypic correlations among traits related to ET and the percentages of fat and protein were near zero (Table 3), except for DE. An increase of DE with increasing fat % was also found by Grunert and Berchthold (1999) who suggested that insufficient energy intake might be a contributing factor. Milk protein content, coupled with milk urea nitrogen levels, is related to energy balance and is a more accurate predictor of ET traits than protein content alone (Kafi and McGowan, 1997; Bosselmann et al., 2005). The genetic correlation between TE and SCS was -0.41 (Table 3) indicating that selection on improved udder health is associated with an increase in TE. A negative impact of SCS on non-return rates of cows was shown by Miller et al. (2001) and König et al. (2006). As indicated by the correlations found in the present study, fertility traits related to ET such as FO, TE, and PTE are also influenced by the status of udder health. Schrick et al. (2001) suggested an influence of clinical or subclinical mastitis on reproductive response by alterations in endocrine profiles and follicular development. Details of this physiological mechanism are given by Schrick et al. (2001) and Moore et al. (1991).

The correlated response in selection for different traits related to ET when selecting on the different production traits is shown in Table 4. Correlated response using the genetic parameters in this study was calculated by $\Delta G_{ET,PT} = \frac{r_g * \sigma_{a(ET)}}{\sigma_{a(PT)}}$ where the subscript *ET* describes the various traits related to ET and the subscript *PT* indicates the investigated production traits. An increase in milk yield by 1000 kg decreased the number of FO by 0.94 and decreased the number of TE by 0.46. As indicated by the low correlations in Table 3, even the unrealistically high increase of 1% for fat or protein% (Table 4) resulted in only minor changes in traits related to ET. The negative impact of SCS on TE, as expected when evaluating the genetic correlations in Table 3, was verified when focusing on the correlated selection response. An increase in SCS by one unit reduced the number of TE by 0.80 embryos. An index for potential bull dams after finishing their test at a central station, as developed by Kandzi (1988), should include non-production traits. An extension to traits related to ET as well as information about health such as SCS can contribute to more success of existing MOET breeding schemes when following the suggestions given in the present study.

Table 4. Correlated selection response for flushed ova (FO), transferable embryos (FE), degenerated embryos (DE), unfertilized oocytes (UO), and the percentage of transferable embryos (PTE) when selecting on various production traits.

Trait	FO	TE	DE	UO	PTE
Per 1000 kg increase in milk yield	-0.94	-0.46	0.01	0.05	-0.04
Per 1% increase in fat %	-0.05	-0.18	0.23	-0.03	-0.01
Per 1% increase in fat %	0.13	0.01	0.07	0.02	0.09
Per 1 unit increase in SCS	-1.64	-0.80	0.05	-0.19	-0.33

[1] PTE = percentage of transferable embryos = no. of transferable embryos / no. of flushed ova

CONCLUSION

Potential accumulation of genetic gain is limited by biological constraints, which in combination with genetic parameters determine the structure of breeding programs to be applied. Several theoretical investigations suggested the application of MOET breeding schemes, but their success often failed due to limited number of offspring per donor. As shown in this study, analyzing traits related to ET includes a complexity of several genetic groups. However, results show the feasibility of estimating variance and covariance among these groups in a synergistic context applying GLMM for different specific distributions (Normal, Binomial, and Poisson) of traits. The present study revealed, based on the estimates for genetic parameters, additional potential to include traits related to ET in a combined breeding goal for potential bull dams. Due to the higher heritability found for FO compared to TE, correlated selection strategies should be applied when improving TE. The most complex model was used for the status of pregnancy of recipients involving genetic effects of recipients and both genetic parents of the embryos. Following the original idea of synergistic models (Willham, 1963), a fourth genetic component describing the vitality of the embryo itself could be included in statistical models. Nevertheless, the attempt presented in this study was the first one utilizing synergistic models in the case of pregnancy after ET. Results revealed a moderate antagonism between the direct effect of the recipient and the maternal and paternal effect contributing to an embryo's vitality. This finding was verified when replacing the maternal and paternal effect by the genetic effect of the embryo itself. The genetic impact of the recipient was nearly 6% of the total variance for pregnancy and therefore, more important for the ultimate success in ET than embryo vitality. However, the practical relevance of this result is limited at the moment, because intensive selection for fertility of recipients is currently not realistic. Nevertheless, selecting for ET-related traits may be of increasing interest with a change to young sire breeding programs, as discussed in the context of introducing genomic selection in dairy cattle (Schaeffer, 2006), which will require short generation intervals and increased reproduction rates on all selection paths.

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CHAPTER V

USE OF REPEATED MEASURES ANALYSIS FOR EVALUATION OF GENETIC BACKGROUND OF DAIRY CATTLE BEHAVIOR IN AUTOMATIC MILKING SYSTEMS

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ABSTRACT

Milking frequencies measured at official test days were used with repeated measurement analysis to reveal environmental and genetic impact on the milking frequency of cows in automatic milking systems (AMS). Repeated measurements were 3 test day observations per cow within days in milk (DIM) classes from 1,216 cows in DIM class 1 (day 0 to day 99), from 1,112 cows in DIM class 2 (day 100 to day 199), and from 1,004 cows in DIM class 3 (day 200 to day 299) kept in 15 farms. Selection criteria for models analyzing repeated measurements were Akaike and Schwarz Bayesian values favoring the autoregressive (AR(1)) covariance structure instead of the compound symmetry (CS) model. Results from the AR(1) model indicated significant impact of fixed herd and parity effects. Milking frequencies decreased with increasing parities and were highest for first parity cows. High daily milk yield was associated with higher milking frequencies. Heritabilities for milking frequency were 0.16, 0.19 and 0.22, in DIM classes 1, 2, and 3, respectively applying the AR(1) model. Higher heritabilities in the later stage of lactation were due to a substantial reduction of the residual variance. Genetic correlations between test day milk yield and daily milking frequency were in a range of 0.46 to 0.57 for all DIM classes and between milking frequency and somatic cell score (SCS) near zero. For verification of results, milking frequencies of the same cows obtained from herd management programs were averaged within DIM classes. Heritabilities were slightly above the values from the AR(1) model. In conclusion, heritabilities for milking frequency in AMS are moderate enough to incorporate this behavioral trait in a combined breeding goal. The inevitable improvement of labor efficiency in dairy cattle farming demands such cows going easily and voluntarily in automatic milking systems.

Key words: automatic milking system, milking frequency, heritability, genetic correlation

INTRODUCTION

Rydhmer (2005) described behavioral genetics as a fascinating and important area of research. The genetic background, the environment and the interaction of heredity and environment result in the phenotypic expression of a behavior. Prior experiences analyzing behavior revealed complicating factors to distinguish between genetic and environmental components and this has to be considered to minimize the confounding from these sources (Buchenauer, 1999). Another concern is that especially in intensive farming systems, domestic animals may not express the full range of innate behavior because of intensive contact with humans (Schutz and Pajor, 2001). Compared with other topics of animal science, relatively little information on behavioral genetics in livestock is available. The ostensible reason is that traits of behavior are difficult to measure and data are often subjective impressions of observers, which increase the residual component. Furthermore, experimental designs for behavioral studies demand a huge amount of work, which probably explains the lack in published studies (Rydhmer, 2005). Beside this, Faure (1994) indicated that measures of behavioral traits were frequently not normally distributed, which complicates the estimation of variance components. Another problem is that cattle are often kept in herds, so that many behavior patterns were adopted by learning from group members and it is difficult or even impossible to distinguish between innate and learned behavioral traits. In a review of the inheritance of behavior in farm animals, Hohenboken (1986) reported genetic differences as determined by estimates of heritabilities. Genetic differences were found between breeds, breed crosses, strains and selection lines. However, most of the published research was conducted in beef cattle (Le Neindre et al., 1995; Gauly et al., 2004). Several working time studies (e.g. Gustafsson, 2004) revealed the importance of temperament in dairy cattle. Trilk et al. (2005) evaluated labor time in farms using robotic milking, which is defined as automatic milking systems (**AMS**). Compared with three times milking in a herringbone parlor, the yearly working hours requirement for milking in the AMS including additional time for milking unsuitable cows was 6.3 hours per cow lower. Nevertheless, the authors identified further potential for working time improvement, because fetching cows to the automatic milking box needed 29.9% of whole working hours for milking. Presupposing a genetic component for behavior, the voluntary entrance of cows in the milking system could be an important behavioral trait for selection decisions. In earliest studies investigating the genetics of behavior in dairy cattle, Burnside et al. (1971) pronounced differences among breeds for percentage culled for "bad" temperament, favoring Ayrshire followed by Jersey, Holstein and Guernsey. A first overview of estimated genetic parameters for temperament in dairy cattle was given by Schutz and Pajor (2001). They reported recent estimates of heritability for temperament in a range from 0.08 to 0.25 and concluded that temperament may have the potential to be included in the breeding goal, although the definition of temperament was not identical in the displayed studies as shown in Table 1.

Table 1. Estimates of heritability for behavioral traits and genetic correlations between behavior and production traits in Holstein dairy cattle (modified from Schutz and Pajor (2001).

Reference	definition of the trait	No. of cows	method	heritability	genetic correlation with milk yield$^{1)}$
Dickson et al. (1970)	Temperament score	1,017	Paternal half sib correlation	0.53	0.05
	Dominance value	921	Paternal half sib correlation	0.07	-0.02
Thompson et al. (1981)	Disposition	8,977	REML, sire model	0.06	
Agyemang et al. (1982)	No trouble	5,601	Henderson I sire model	0.07	
	Slight trouble	5,601	Henderson I sire model	0.06	
Baehr (1983)	feeding frequency	102	Paternal half sib correlation	0.61	
	resting period	102	Paternal half sib correlation	0.23	
Sullivan and Burnside (1988)	Ease of handling	18,178	Sire model	0.12	-0.15
	Milking behavior	18,178	Sire model	0.16	-0.17
	Aggressiveness at feeding	18,178	Sire model	0.11	0.23
Foster et al. (1988)	Disposition	43,428	REML, sire model	0.08	
Lawstuen et al. (1988)	Temperament	9,546	REML, sire model	0.12	0.12
Erf et al. (1992)	Trouble-free workability	5,353	REML, threshold model	0.11	0.25
	Overall satisfaction	5,653	REML, threshold model	0.08	0.69
Visscher and Goddard (1994)	Temperament score	14,596	REML, sire model	0.22	0.11
	Likeability	14,596	REML, sire model	0.18	0.50
Sewalem et al. (2001)	Milking temperament	706,826	Animal model		0.06$^{2)}$

[1] Positive correlations are favorable, i.e. cows giving more milk have the desired temperament.

[2] Correlation between estimated breeding values of bulls.

The definition of an automatic milking installation is that the cows decide when they will come to the milking area. Apart from the study conducted by Baehr (1983) the displayed results for genetic parameters in Table 1 were from subjective impressions of investigators. Baehr (1983) favored objective measurements, i.e. the records of voluntary entrances of cows in a feeding station or the resting period of cows in their boxes. Estimated heritabilities using average observations per cow and day were in a range from 0.23 to 0.61. Recent developments in mixed model theory and advances in computer software enabled the implementation of random effects in the statistical model and the modeling of the covariance structure of the data. Modeling the covariance structure is especially important for the analysis of repeated measurements, because measurements taken close in time are potentially higher correlated than those taken far apart from time (Littel et al., 1997).

The objective of our study was to estimate genetic parameters for the automatically recorded behavioral trait ‘milking frequency’ of cows in an AMS and its correlation with production traits using different methods for analyzing repeated measurements. For selection to be effective, reliable estimates of genetic parameters of behavioral traits are needed to determine the amount of genetic variation available. Correlations with other traits of economic importance are also required to define a combined breeding value in dairy cattle.

MATERIALS AND METHODS

Data

15 milking farms located in the north-western part of Germany using the same type of AMS were used in the study. The main characteristic for the chosen sample of farms was the fact that the entrance of cows in the milking box was mainly voluntary and regulations by employees were restricted to a minimal level. The feeding and management strategies in our research design over the whole period within and across farms were kept to be as constant as possible.

The general floor plan for voluntary traffic of cows is depicted in Figure 1. Some tasty concentrate feeds offered in the milking box in addition to the wish to be milked were the only known motivators for cows to move voluntarily into the AMS.

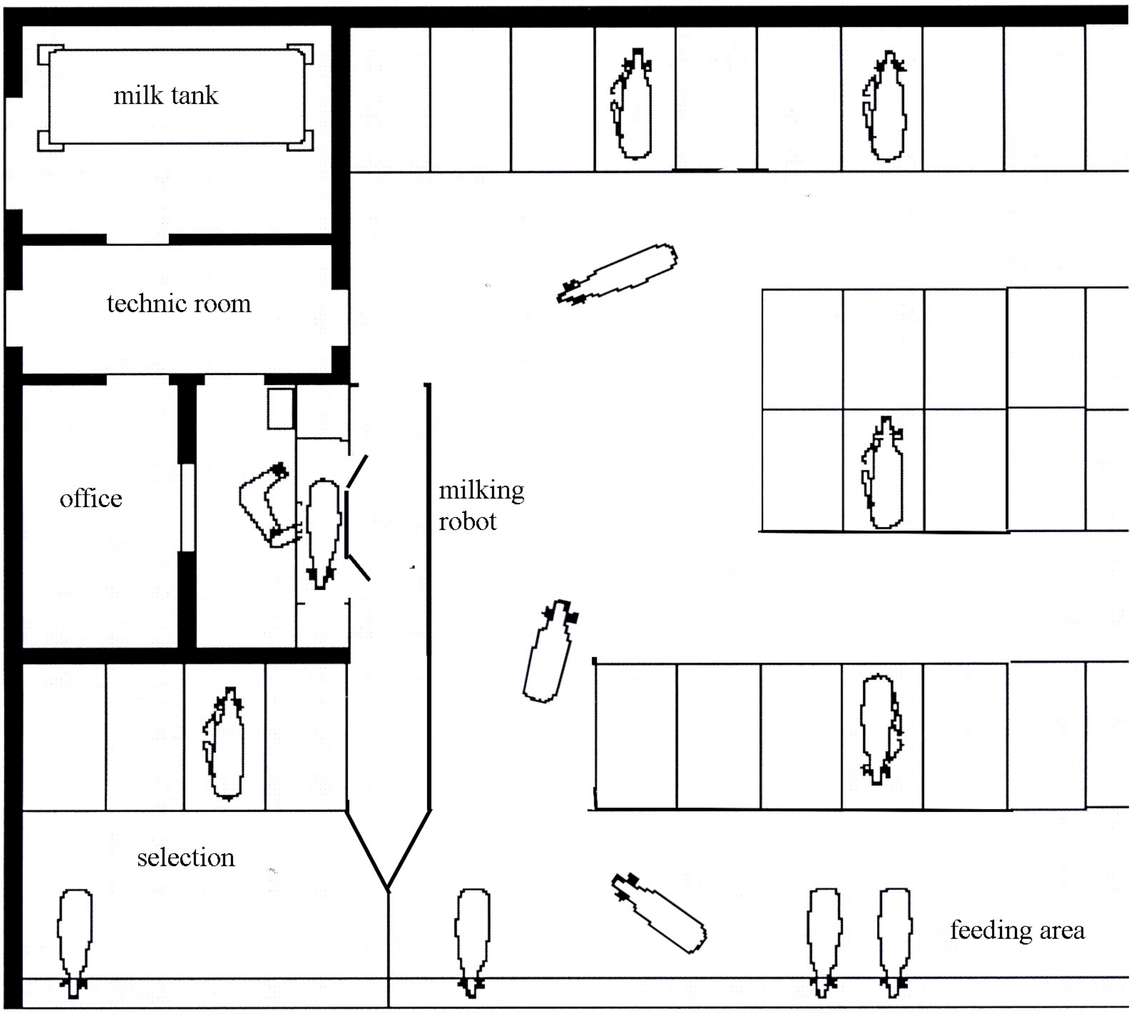

Figure 1. Schematic floor plan for voluntary traffic of cows in an AMS as used for our research design.

Milking frequency entries and production records were available from two different datasets. Dataset 1 comprised the results from the official milk recording scheme in intervals of four weeks which are utilized for the official national breeding value estimation. For the official milk recording in intervals of four weeks, a shuttle is connected to the AMS and over a period of 24 hours a sample is taken of each milking and milking frequency was counted. The sample provided data about the somatic cell count. The transformation procedure of AMS records for electronically measured milk yield and contents to 24 hour equivalents was applied as described by Buenger et al. (2001). Dataset 1 included cows calving in either 2003 or 2004 and therefore, no repeated measurements of cows across parities were available. Bohlsen (2000) indicated different behavior of cows in AMS related to their lactation stages. Based on these results, a general stratification of the data according to days in milk (**DIM**) after calving was done. The DIM class 1 was from day zero to day 99, the DIM class 2 from day 100 to day 199 and the DIM class 3 from day 200 to day 299 after calving. Data for repeated measure analysis (dataset 1) were 3 test day observations per cow within DIM classes from 1,216 cows in DIM class 1 (day 0 to day 99), from 1,112 cows in DIM class 2 (day 100 to day 199), and from 1,004 cows in DIM class 3 (day 200 to day 299).

In addition, milk yields from each visit in the milking box of these cows from dataset 1 were recorded by the farmers using herd management programs. Daily milk yields and daily milking frequencies from all available entrances in the milking box were stored in dataset 2. Cows that were less than 80 days present in the AMS within DIM classes were excluded from both datasets. A complete overview of the data and the genetic structure is given in Table 2.

Table 2. No. of cows, no. of milking days, no. of daughters per sire and average milking frequency (MF), milk yield (MY) and SCS for model 1 (repeated measure analysis) and model 2 (average observations) stratified by days in milk (DIM) classes.

	DIM class 1		DIM class 2		DIM class 3	
	model 1	model 2	model 1	model 2	model 1	model 2
No. of cows	1216	1216	1112	1112	1004	1004
No. of milking days[1]	3648	99,712	3336	96,744	3012	89,356
Average no. of daughters per sire[2]	9.7 (1 to 56)	9.7 (1 to 56)	9.1 (1 to 51)	9.1 (1 to 51)	8.4 (1 to 47)	8.4 (1 to 47)
Average MF per day	3.00	3.05	2.97	2.98	2.70	2.81
Average MY per day	32.41	32.60	28.16	28.02	22.45	22.65
Average SCS per day	3.44	3.53	3.51	3.54	3.69	3.69

[1] For model 1: 3 repeated measurements (official test days per

Statistical Models

Repeated measure analysis.

Milking frequencies in the AMS were available from 3 different test days for each cow within distinct DIM classes (dataset 1). This definition implied 3 repeated measurements within cow and DIM class for the behavioral trait milking frequency per cow and day. The statistical model included the fixed effects of the herd and the parity as well as a regression on milk yield and days in milk up to the third polynomial degree in order to fit regression curves. Interaction between parity and milk yield in linear and exponential terms was also considered in the model. The none significant regression coefficients of different polynomial structures were removed from the model by using F-statistics sum of square type I tests at $P < 0.05$ rather than likelihood ratio tests. Based on type I sums of squares at $P < 0.05$, a sequential analysis approach is appropriate for polynomial formulated models (Littel et al., 1999). The final model 1 for analyzing repeated measurements within DIM classes only included significant fixed effects and covariates as well as random additive genetic and permanent environmental effects of cows and was formulated as:

$$y_{ijkl} = \mu + H_i + parity_j + a_k + pe_k + \beta_1 MY_{ijk} + \alpha_1 DIM_{ijk} + e_{ijkl}$$

where

y_{ijkl} = milking frequency of cow k in the AMS per test day

μ = overall mean effect

H_i = fixed effect of herd i

$parity_j$ = fixed effect of parity j

a_k = random additive genetic effect of cow k

pe_k = random permanent environment effect of cow k

MY_{ijk} = milk yield of cow k in herd i and parity j

β_1 = linear regression of milking frequency on milk yield

DIM_{ijk} = days in milk of cow k in herd i and parity j

α_1 = linear regression of milking frequency on days in milk

e_{ijkl} = random residual effect belonging to observation

The ASREML program (Gilmour et al., 1998) was applied, which enables the user to directly address the covariance structure when analyzing repeated measures. Two covariance structures were investigated, the compound symmetry (**CS**) and the first-order autoregressive

AR(1) structure. First, the CS structure was fitted. This modeling implies that all measures over time have same variances and all pairs of correlations within the same animal, parity and DIM class are equal. The CS structure assumes equal correlation between all possible pairs of measurements. The AR(1) covariance structure allows for nonconstant covariances (Wade and Quaas, 1993). As suggested by Quaas (1984), the AR(1) structure was used for modeling the residual covariance structure when animals have repeated measures. The lag between measures was defined as the time dependent covariate 'days in milk' in model 1. The equation for the linear mixed model in matrix notation and the modeling of matrices for the CS model and the AR(1) model is given in detail by Sawalha et al. (2005a). Selection of the most appropriate covariance structure was based on Akaike's information criterion (Akaike, 1973). Akaike (1973) proposed a simple and useful criterion (**AIC**) for selecting the best-fit model among alternative models:

$$\text{AIC} = -2\ (\text{log likelihood}) + 2\ (\text{number of variance parameters})$$

Here, the model with the lowest value for AIC is favorable and should be applied. Another widely used information criterion is the Bayesian Schwarz information criterion (**BIC**). The BIC is defined as:

$$\text{BIC} = -2\ (\text{log likelihood}) - \log(n) \times \text{number of variance parameters}$$

where n is equal to the number of records used in the analysis as shown by Huisman et al. (2001). The third possibility to compare the goodness of fit between the two models was the application of the likelihood ratio test.

Average observations. Milking frequencies and milk yields per cow and day obtained from the herd management program (dataset 2) were averaged within cows and DIM classes. Using average observations of repeated measurements is a commonly used procedure, i.e. for achieving normality of data as was applied by Gregory et al. (1997) for the ovulation rate of six following estrous cycles in a beef cattle population. The ASREML software (Gilmour et al., 1998) was used to check significance of the fixed herd and parity effects as well as the effect of the covariate average daily milk yield up to the third polynomial degree. None significant effects at $P < 0.05$ were removed from the model 2, which was finally formulated as follows:

$y_{ijkl} = \mu + H_i + parity_j + a_k + \beta_1 MY_{ijk} + e_{ijkl}$

where

y_{ijkl} = average milking frequency per day of cow k in the AMS within DIM class
μ = overall mean effect
H_i = fixed effect of herd i
$parity_j$ = fixed effect of parity j
c_k = random additive genetic effect of cow k
MY_{ijk} = average milk yield per day of cow k in herd i and parity j within DIM class
β_1 = linear regression of milking frequency per day on average milk yield per day
e_{ijkl} = random residual effect belonging to observation

The AR(1) structure for modeling repeated measurements (model 1) and model 2 for average observations from the herd management program were used to estimate genetic correlations between traits. Genetic correlations between the daily milking frequency, daily milk yield and SCS were estimated in multivariate analysis by removing the covariate milk yield from model 1 and model 2. The daily somatic cell count was log-transformed into daily SCS to achieve normality and homogeneity of variances as given by Ali and Shook (1980). For all analysis, relationships of cows were considered in an animal model traced back to base animals born in 1940.

RESULTS AND DISCUSSION

Covariance structures

The AIC and BIC information criteria as well as the likelihood ratio test were used for the selection of the best covariance structure for analyzing repeated measures (Table 3). The smallest values were obtained when applying the AR(1) structure. In addition, all of the calculated likelihood ratio statistics were larger than the critical χ^2 values. The smallest calculated statistic was 25 between the AR(1) model and the CS model for DIM class 2. This value is larger than the critical χ^2 value at $P = 0.001$ with 1 degree of freedom, which is 10.83. The best fit comparing covariance structures for different models applying the SAS mixed procedure was also found by

Littel el al. (1997) when defining the AR(1) covariance structure for repeated measurements. Based on the results for fertility in laying hens, Sharifi (2004) suggested to include the time interval defined as the lag between repeated measurements in statistical models. Similar to our study, AIC values and BIC values were smaller for the AR(1) structure compared with the CS structure. Sawalha et al. (2005a) modeled first-order autoregressive covariance structures for test day permanent and environmental effects. The AIC criterion was better for the AR(1) structure compared with the CS model. They concluded the advantage of AR(1) models for variance component estimations and found smaller estimates for heritabilities than with the CS model. A second analysis conducted by Sawalha et al. (2005b) clearly pointed out that the use of an autoregressive covariance structure for short-term environmental effects is more adequate for breeding value estimation than the simple CS structure. The criterion for the goodness of fit was the highest accuracy for estimated breeding values utilizing autoregressive models.

Table 3. Akaike information criteria (AIC), Schwarz Bayesian information criteria (BIC), 2 log -L values for the CS[1] and AR(1)[1] covariance structure analyzing repeated measures and the AR(1) correlation coefficient ρ stratified by days in milk (DIM) classes (smaller values within DIM classes indicate the better model).

	DIM class1		DIM class2		DIM class3	
	Covariance structure		Covariance structure		Covariance structure	
Criterion / parameter	CS	AR(1)	CS	AR(1)	CS	AR(1)
AIC	12,406	12,329	11,201	11,076	8,633	8,546
BIC	12,416	12,329	11,211	11,086	8,642	8,556
2 log -L	12,402	12,325	11,097	11,072	8,629	8,542
LRT[2]	77		25		87	
ρ[3]		0.53		0.52		0.61

[1] CS model is a simple repeatability model with compound symmetry covariance structure for milking frequency per day environmental effects; AR(1) model assumes autoregressive covariance structure for milking frequency per day environmental effects.

[2] LRT = likelihood ratio test statistic for comparing CS models with AR(1) models.

[3] AR(1) correlation coefficient.

Estimates of autoregressive correlation coefficients (ρ) for the residuals with the AR(1) model were in the range of 0.52 to 0.61. Sawalha et al. (2005a) found lower estimates in the range of 0.23 to 0.38 for test day milk yields. They concluded that the small estimates of the correlation coefficient for residual effects is due to fact that the AR(1) model also included permanent environmental effects that were assumed to be common for all test day records for each cow.

Fixed effects and covariates

Analysis of variance for repeated measurements (AR(1) covariance structure) revealed significance for fixed effects of the herd ($P < 0.001$) and parity ($P < 0.01$) on the milking frequency per cow and day within all DIM classes. Similar results were obtained using model 2 and analyzing average observations within DIM classes. The least squares means for the milking frequency by parities analyzed separately for different DIM classes with both models are given in Table 4.

Table 4. Least-Square-Means for milking frequency by parities for different days in milk classes using repeated measurements and the AR(1)[1] covariance structure (model 1) and average observations (model 2). Standard errors of means are in brackets.

	Parity 1		Parity 2		Parity >2	
Days in milk	model 1[2]	model 2[2]	model 1[2]	model 2[2]	model 1[2]	model 2[2]
1-100	3.35^a	3.12^a	3.01^b	3.04^b	2.865^c	2.74^c
(DIM class 1)	(± 0.026)	(± 0.027)	(± 0.022)	(± 0.027)	(± 0.021)	(± 0.026)
101-200	3.26^a	3.03^a	2.95^b	2.99^b	2.802^c	2.69^c
(DIM class 2)	(± 0.026)	(± 0.027)	(± 0.021)	(± 0.030)	(± 0.023)	(± 0.028)
201-300	2.75^a	2.86^a	2.69^b	2.80^b	2.551^c	2.48^c
(DIM class 3)	(± 0.019)	(± 0.024)	(± 0.020)	(± 0.026)	(± 0.021)	(± 0.024)

[1] AR(1) model assumes autoregressive covariance structure for milking frequency per day environmental effects.

[2] Different superscripts within DIM classes and models indicate significant differences ($P < 0.01$, t-test).

Values for milking frequencies were higher for first parity cows when compared with cows at later parities. The effect of better locomotion due to reduced feet and leg disorders (König et al., 2005) or the effect of their smaller udder capacity can be anticipated. Cows in the earliest DIM class have higher milking frequencies compared with the following two classes. These findings agree with results described by Halm (2003) and Dzidic et al. (2004). Dzidic et al. (2004) divided the lactation stage in DIM classes identical to our study and they found out milking frequencies of 2.93, 2.50, and 2.16 in DIM classes 1, 2 and 3, respectively. They concluded an effect of higher milk yield in the early lactation stage on the milking frequency. We have included milk production as covariate in statistical models. The effect of higher milking frequencies at the early stages of lactation seemed to be influenced by additional effects, e.g. the human interference with cow movement could have an effect in this case. The association between the production level in daily milk yield and daily milking frequencies in our study is illustrated in Figure 2 for repeated measurements (model 1) and is also valid for DIM class 2 and DIM class 3. High milk yield increases cows' mobilization towards the milking box. This phenomenon was observed for all DIM classes. But even for the same values of daily milk yield in different DIM classes, milking frequencies in DIM class 1 were higher than in DIM class 2 and lowest in DIM class 3.

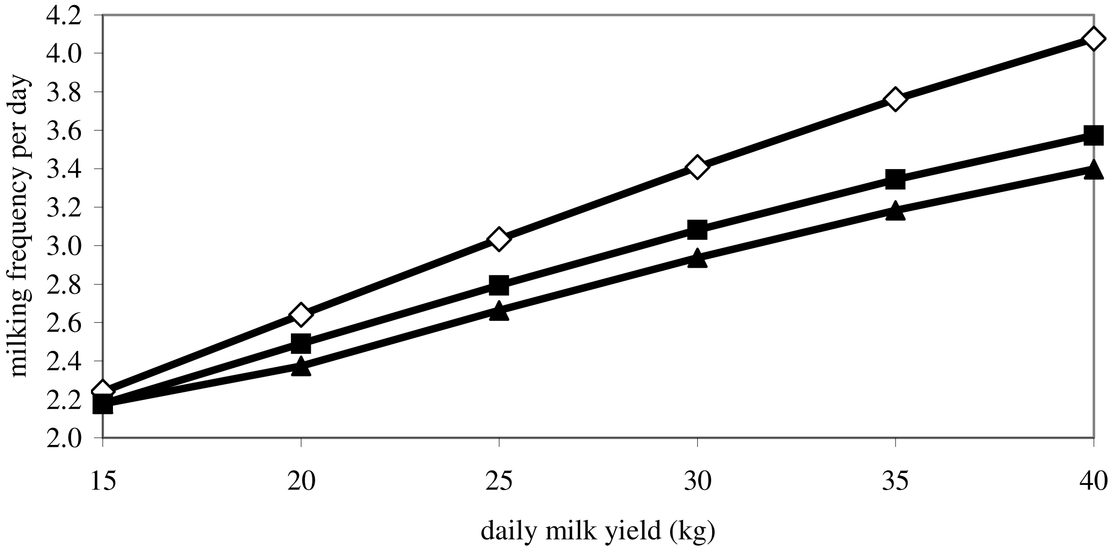

Figure 2. Least Square Means for milking frequency per day in parity 1(◊), 2 (■), and above 2 (▲) dependent on daily milk yield for DIM class 1 from 1 to 100 days after calving.

Genetic parameters

The models for repeated measures with the AR(1) covariance structure among the residual effects resulted in smaller estimates of heritability for milking frequency than with the CS model (Table 5). Heritabilities estimated with model 1were moderate and in the range of 0.16 in DIM class 1 to 0.22 in DIM class 3 with the AR(1) model and in the range of 0.17 to 0.23 with the CS model (Table 5). Sawalha et al. (2005a) estimated smaller additive genetic and permanent environmental variances for yield traits with the AR(1) model than with the CS model which resulted in marginal smaller heritabilities. Heritabilities using average observations (model 2) were slightly above the values from model 1 (Table 5).

Table 5. Variance components, heritabilities and standard error of heritabilities for milking frequency for different days in milk (DIM) classes using repeated measurements (model 1) and average observations (model 2).

	DIM class 1			DIM class 2			DIM class 3		
	model 1[1]		model2	model 1[1]		model 2	model 1[1]		model 2
Component	AR(1)	CS		AR(1)	CS		AR(1)	CS	
σ_a^2	0.083	0.088	0.058	0.087	0.089	0.086	0.084	0.087	0.070
σ_e^2	0.341	0.340	0.262	0.299	0.295	0.259	0.259	0.256	0.183
σ_{pe}^2	0.082	0.080	-	0.084	0.081	-	0.040	0.038	-
σ_p^2	0.506	0.508	0.320	0.470	0.465	0.343	0.383	0.381	0.246
h^2	0.164	0.173	0.182	0.185	0.191	0.249	0.219	0.228	0.276
$S.E._{h}^2$	0.041	0.041	0.039	0.052	0.051	0.048	0.049	0.049	0.048

[1] CS model is a simple repeatability model with compound symmetry covariance structure for milking frequency per day environmental effects; AR(1) model assumes autoregressive covariance structure for milking frequency per day environmental effects.

Higher heritabilities in the later stage of lactation were due to a substantial reduction of the residual component. It could be assumed that disturbing effects of farmers in the early lactation stage are mandatory for a cow's acclimatization to the automatic milking area, whereas in the following lactation stage after initial acclimatization, cows are more self-adjusting the milking process. A comparable research design to our study was developed by Baehr (1983). She estimated a heritability of 0.55 for the entrance frequency of cows in a feeding station and of 0.28 for the number of a cow's lay down period per day. Heritabilities for behavior or temperament of cows using subjective impressions or subjective given scores as compiled in Table 1 or outlined by Schutz and Pajor (2001) were generally lower than the values found in our study.

In conclusion, the amount of additive genetic variance is sufficient enough for breeding policies, but the integration of temperament in a combined breeding goal requires an exact definition of this trait. Temperament in dairy cattle can include milking behavior, easy handling and the dominance or aggressiveness of cows. The traditional meaning of milking behavior concerns a cow's ability to be calm and easy to handle during the milking process. Sullivan and Burnside (1988) reported a positive genetic correlation of 0.74 between milking behavior and ease of handling. Our definition of behavior in terms of milking frequency in the milking box also incorporated the dominance or aggressiveness of cows. Cows having a lower rank or status within the herd are likely to be suppressed from the milking box by cows having a higher rank. Sullivan and Burnside (1988) estimated the genetic correlation between milking behavior and aggressiveness to be close to zero. Presupposing such a negligible genetic correlation between milking frequency and milking behavior, selection on milking frequency will have no disadvantages on milkability. But for final breeding strategies, further investigations for relationships between different types of behavioral traits in automatic milking systems have to be done.

Genetic correlations between milking frequency and other production traits are of substantial interest, because selection in German dairy cattle is mainly focused on improved production (Rensing et al., 2002). Genetic correlations between milking frequency and daily milk yield were in a range between 0.46 to 0.57 for the model 1 applying the AR(1) covariance structure und model 2 for average observations within DIM classes (Table 6). These findings suggest that sires that have high proofs for production traits will tend to have daughters that come easily or voluntarily into the milking box. The positive genetic correlations for all DIM classes indicated that selection towards increased milk production would have desirable effects on the voluntary visits of cows in the milking box. However, the direct recording of temperament of cows will ensure additional genetic gain in a combined breeding goal composed of production and functional traits as well as temperament of cows. The derivation of economic weights for temperament of cows should be regarded as a crucial part for further breeding objectives, because fetching cows to the automatic milking box needed one third of whole working hours for milking (Trilk et al., 2005). The entrances of cows in an AMS is a measurement of behavior free of subjective impressions of investigators and can also contribute for the selection of cows coming voluntarily in conventional herringbone parlors.

Table 6. Genetic correlations (r_g) between milking frequency (MF), milk yield (MY) and SCS for different days in milk (DIM) classes using repeated measurements and AR(1)[1] covariance structure (model 1) and average observations. Standard errors or r_g in brackets.

	DIM class 1		DIM class 2		DIM class 3	
r_g	model 1	model 2	model 1	model 2	model 1	model 2
MF : MY	0.57	0.47	0.48	0.46	0.53	0.49
	(± 0.11)	(± 0.09)	(± 0.14)	(± 0.11)	(± 0.15)	(± 0.13)
MF : SCS	0.04	0.06	0.03	0.01	0.01	0.04
	(± 0.14)	(± 0.13)	(± 0.16)	(± 0.14)	(± 0.17)	(± 0.14)
MY : SCS	0.18	0.16	0.17	0.16	0.20	0.15
	(± 0.11	(± 0.10)	(± 0.12)	(± 0.10)	(± 0.14)	(± 0.12)

[1] AR(1) model assumes autoregressive covariance structure for milking frequency per day environmental effects.

Other studies estimating correlations between the production level in milk yield and behavior should be carefully compared to our results, because the definition of temperament differs between studies or experimental designs. Most correlations in dairy cattle between milk yield and milking temperament or between milk yield and social dominance, respectively, were near zero and therefore negligible (e.g. Dickson et al., 1970; Sewalem et al., 2001). Sullivan and Burnside (1988) identified cows that were genetically superior in production as the more aggressive ones during the feeding process. The displayed correlations were undesirable between EBVs for milk yield and EBVs for milking behavior and between EBVs for milk yield and EBVs for ease of handling of cows. Visscher and Goddard (1994) analyzed workability traits scored by farmers on heifers with a five-point linear scale. Good temperament and high likeability was genetically positively associated with higher milk yield. The same was found by Erf et al. (1992), i.e. overall satisfaction of cows or trouble free workability was favorably correlated with fat corrected milk. Discussing these results, the question remains whether such owner surveys are the best method to find out the genetic background of behavior. Our attempt to characterize behavior in dairy cattle is relatively free from subjective impressions of farmers, but further analysis should focus on correlations between different types of temperament, i.e. to find the relationship between the milking frequency of cows in AMS and behavior during the milking process.

Genetic correlations between milking frequency and SCS were near zero, regardless the choice of the model (Table 6). Estimates for genetic correlations were in a range of 0.01 to 0.06 with the AR(1) model for repeated measures and the model 2 analyzing average observations. Devir et al. (1993) suggested to utilize milking frequencies per day in the AMS as a controlling or management system, e.g. to control the status of udder health. Based on our results, there is none genetic background between milking frequency and SCS which indicates mastitis.

For completeness of results, genetic correlations between daily milk yield and SCS are presented in Table 6. The positive genetic correlation in a range of 0.15 to 0.20 confirmed results from previous studies (e.g. König et al., 2005) and indicates that selection or breeding on increased milk yield increases the susceptibility to udder diseases.

CONCLUSION

The present study has clearly shown the genetic background of dairy cattle behavior by analyzing objective measurements regardless of the method of analyzing the data. Genetic parameters from repeated measurement analysis using the AR(1) and CS covariance structures were in agreement with estimates from average observations. Heritability estimates were high enough for direct selection on behavior of cows, in our case the voluntary entrances of cows in the milking box. The positive genetic correlation between daily milk yield and daily milking frequency indicated that continued selection for high production may increase the proportion of cows going voluntary in the AMS. Genetic correlations between milking frequency and SCS were near zero.

The inevitable improvement of labor efficiency in dairy cattle farming as emphasized by Devir et al. (1993) and Trilk et al. (2005) as well as the effect of increasing robotic milking in Germany demand such cows going easily and voluntarily in automatic milking systems. The definition of the breeding goal, i.e. to include different aspects for temperament can make a contribution towards farmers and animals welfare. But nevertheless, beyond the possibilities towards genetic improvement of behavior, the fixed herd effect prevalently describing husbandry and feeding strategies was the most important factor in our study affecting the milking frequency of cows.

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CHAPTER VI

APPROACHES TO THE MANAGEMENT OF INBREEDING AND REALTIONSHIPS 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 8,030 bull dams was much more 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%. 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. Significant 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

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.

An increase of genetic relationships between parents implies, that the probability increases that the offspring receives identical copies of a single gene from male and female pathway of inheritance. Such alleles are "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; Kearny 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.

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 und 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-d milk yield	- 26,7 kg
			305-d fat yield	- 0,6 kg
			fat-%	- 0,0028 %
Casanova et al., 1992	Brown S.	Switzerland	305-d milk yield	- 28,0 kg
			305-d fat yield	- 0,1 kg
			fat-%	- 0,0005 %
Short et al., 1992	HOL	USA	305-d milk yield	- 22,6 kg
			305-d fat yield	- 0,8 kg
			305-d protein yield	- 0,9 kg
Miglior et al., 1995	Canada	Canada	SCS	+0,0012
Wiggans et al., 1997	Brown S.	USA	305-d milk yield	- 24,6 kg
			305-d fat yield	- 1,1 kg
			305-d protein yield	- 0,9 kg
	HOL	USA	305-d milk yield	- 29,6 kg
			305-d fat yield	- 1,1 kg
			305-d protein yield	-0,9 kg
	JER	USA	305-d milk yield	- 21,3 kg
			305-d fat yield	-1,0 kg
			305-d protein yield	- 0,8 kg
Smith et al., 1998	HOL	USA	305-d milk yield	-26,7 kg
			305-d fat yield	-0,9 kg
			305-d protein yield	-0,8 kg
			SCS	+0,002
			productive life	-5,9 days
Thompson et al., 2000	HOL	USA	305-d milk yield	-52 kg
			SCS	0.0

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 3,024 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 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.

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. 8,030 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 7,933 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 ten 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 ten sires were calculated. The last scenario for calculating relationships considered 7,933 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.

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-F. Ned Boy	3.6	2.9	2.6	3.4	3.3	3.6

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. 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. (1997), the depression per 1% of inbreeding is roughly about 1 kg protein considering 305-d 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 $(\frac{1}{2}\bar{R}_{ij} \times 1\ kg) \times 2$. 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: RZM_ad = RZM + $(\frac{1}{2}\bar{R}_{ij} \times 1\ kg) \times 2 \times 0.69$. 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.

RESULTS

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 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 x 0.095) = 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.

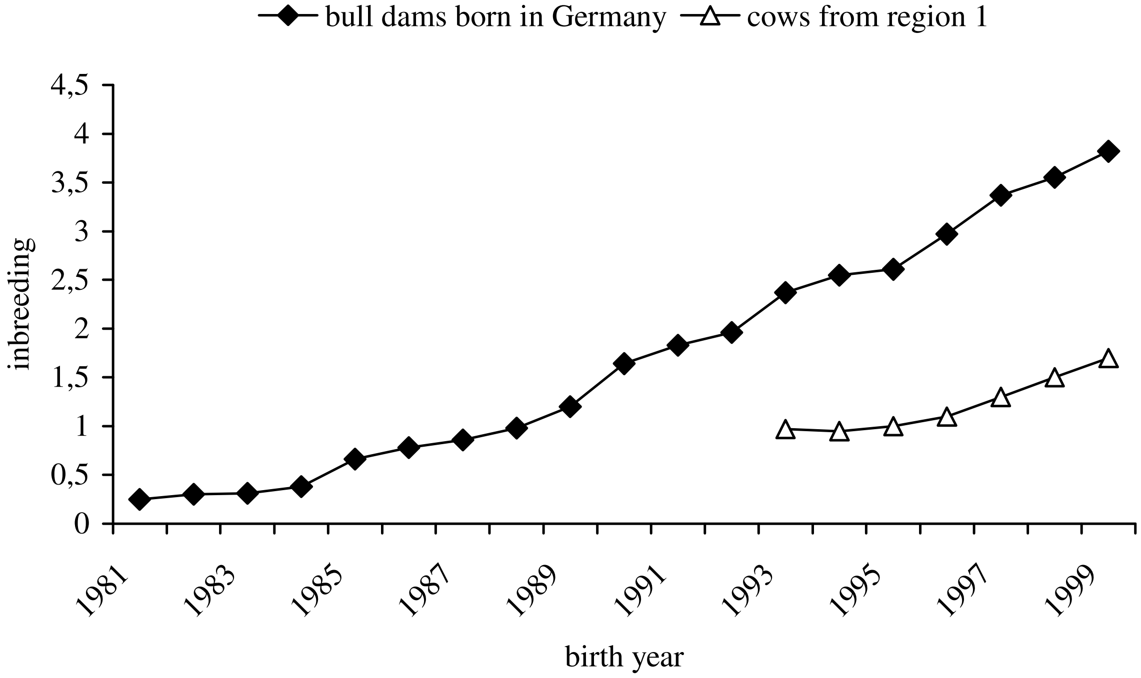

Fig. 1. Inbreeding coefficients (in %) for a subset of Holstein cows within one region of Germany and for bull dams of German young bulls by birth years

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.

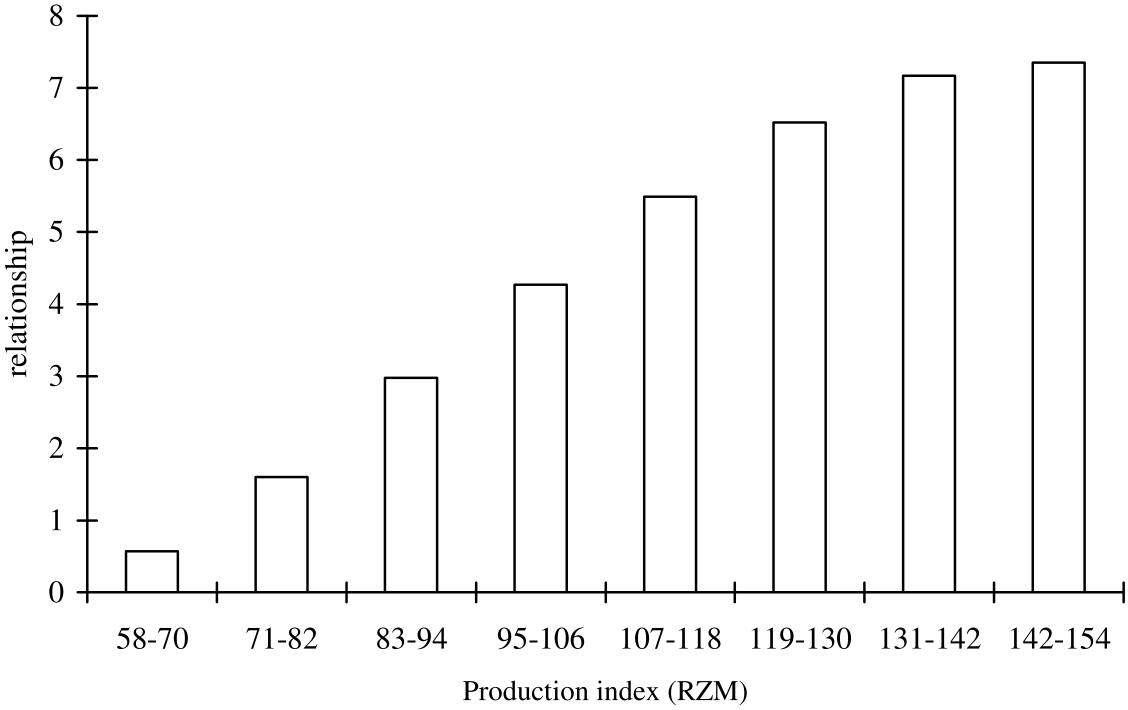

Fig. 2. Average relationship (in %) between AI bulls and cows from one region within Germany by RZM-classes for production traits

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. 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.

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	95.9^{a}	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

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.

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

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 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 is shown in Fig. 3.

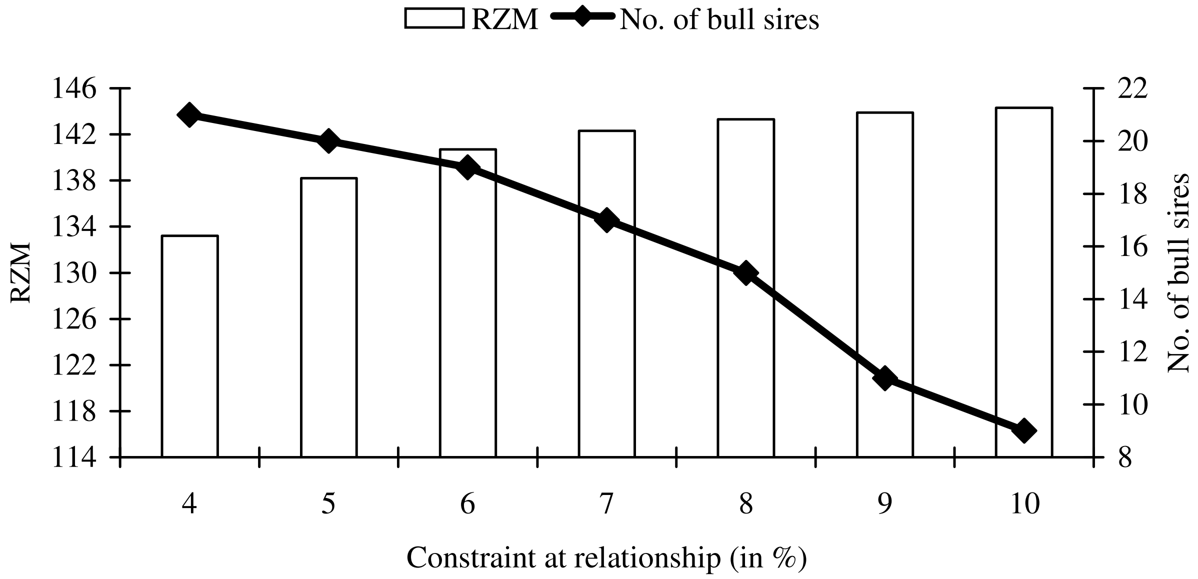

Fig. 3. Production index (RZM) of selected animals and number of bull sires at different constraints for average relationships

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.

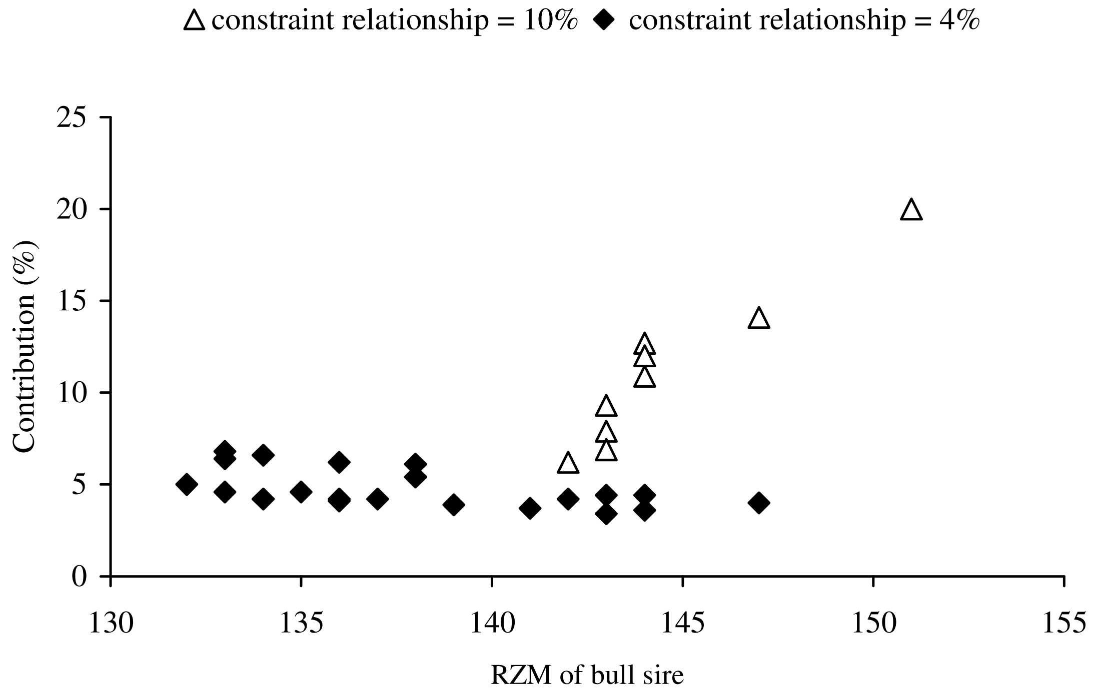

Fig. 4. Association between optimised contributions of bull sires and their production index (RZM) for two levels of constraint on average relationship

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 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 more 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 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.

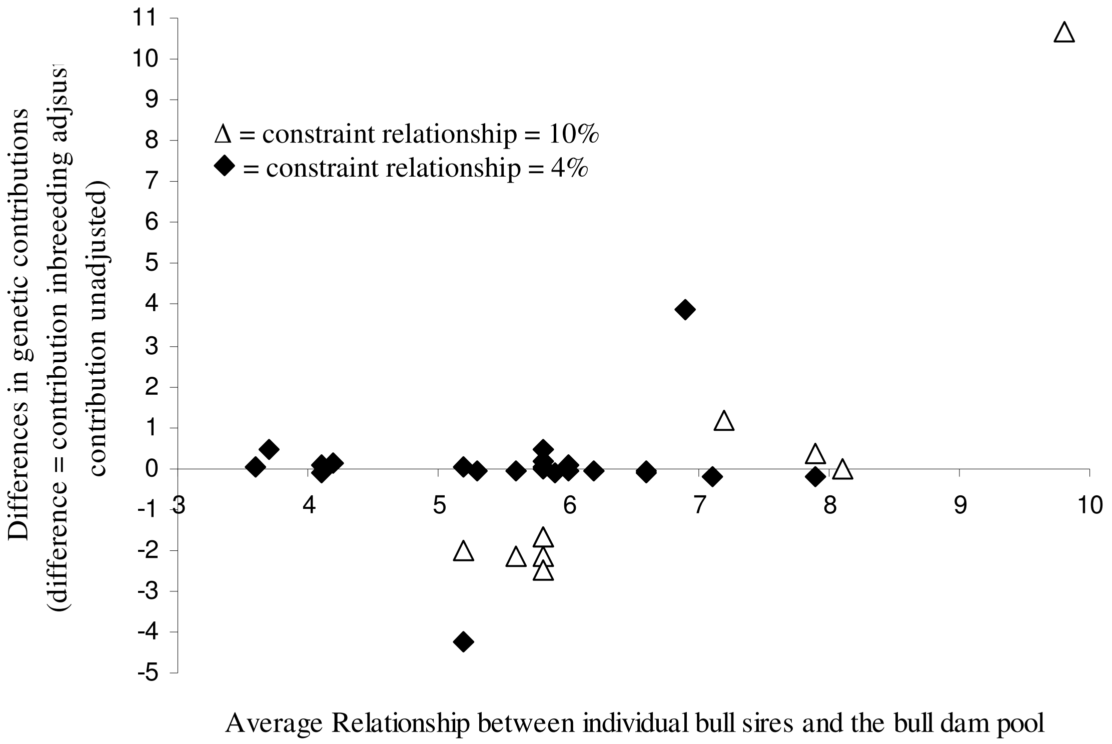

Fig. 5. Differences in genetic contributions for selected bull sires using inbreeding adjusted EBVs and non adjusted EBVs for two levels of constraint on average relationship

DISCUSSION

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 Kearny 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-carrries. 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 apporoximately 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.

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 an 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; Kearny et al., 2004), a substantial decrease of the average relationship coefficient would have been possible at each selection step without penalizing the average EBV. Kearny 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 fullfilling 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 substantial improvements in genetic gain greater than 20% compared to "conventional" BLUP strategies by maintaing same rates 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. Woolliams et al. (2002) have described the rate of inbreeding as a measure of risk from the perspective of the breeding program.

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. The approach seemes 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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CHAPTER VII

APPLICATION OF CONTROLLING INSTRUMENTS FOR IMPROVEMENTS IN COW SIRE SELECTION

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ABSTRACT

National estimated breeding values of bulls from 12 different German AI organizations from 1998 through 2006 were used to determine the differences in expected and realized selection intensities for cow sire selection considering the total merit index as well as sub-indices for production, conformation, somatic cell count, fertility, and functional herd life. The expected selection intensity was derived from the Gaussian distribution and the replacement rate describing the percentage of bulls graduated as cow sires from the total amount of progeny tested young bulls within AI organization and birth year. Realized selection intensities for all indices were derived from the selection differential of cow sires defined as the deviation of the average index of selected cow sires from the average index of the total amount of progeny tested young bulls. A low replacement rate of cow sires was associated with relatively high realized selection intensities for the total merit index, production and conformation index, but not related to the somatic cell count, fertility, and functional herd life index. The controlling value, defined as the ratio of realized and expected selection intensities, indicates the effectiveness of cow sire selection for different traits. Low controlling values, i.e. low realized selection intensities in combination with moderate or high expected selection intensities, suggest improvements in the step of cow sire selection, especially when discussing the total merit index. Analysis of variance revealed significant differences in expected selection intensities, realized selection intensities and controlling values for the total merit, production and conformation index between AI organizations and birth years of bulls. AI organizations applying well defined breeding policies (e.g. high controlling values for the total merit index) were successful in the national competition when evaluating the national common top list for the respective index regardless of the active population size. The suggested method also allows the comparison of the importance of different indices in selection decisions. Furthermore, controlling values can monitor additional potential in the improvement of cow sire selection with respect to the improvement of the genetic level in the whole population. The development of appropriate selection tools or controlling instruments is of increasing concern to monitor selection policies in the short term as well as for establishing sustainable breeding policies.

Key words: breeding programs, selection intensity, controlling cow sire selection

INTRODUCTION

The availability of artificial insemination (**AI**) led to breeding programs based on progeny testing (**PT**) as suggested by Henderson (1964) and Skjervold and Langholz (1964). Substantial genetic progress in production traits has resulted from conventional PT since the 1970's (e.g. Van Vleck and Van Tassel, 1991; Swalve and Höver, 2003), but some authors (e.g. Bolgiano et al., 1979; Van Vleck, 1987) expected additional genetic gain due to improved selection strategies.

The design parameters which have attracted the most attention for the optimization of PT were the proportion of cows mated to young bulls, the number of young bulls progeny tested per year and the number of daughters per young bull. For a given population size, the percentage of cows mated to young bulls and the number of daughters per young bull determine the number of young bulls to be progeny tested. Several papers focus on the optimization of these parameters during the last few decades (Skjervold and Langholz, 1964; Van Vleck, 1964; Oltenacu and Young, 1974; Dekkers et al., 1996). The optima for design parameters varied widely among studies depending on the objective. Including economical aspects, the optimum number of daughters per bull was higher and the proportion of mating to young bulls was reduced compared to studies whose objectives focused only on the maximization of genetic gain. These recommendations concerning test capacities and economics, mostly based on results from Dekkers and Shook (1990) and Dekkers et al. (1996), were implemented in dairy cattle breeding programs in Germany.

Despite the optimization of the number of bulls selected for PT and the number of daughters per bull produced, speed and accuracy of the PT, net merit of bull sires and bull dams as well as the intensity of selection after the test mainly determine the rate of genetic gain. Selection of superior bulls accounts for 70 to 76% of the total genetic gain that is possible in the dairy cattle population (Robertson and Rendel, 1950; Van Vleck and Murphy, 1983). Bull sires generate test bulls and their selection is one important tool in dairy cattle breeding programs regarding the level of inbreeding and relationships between animals as well as the genetic merit in future generations (König and Simianer, 2006). However, the selection of superior cow sires (**CS**) for AI among the total pool of young bulls also drew the attention of AI organizations. Evaluating the annual statistics of the German Cattle Breeders' Federation (ADR, 2004), 60% of the inseminations of cows were made with cow sires stemming from the own PT program. Based on this high proportion, selected cow sires out of the pool of pre-selected young bulls have an essential direct impact on phenotypic performances and also on estimated breeding values (**EBV**) of cows. Optimization and controlling of selection intensities for the most important traits following PT will be a crucial part in future dairy cattle breeding programs. Swalve and Höver (2003) analyzed genetic trends for production traits of cows within 4 distinct regions of Germany and they suggested additional genetic gain when focusing breeding objectives on a selection index closely related to the RZG. Following Swalve and Höver (2003) and the annual published statistics for AI (ADR, 2004), cow sire selection practiced by AI organizations not only depended on their total merit index, but was determined by traits such as direct calving ease or direct stillbirth increasing the market share for a short period. In the long term, success of AI organizations and accumulation of genetic gain will strongly depend on selection of superior sires according to their total merit index which combines all traits based on their genetic parameters and economic importance.

In this study, data of national breeding values over a period of eight years were used to compare selection policies in different traits and breeding programs. Evaluation of realized selection intensities of cow sires in most relevant indices and the comparison to expected possibilities, defined in this study as controlling values, can be a powerful instrument to verify selection decisions and eventually explain pronounced differences of success of AI organizations.

MATERIALS AND METHODS

Data were 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**) of Holstein bulls from EBV databases in August 1998 through February 2006 from 12 different AI organizations located in Germany.

In Germany, all indices are expressed as relative breeding values, standardized to a yearly rolling base with a mean of 100 and a standard deviation of 12 points. 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. The RZM includes fat kg and protein kg in the ratio of 1:4. Estimated breeding values of 18 linear conformation traits and 4 EBV for the general characteristics (angularity, body, feet and legs, and udder) are combined in the total composites for dairy type, body, feet and legs, and udder. The 4 total composites are then combined into a sub-index for total conformation called RZE. The reproduction sub-index (RZZ) is defined as an index combining the direct and maternal EBV for calving ease, stillbirth and non return rate. The solutions from the genetic evaluation of length of productive life are combined in the RZN sub-index with evaluations of indicator traits, i.e. predictors of longevity, through selection index calculations.

The decision of an AI organization to return a bull to service (cow sire for AI) or to cull the bull is generally made at the time of his first appearance in the quarter-annual data file (**EBV-1**) for national genetic evaluation having at least a reliability of 0.70 for production traits. Later evaluations (**EBV-2**) were analyzed to identify if the sire had second crop daughters or not, because EBV based on daughters from graduated sires are marked in the data file and therefore are distinguishable from EBV only based on PT. A bull is identified in the data file for second crop daughters when at least five additional daughters with test day records seven years after the birth of the bull are identified. Due to the time lag between EBV-1 and EBV-2, the study is restricted to historical data encompassing bulls of the birth years between 1992 and 1996. Exemplarily for two bulls born in December 1992 and December 1996, Table 1 characterizes the main events in the bulls' lifetime which were essential for the applied method. A similar method for evaluating international EBV and to identify differences in breeding objectives across countries was used by Powell et al. (2003).

Table 1. Stations in life of sires born in 12/1992 and 12/1996: From birth until breeding value estimation based on second crop daughters.

	Information based on PT[3]					Graduated cow sire		
Birth	Start PT	End of PT	Birth of calves	Calving of daughters	EBV-1[1)]	Birth of calves	Calving of daughters	EBV-2[2)]
12/1992	05/1994	09/1994	06/1995	12/1997	08/1998	04/1999	10/2001	02/2002
12/1996	05/1998	09/1998	06/1999	12/2001	08/2002	04/2003	10/2005	02/2006

[1)] EBV-1 = decision of cow sire selection (graduating or culling) and station of life when calculating pedigree indices

[2)] EBV-2 = database of estimated breeding values for the applied method for verification of culling or graduating at EBV-1

[3)] PT = Progeny testing

Table 2. Number of young bulls (test capacity), replacement rates (p in %) and expected selection intensities (i_e) for cow sires stratified by AI organizations averaged over birth years of bulls from 1992 to 1996.

AI organization	Test capacity		Replacement rate		Expected selection intensity	
	Mean	SD	Mean	SD	Mean	SD
A	42.0	4.6	13.8	5.3	1.60	0.19
B	22.6	2.2	14.0	6.1	1.59	0.22
C	61.8	2.5	14.8	3.5	1.56	0.12
D	61.6	5.4	26.4	8.5	1.24	0.20
E	139.2	8.9	8.4	2.1	1.84	0.11
F	53.8	2.5	18.8	9.2	1.43	0.25
G	52.8	3.7	12.2	4.6	1.66	0.18
H	118.2	4.5	8.2	2.8	1.85	0.09
I	43.4	2.4	20.0	5.6	1.40	0.16
J	40.2	2,8	16.1	6.2	1.52	0.21
K	64.2	3.3	8.0	1.1	1.86	0.06
L	42.2	4.6	10.6	3.1	1.73	0.13
Mean	61.8	3.9	14.3	5.3	1.58	0.17

Realized selection intensities ($\mathbf{i}_{\mathbf{r(j)}}$) for cow sires in indices for RZG, RZM, RZE, RZS, RZZ, and RZN were calculated as follows:

$$i_{r(j)} = \frac{\mu_{\text{index}_{(j)}-\text{CS}} - \mu_{\text{index}_{(j)}-\text{PT}}}{\sigma_{\text{index}_{(j)}}}$$

where $\mu_{\text{index}-\text{CS}}$ is the average index of selected cow sires within AI organization and birth year at EBV-1, $\mu_{\text{index}-\text{PT}}$ is the average index of all progeny tested bulls from the same AI organization and birth year at EBV-1, and σ_{index} is the respective standard deviation. The subscript *j* indicates the different indices. The expected selection intensity ($\mathbf{i}_\mathbf{e}$) was derived from the Gaussian distribution and the replacement rate. This indicates that i_e is equal for all indices within birth year and AI organization, whereas $i_{r(j)}$ depends on the different indices *j*. The replacement rate describes the percentage of bulls graduated as cow sires from the total amount of progeny tested young bulls within AI organization and birth year. A more stringent selection of cow sires increases the expected selection intensity and should increase the realized selection intensity in most important indices, supposing the graduation of superior bulls according to their total merit index. Table 2 gives an overview of test capacities, replacements and expected selection intensities stratified by AI organizations and averaged over the birth years of bulls. Replacement rates of cow sires varied highly among AI organizations and were extremely low and constant for organizations E and K showing values of 8.4 and 8.5% for replacements with a standard deviation of only 2.1 and 1.1, respectively. In AI organization D a less stringent selection was applied. Over one quarter (26.4 %) of all bulls were graduated as cow sires regarding birth years from 1992 to 1996.

Table 3. Steps for monitoring or controlling cow sire selection and interpretation of results

Step for monitoring or controlling[1]	Indicator	Practical relevance and suggestion for the AI organization
(1) Comparison of $i_{r(j)}$ over time	Relevance of traits in cow sire selection decisions over time	Verification of historical selection decisions
(2) Analyses of $i_{r(j)}$ over AI stations within birth years of bulls	Relevance of traits in current cow sire selection decisions	Low values of $i_{r(j)}$: Verification of reasons; increase of $i_{r(j)}$
(3) Analyses of i_e	Intensity of graduation of cow sires (replacement rate)	Low values of i_e: Stronger graduation of cow sires
(4) Analyses of $co_{(j)} = \frac{i_{r(j)}}{i_e}$	Controlling cow sire selection: Realized selection intensity in dependency of the expected potential	Low values of $co_{(j)}$: Verification of reasons; increase of $i_{r(j)}$

[1] $i_{r(j)}$ = realized selection intensity for index j, i_e = expected selection intensity, $co_{(j)}$ = controlling value for index j

Comparing $i_{r(j)}$ or i_e, or a combination of both, four different analyses of practical relevance are given in Table 3. First of all, results for $i_{r(j)}$ across the different trait complexes allow the comparison of the relevance of traits for selecting cow sires over time. Secondly, the comparison of $i_{r(j)}$ over AI organizations can give hints for the improvement in current cow sire selection decisions. Thirdly, low values for i_e suggest to decrease the replacement rate of cow sires to increase the genetic level in the population through a restricted selection of superior sires. And, at last and most important, low values for $i_{r(j)}$ in combination with moderate or high values for i_e suggest to focus selection more on the respective index, especially when discussing the total merit index. This last case emphasizes the magnitude of one essential controlling instrument in practical dairy cattle breeding programs: The comparison of realized values ($i_{r(j)}$) in different indices from the expected potential (i_e) defined as controlling value $co_{(j)} = \frac{i_{r(j)}}{i_e}$. Low controlling values indicate an intensive graduation of cow sires, i.e. a small number of selected sires to produce second crop daughters, but low realized selection intensity in the respective index j. The realized selection intensity should be of the same dimension compared with the expected potential, especially for the most important index, the RZG. However, without inclusion of the pre selection of young bulls into the analyses (e.g. the genetic merit of bull dams and bull sires) the suggested method might not allow for the optimal comparison of the importance of different indices in selection decisions. An additional approximate calculation was done to derive the impact of indices adjusted for pre selection on $i_{r(j)}$ and $co_{(j)}$. A pedigree index (**$PI_{(j)}$**) for all traits and bulls, also standardized on a mean of 100 and a standard deviation of 12 points, like the relative breeding values, was calculated considering indices of sires and maternal grandsires (**MGS**) weighted by the coefficients of relationship as follows:

$$PI_{(j)} = 0.5*(\text{index}_{(j)}\text{-sire}) + 0.25*(\text{index}_{(j)}\text{-MGS})$$

$PI_{(j)}$ were also calculated for each bull at the time of his first appearance in the quarter-annual data file (Table 1) for national genetic evaluation having at least a reliability of 0.70 for production traits. Ignoring indices of bull dams when constructing the $PI_{(j)}$ does not account for possible Mendelian sampling effects. On the other hand, potential biases in results of the current study due to preferential treatment of cows may have been avoided (Kuhn et. al., 1994).

The adjustment of realized selection intensities was:

$$i_{r(j)}\text{adjusted} = \frac{(\mu_{\text{index}_{(j)}-CS} - \mu_{\text{index}_{(j)}-PT}) + \Delta PI_{(j)}}{\sigma_{\text{index}_{(j)}}} \quad \text{with } \Delta PI_{(j)} = PI_{(j)} - (\sum_{k=1}^{k=n} PI_{(jk)})/n \text{ and}$$

k = numbers of bulls within birth years. The adjustment procedure rewards a more intensive preselection and allows a more accurate comparison of the importance of different traits in selection decisions.

Analysis of variance was applied to identify the impact of birth years and AI organizations on i_e, $i_{r(j)}$, and $co_{(j)}$. Beyond the overall mean effect and the random residual component, the statistical models included fixed effects of the AI organization and the birth year of bulls.

In a second step, the impact of controlling values on success of AI organizations was investigated for the different indices. In Germany, the estimation of breeding values for the Holstein breed is centralized and results are ranked nationally, but the 12 different AI organizations operate regionally. This means that PT is performed within distinct regions and the main intention of AI organizations is to increase the number of own bulls at the top of the common list for RZG. A success rate (**SR**) for AI stations stratified by birth years of bulls was computed as follows:

$$\mathrm{SR}_{(j)} = \frac{\text{percentage of own bulls in a top list of } \mathrm{N} = 100 \text{ for trait } j}{\text{percentage of own bulls at the total test capacity}}$$

The higher the value for SR, the more successful was the respective AI organization. Analysis of variance applying the procedure MIXED (SAS, 1994) was used to identify the impact of several effects on SR in RZG, RZM, RZE, RZS, RZZ, and RZN. The statistical model included the fixed effects of the birth year of bulls and the population size of the distinct AI region as well as a regression on controlling values up to the fourth polynomial degree in order to fit regression curves. Population size was divided in 3 classes: ≤ 100,000 cows, from 100,001 to 150,000 cows, and > 150,000 cows.

The non significant regression coefficients of different polynomial structures were removed from the model by using F-statistics sum of square type I tests at $P < 0.05$ rather than likelihood ratio tests. Based on type I sums of squares at $P < 0.05$, a sequential analysis approach is appropriate for polynomial formulated models (Littel et al., 1999).

RESULTS AND DISCUSSION

Realized selection intensities in relation to expected selection intensities

Realized and expected selection intensities for AI organizations and different birth years of bulls are shown for RZG, RZM, RZE, RZS, RZZ, and RZN in Figures 1 to 6, respectively.

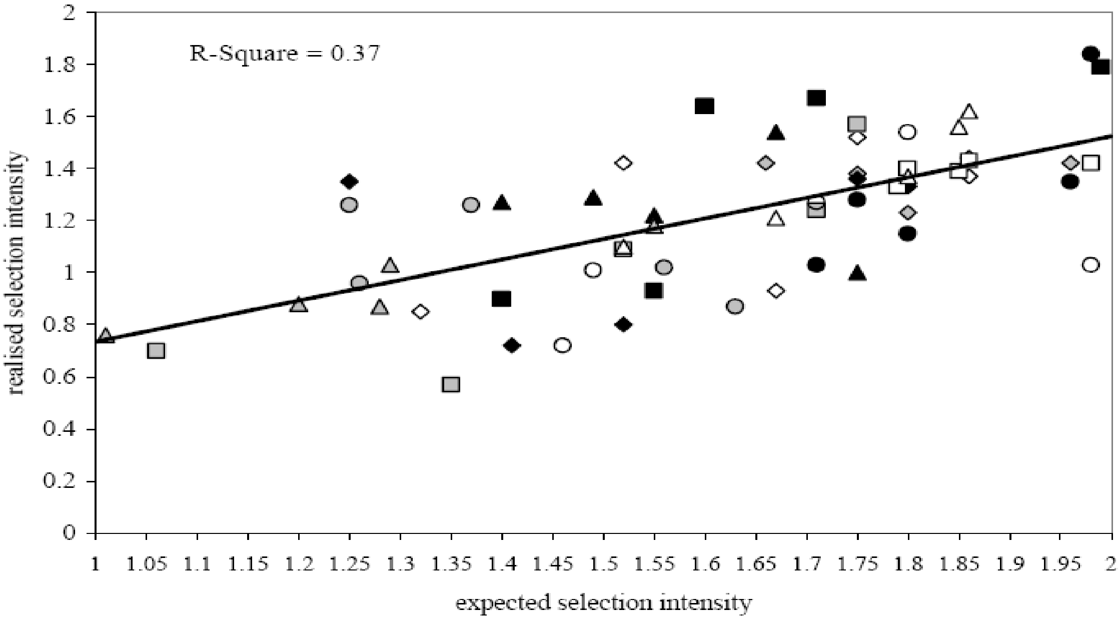

Figure 1. Realized selection intensities ($i_{r(RZG)}$) in dependency of expected selection intensities (i_e) for 12 different AI organizations stratified by birth years of bulls from 1992 to 1996 for the total merit index (RZG). (Different symbols denote different AI organizations, solid line = linear regression of $i_{r(RZG)}$ on i_e).

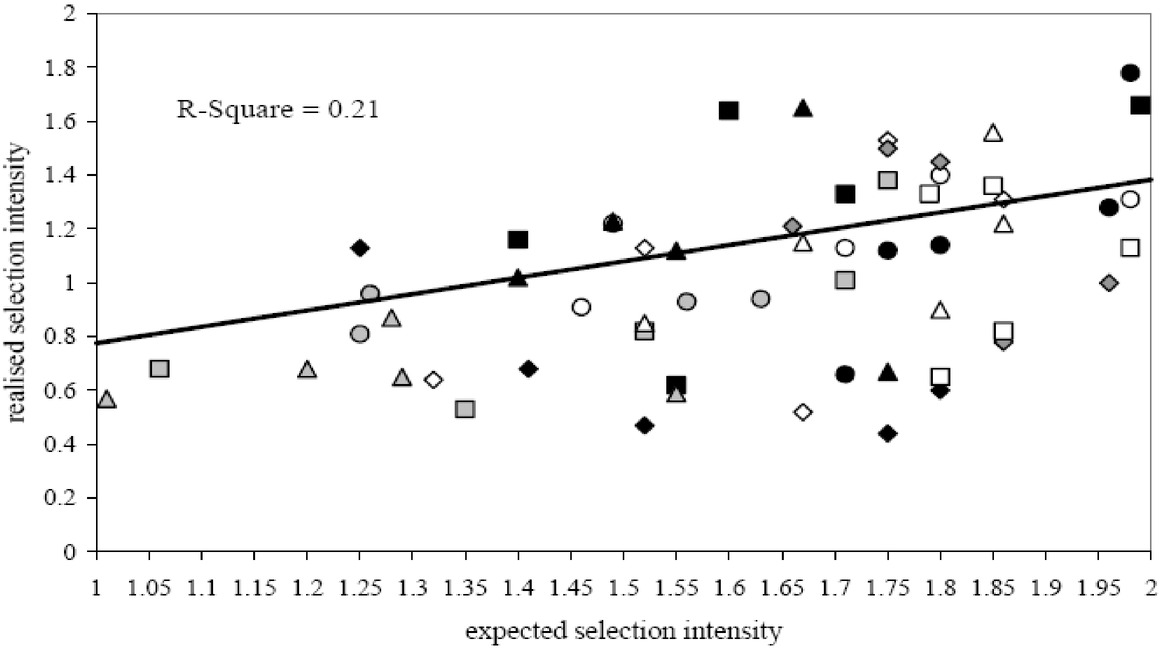

Figure 2. Realized selection intensities ($i_{r(RZM)}$) in dependency of expected selection intensities (i_e) for 12 different AI organizations stratified by birth years of bulls from 1992 to 1996 for the production index (RZM). (Different symbols denote different AI organizations, solid line = linear regression of $i_{r(RZM)}$ on i_e).

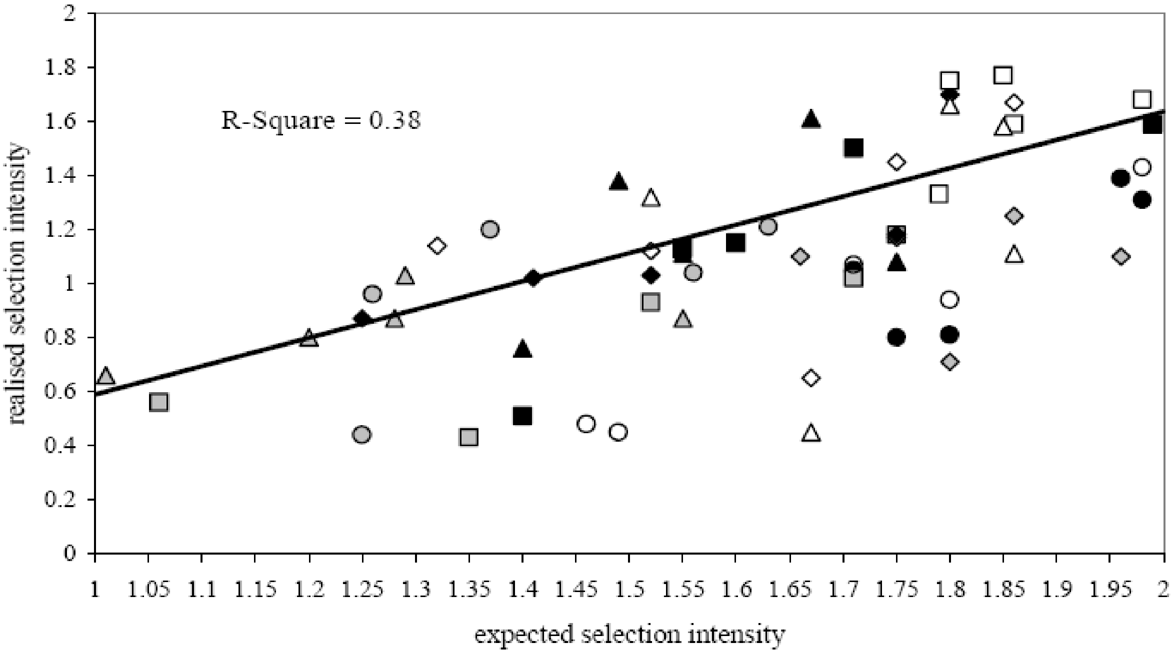

Figure 3. Realized selection intensities ($i_{r(RZE)}$) in dependency of expected selection intensities (i_e) for 12 different AI organizations stratified by birth years of bulls from 1992 to 1996 for the conformation index (RZE). (Different symbols denote different AI organizations; solid line = linear regression of $i_{r(RZE)}$ on i_e).

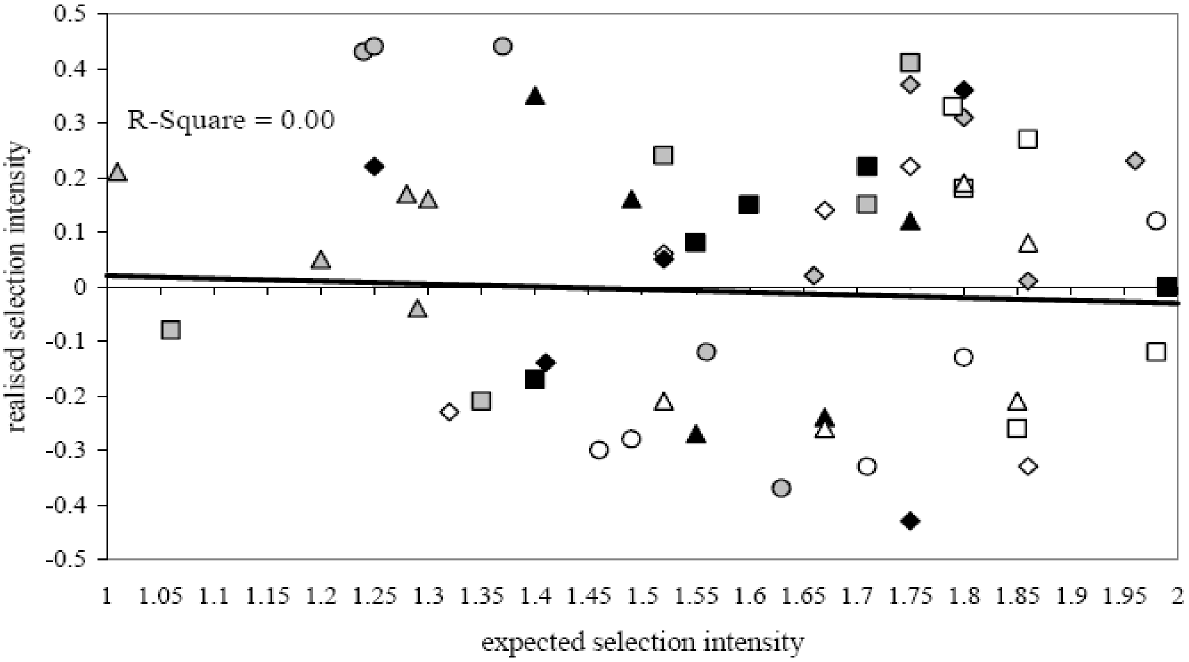

Figure 4. Realized selection intensities ($i_{r(RZS)}$) in dependency of expected selection intensities (i_e) for 12 different AI organizations stratified by birth years of bulls from 1992 to 1996 for the somatic cell count index (RZS). (Different symbols denote different AI organizations, solid line = linear regression of $i_{r(RZS)}$ on i_e).

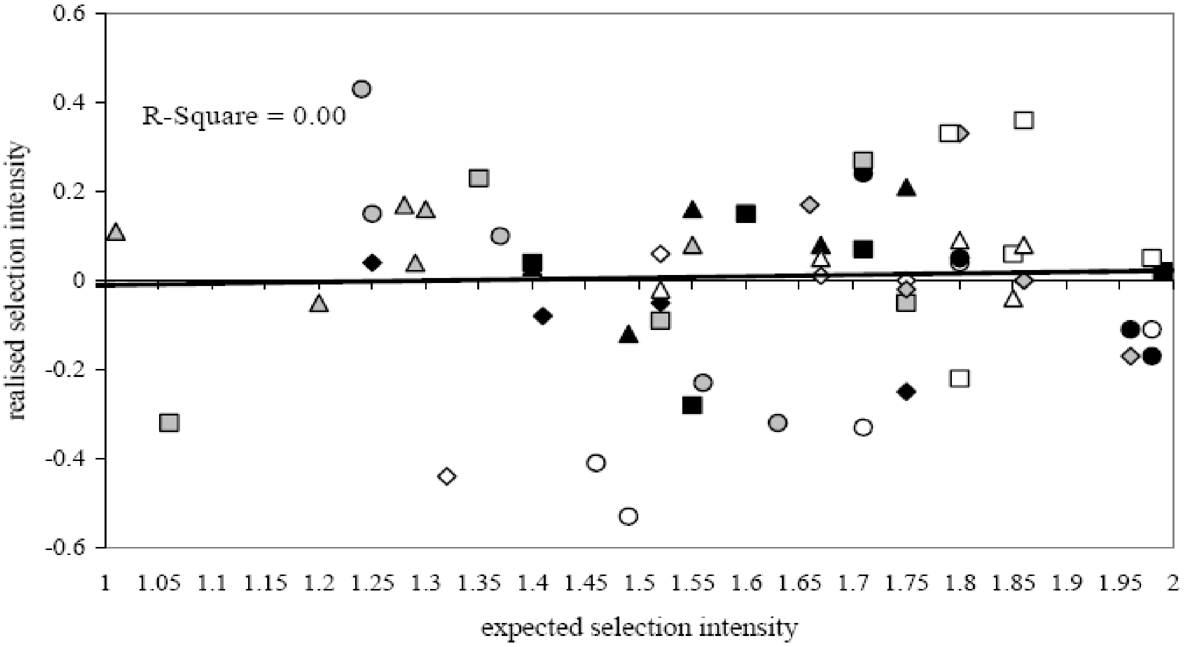

Figure 5. Realized selection intensities ($i_{r(RZZ)}$) in dependency of expected selection intensities (i_e) for 12 different AI organizations stratified by birth years of bulls from 1992 to 1996 for the fertility index (RZZ). (Different symbols denote different AI organizations, solid line = linear regression of $i_{r(RZZ)}$ on i_e).

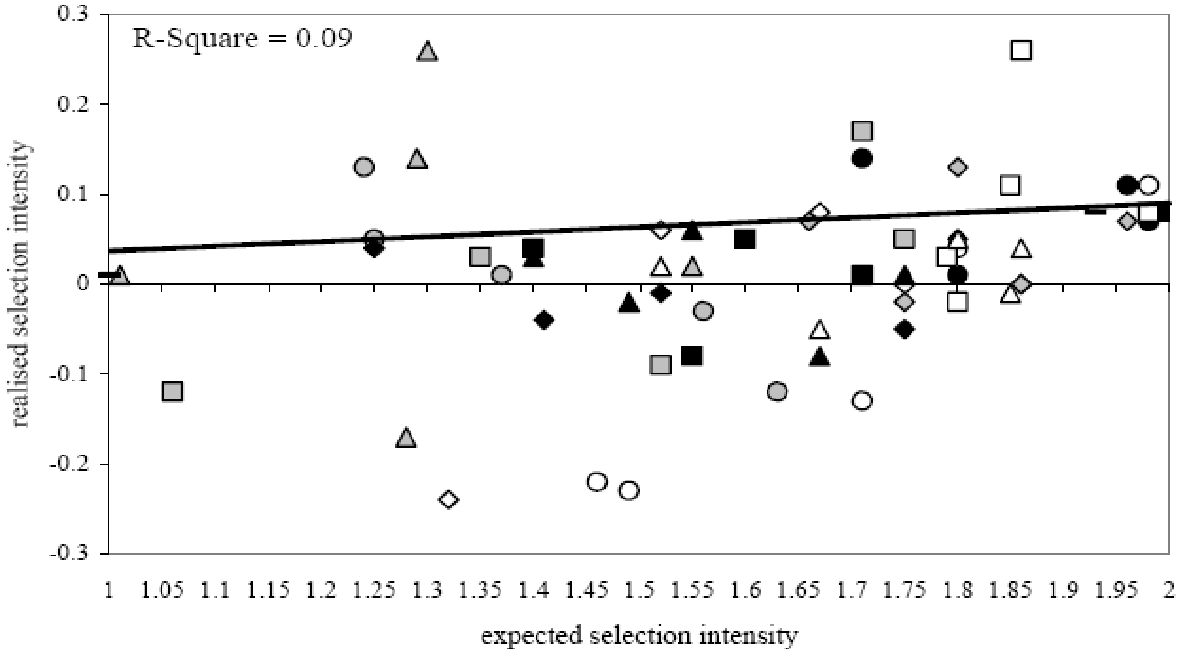

Figure 6. Realized selection intensities ($i_{r(RZN)}$) in dependency of expected selection intensities (i_e) for 12 different AI organizations stratified by birth years of bulls from 1992 to 1996 for the functional herd life index (RZN). (Different symbols denote different AI organizations, solid line = linear regression of $i_{r(RZN)}$ on i_e).

Each data point in the Figures indicates a combination of $i_{r(j)}$ and i_e, where for one AI organization and one birth year one symbol was used. For RZG, RZM and RZE, a pronounced dependency of $i_{r(j)}$ on i_e was found, whereas realized selection intensities for the sub-indices of functional traits (RZS, RZZ, and RZN) were not or less affected from the expected potential. Regression coefficients for $i_{r(RZG)}$, $i_{r(RZM)}$, $i_{r(RZE)}$, in dependency of i_e were 0.74, 0.45, and 0.89, respectively, but were near zero for RZS (-0.01), for RZZ (0.04), and for RZN (0.06). These results indicate that the graduation of cow sires in Germany born between1992 and 1996 was mainly based on the total merit (RZG) as well as on RZE and RZM. Intensive selection on RZG indirectly improved selection intensities of RZM and RZE, and vice versa, because RZM and RZE have the highest impact on the total merit index (Rensing et al., 2002). In the middle and at the end of the 1990's, the weights for RZS, RZZ, and RZN in the total merit index were only 14% , 4%, and 6%, respectively, which encouraged AI stations to select on indices for production and conformation regardless of the index for somatic cell count or fertility. Due to the negative correlations or correlations near zero between production and so called functional traits as summarized by Thaller (1997), selection on production has led to slightly negative or negligible realized selection intensities for RZS and RZZ.

Expected selection intensities

Least square means for expected selection intensities are shown in Table 4. A range from 1.25 to 1.86 for expected selection intensities indicate quite different breeding strategies of the German AI organizations. An expected selection intensity of 1.25 means that one of four young bulls was selected as a cow sire, whereas other AI organizations accomplished a more stringent selection program applying replacement rates for cow sires of about 6%. Analysis of variance for i_e revealed pronounced significant effects of the AI organization ($P < 0.001$) and birth year of bulls ($P < 0.01$). Both effects together explained 67.9% of the total variation in i_e. Results indicate that expected selection intensities or replacement rates of cow sires were not at random, but rather determined by the breeding policy of AI organizations (Table 4). Least Square means for i_e indicate a more severe selection of cow sires in younger birth years (Table 5). Utilizing Interbull data from 1995 through 2002, Powell et al. (2003) calculated a replacement rate of 15.8% (i_e = 1.53) for German cow sires which is close to the expected selection intensities found in this study for individual AI organizations.

Table 4. Least Square Means for expected selection intensities (i_e), realized selection intensities ($i_{r(j)}$) and controlling values ($co_{(j)}$) in indices j = RZG, RZM, RZE, RZS, RZZ, and RZN for different AI organizations.

		Index[1]											
		RZG		RZM		RZE		RZS		RZZ		RZN	
AI organization	i_e	i_r	co	i_r	co	i_r	co	i_r	co	i_r	co	i_r	co
A	1.58	1.14	0.72	0.94	0.59	1.13	0.72	0.03	0.01	-0.11	-0.07	0.11	0.07
B	1.61	1.39	0.86	1.14	0.70	1.18	0.72	0.08	0.05	-0.02	-0.01	0.07	0.04
C	1.57	1.25	0.80	1.15	0.73	1.19	0.75	0.02	0.02	0.07	0.04	0.08	0.05
D	1.25	0.94	0.75	0.69	0.55	0.80	0.65	0.14	0.11	0.08	0.07	-0.01	-0.01
E	1.84	1.33	0.72	1.20	0.64	1.07	0.58	0.03	0.02	0.01	0.01	0.09	0.05
F	1.48	1.03	0.68	0.88	0.59	0.82	0.55	0.04	0.02	0.01	-0.01	0.00	0.00
G	1.69	1.11	0.66	1.19	0.71	0.87	0.50	-0.07	-0.05	-0.27	-0.17	0.01	0.01
H	1.81	1.35	0.75	0.71	0.39	1.07	0.59	0.19	0.10	0.10	0.06	0.10	0.06
I	1.41	1.07	0.78	1.05	0.75	0.93	0.67	0.18	0.15	-0.05	-0.02	-0.02	-0.01
J	1.55	1.11	0.73	0.66	0.43	1.16	0.74	-0.08	-0.04	-0.06	-0.03	-0.01	-0.01
K	1.86	1.39	0.75	0.99	0.52	1.58	0.85	0.17	0.09	0.02	0.01	0.09	0.05
L	1.74	1.37	0.78	1.05	0.60	1.22	0.70	0.06	0.03	0.03	0.02	0.03	0.02
East	1.54	1.20	0.78	1.04	0.68	1.03	0.67	0.09	0.06	0.04	0.03	0.06	0.04
West	1.67	1.20	0.72	0.92	0.55	1.12	0.67	0.04	0.02	-0.04	-0.02	0.02	0.01
Mean	1.62	1.20	0.75	0.97	0.62	1.09	0.67	0.07	0.04	-0.01	-0.01	0.04	0.02

[1] RZG = total merit index, RZM = production index, RZE = conformation index, RZS = somatic cell count index, RZZ = fertility index, RZN = functional herd life index

However, following the results of an international comparison, replacement rates for German cow sires are too high. In other influential countries for Holstein genetics, e.g. Canada, The Netherlands, or the United States, replacement rates for cow sires were in a range from 5.4 to 7.9% (Powell et al., 2003). A comparably intensive selection was only practiced within AI organizations E, H, K and L. The relatively high percentage of bulls graduated in Germany could likely be impacted by the existence of several independent AI organizations as supposed by Powell et al. (2003). A study of test capacities for young bulls across country borders (König et al., 2002) also revealed disadvantages for the German Holstein breeding program when focusing on the international comparison of size parameters. However, the size of the test capacity is not inevitably a reason for applying high replacements or low selection intensities and was not related to the success of German AI organizations (Grandke and Simianer, 1998).

Table 5. Least Square Means for expected selection intensities (i_e), realized selection intensities ($i_{r(j)}$) and controlling values ($co_{(j)}$) in indices j = RZG, RZM, RZE, RZS, RZZ, and RZN for different birth years of bulls.

		Index[1]											
		RZG		RZM		RZE		RZS		RZZ		RZN	
Birth year	i_e	i_r	co	i_r	co	i_r	co	i_r	co	i_r	co	i_r	co
1992	1.48	1.01	0.68	0.93	0.63	0.93	0.63	0.13	0.07	-0.01	-0.01	-0.02	-0.01
1993	1.57	1.11	0.71	0.86	0.55	0.94	0.58	0.01	0.02	0.04	0.03	0.06	0.04
1994	1.58	1.20	0.76	0.88	0.57	0.96	0.61	0.13	0.09	-0.01	-0.01	0.05	0.03
1995	1.67	1.29	0.76	0.91	0.55	1.26	0.76	0.02	0.01	-0.07	-0.04	-0.03	-0.02
1996	1.77	1.39	0.79	1.27	0.72	1.34	0.76	0.05	0.03	-0.02	-0.01	0.07	0.04
Mean	1.62	1.20	0.75	0.97	0.62	1.09	0.67	0.07	0.04	-0.01	-0.01	0.03	0.02

1) RZG = total merit index, RZM = production index, RZE = conformation index, RZS = somatic cell count index, RZZ = fertility index, RZN = functional herd life index

Realized selection intensities

Analysis of variance revealed a significant impact *($P < 0.05$)* of the fixed effects (AI organization and birth year of bulls) on $i_{r(j)}$ for the total merit index and indices for production and conformation, respectively. Least Square means for $i_{r(RZG)}$, $i_{r(RZM)}$ and $i_{r(RZE)}$ increased with decreasing age of bulls but were in a non-systematic order for RZS, RZZ, and RZN (Table 5). Realized selection intensities for all sub-indices (Table 4) were in the range as found in an international study conducted by Powell et al. (2003). Realized selection intensities for yield traits in their study tended to be around 1.0 for the overall data but ranged from 0.24 to 1.31 in different countries. Least square means for $i_{r(RZM)}$ for different AI organizations within Germany varied from 0.66 to 1.20 (Table 4). Powell et al. (2003) expected the relatively low selection intensity for milk yield in The Netherlands based on the fact that the total merit index in The Netherlands included a negative weight for milk (Miglior et al., 2005). Differences of $i_{r(j)}$ for AI organizations within Germany in the same year and for the same index cannot be explained by differences of weights in the total merit index. One reason could be that some German AI organizations have developed an own total merit index deviating from the official RZG and specially adapted to the environmental effects and market conditions within their region. One example is the so called Saxony Breeding Index (ZIS), which for instance has a higher emphasis on somatic cell count compared to the RZG (Brade, 2004).

Low or even negative realized selection intensities in a range from –0.07 to 0.17 for RZS are of increasing concern regarding the international trend and efforts in improving udder health in the cow population. A substantial improvement in such functional traits requires a special recording system, good data quality, appropriate statistical methods for the estimation of EBV as well as the willingness of AI organizations to change their breeding strategy towards more functionality. Such a system was successfully implemented in the Nordic countries (Heringstad et al., 2003). The advantage of the Nordic Holstein cattle population when compared with populations in other countries for RZS (Simianer and König, 2002) justify all efforts, like the consequent selection on RZS for graduating cow sires in Sweden (Powell et al., 2003).

AI organizations B, C, D, E, and I belong to the former Eastern part and A, F, G, H, J, K, and L to the former Western part of Germany. Since the reunification of the two formerly separated German states in 1990, the German dairy cattle population is exhibiting substantial heterogeneity in housing and management conditions. In Western Germany, small farms with herd sizes of around 30 to 100 cows are prevalent whereas in Eastern Germany large-scale dairy farms with herd sizes of 500 to 2000 cows are common. In addition to the heterogeneity of genetic parameters in the Eastern and Western part (König et al., 2005), different selection strategies for cow sires due to the variation in environmental conditions can be anticipated. Least square means for realized selection intensities of AI stations were averaged within the Eastern and Western states, respectively, and were higher for RZM, RZS, RZZ, and RZN in the Eastern part of Germany (Table 4). It can be concluded that production and functionality of cows is of more importance in regions representing large scale farms compared with family farms in the Western part of Germany. Family farms are traditionally more interested in type components as recently pointed out when analyzing the impact of conformation traits on auction prices of heifers (König et al., 2006). Average realized selection intensity for RZE was 1.12 in the western part compared with $i_{r(RZE)}$ = 1.03 in the regions of eastern Germany.

Discussing the importance of different traits based on $i_{r(j)}$ of cow sires, the influence of pre-selection (e.g. the genetic merit of bull dams and bull sires) should be evaluated. However, the $PI_{(RZG)}$ of test bulls was relatively equal for all AI organizations in the range from 107.8 to

108.7 and not affected from $i_{r(RZG)}$, and vice versa (Figure 7). Selection of young bulls in German Holstein breeding programs is only focused on the same few sires per year. Also, the maternal path of pre-selection is relatively equal, as pointed out by König and Simianer (2006). Selection of bull dams within and across country borders for German breeding programs is often done in cooperation between different AI organizations (König, 2001), keeping in mind the reduction of variable costs. Due to the minor impact of PI on the graduation of cow sires, differences between $i_{r(RZG)}$ and $i_{r(RZG)}$adjusted were marginal (Figure 7). Comparing $i_{r(j)}$ and further on $co_{(j)}$ without adjustments for pre-selection seemed to be a proper approach to monitor and control cow sire selection in dairy cattle breeding programs.

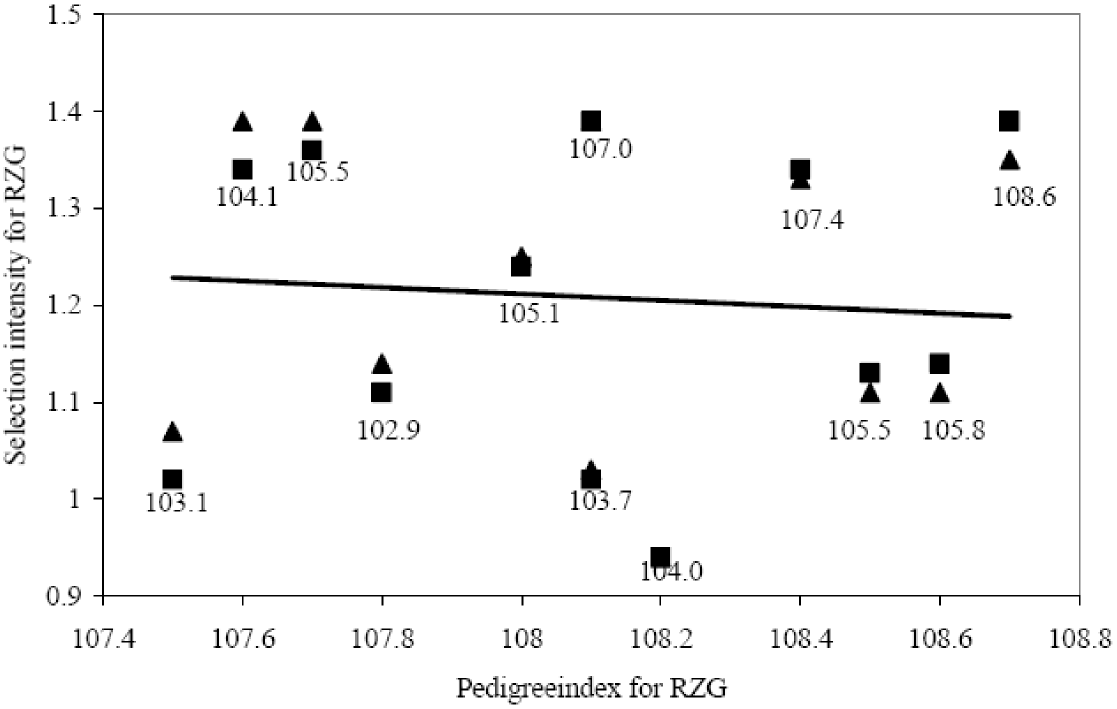

Figure 7. Realized selection intensity ($i_{r(RZG)}$) (■) and for pre selection adjusted realized selection intensity ($i_{r(RZG)}$adjusted) (▲) in dependency of the pedigree index for RZG ($PI_{(RZG)}$) for 12 different AI organizations. (Solid line = linear regression of $i_{r(RZG)}$ on $PI_{(RZG)}$, figures below symbols denote average RZG of progeny test bulls in each AI organization)

Controlling values

Least Square Means for the controlling values for different AI organizations are given in Table 4. A maximal or optimal value of 1.0 indicates a stringent realized selection intensity according to the expected guidelines derived from the replacement rate of cow sires. Least Square means for the controlling value were in the range from 0.39 to 0.85 for RZG, RZM, and RZE, respectively. Results revealed a much higher potential for the improvement of RZS, RZZ, and RZN. Partially negative controlling values for individual AI stations and birth years were found, obviously due to their minor impact on the total breeding goal. It can be anticipated that the increase of the weight for RZN in the total merit index from 6% to 25% should have positive effects on $i_{r(RZN)}$ as well as on $co_{(RZN)}$.

However, analysis of variance also revealed significance *(*$P < 0.05$*)* of fixed effects of AI organizations and birth year of bulls on controlling values for RZG, RZM and RZE, indicating potential for improvement in realized selection intensities for some AI organizations without changing the replacement rate of cow sires. In analogy to increased expected and realized selection intensities for younger bulls, higher controlling values were also found for RZG, RZM, and RZE in younger birth years (Table 5). Following the original ideas of animal breeding, it is strongly recommended to orient breeding strategies towards the total merit index (e.g. Beekman and Van Arendonk, 1993), assuming that weights for individual traits in a total merit index are correctly derived. Preliminary results of a current analysis conducted by Lind et al. (2006) for the derivation of economic weights in German dairy cattle underline the importance of higher weights of functional traits in the total merit index. Essential changes of weights of individual traits in the RZG will have impact on realized selection strategies.

In conclusion, controlling values for RZG are the most important controlling instruments and potential for the increase in $i_{r(RZG)}$ and $co_{(RZG)}$ within several AI organizations was identified. Due to the minor importance of functional traits in the total merit index (Rensing et al., 2002), it could be expected that AI organizations applying less stringent selection intensities for RZG focus their breeding strategies on RZS, RZZ, or RZN, respectively. Such hypothesis would suggest negative correlations between the controlling values for RZG with controlling values for functional traits, but correlations were near zero in our study. Some German AI organizations operate below their theoretical possibilities in all selection decisions, for the total merit index as well as for functional traits.

Van Tassel and Van Vleck (1991) concluded that the estimates of genetic selection differentials provide a measure of selection practices used historically and can help to determine strengths and weaknesses in selection programs. Up to the 1990s, the main breeding goal in dairy cattle around the world was milk production. Also, from 1960 to 1990, Van Tassel and Van Vleck (1991) found much smaller realized selection differentials on the cow sire path than expected. Results indicate that in the past as well as in this study, selection of cow sires was not consequently focusing on the aggregate breeding goal. There is a clear potential for additional benefit of dairy cattle producers due to improved selection strategies, because maximum income on the farm gate level will be realized when selection is strongly oriented towards the total merit index.

Controlling values for all indices except RZE were slightly higher in the Eastern part of Germany compared with the regions located in the West (Table 4), mainly due to a lower i_e (1.54 versus 1.67) and higher $i_{r(RZM)}$, $i_{r(RZS)}$, $i_{r(RZZ)}$ and $i_{r(RZN)}$, respectively. AI organizations from the Western regions are giving away more potential than the competitors in the East. They graduate a smaller percentage of sires, but several unimportant criteria seemed to be applied in selection decisions.

Success Rate

The SR in dependency of the controlling value is depicted in Figure 8 for RZG, RZM, and RZE. For $SR_{(RZG)}$, the regression on controlling values up to the third polynomial degree was significant ($P < 0.05$), whereas for RZM and RZE, only the linear term was considered in the statistical model. When analyzing success of AI organizations in top lists for RZS, RZZ, and RZN, neither fixed effects nor covariates of different polynomial structures were significant at $P < 0.05$. Results indicate that an intensive selection in most important traits towards the expected potential was the reason for a higher success of AI organizations, e.g. higher number of own bulls in the top list. Hence, well-defined breeding policies as the intensive selection of sires to produce second crop daughters or an increase in PI have positive effects on the presence of bulls in a top list and on their average total merit index. As shown in Figure 7, a high $PI_{(RZG)}$ in combination with high values for $i_{r(RZG)}$ slightly increased the average RZG of young bulls within AI organizations.

Referring to the annual statistics of the German Cattle Breeders' Federation (ADR, 2004), 60% of the inseminations of cows are made with cow sires originating from the own region. Hence, intensively selected and genetically superior cow sires are mainly responsible for the average genetic level of the cow population and also for the genetic trend within the distinct AI region. These cows from the own region are potential mating partners for the next generation of young bulls. A previous investigation conducted in the German Holstein population (König, 2001) has shown that regions characterized by a superior average genetic level for cows are more present in top lists of bulls. Details or reasons for these findings should be analyzed in future studies.

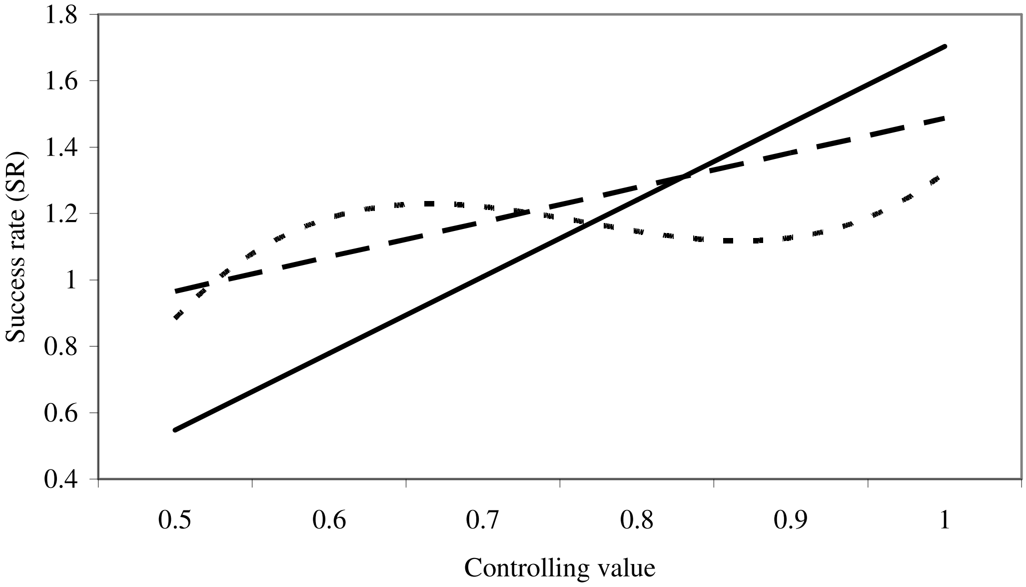

Figure 8. Least Square Means for the success rate in the total merit index (RZG, dotted line), the production index (RZM, dashed line), and the conformation index (RZE, solid line) in dependency of controlling values for respective indices.

The final impact of individual sires on the cow population may vary widely depending on selection decisions of dairy cattle farmers. If the replacement rate of cow sires for an AI organization is high and most inseminations were done with the best two or three cow sires for RZG, no negative effect could be expected on the cow population. But the crucial points in each dairy cattle breeding program are previous selection steps done by AI organizations. Dairy producers only have the possibility to select out of the pool of pre-selected bull sires, and inappropriate selection decisions done by AI organizations are really difficult to compensate at the farm-gate level.

Following the results from this study, the practical recommendation for AI organizations to be successful in the national and international competition is to increase the genetic level of the cows in the most important traits. In a first step, they have the possibility to increase selection intensities of cow sires originating from their own breeding program. Secondly, and much faster, they can improve the genetic level in the whole population due to the increase of AI from superior bulls of other regions or from foreign countries. Such a method implies the willingness of milk producers to inseminate their cows with foreign bulls, but the percentage of these bulls used for AI is actually below 10%. Also, semen exchange of superior sires between different regions within Germany is limited to 15% (ADR, 2004).

Breeding plans developed at the beginning of AI in Germany (e.g. Skjervold and Langholz, 1964; Lindhe, 1968; Langholz, 1979) found a pronounced dependency of genetic gain on the population size. These findings could be of practical relevance considering populations below 10,000 cows, but current German breeding programs consist of at least 50,000 cows. Swalve and Höver (2003) compared the genetic trend within four different regions of Germany, but marginal differences in annual changes of EBV were independent of the population size.

Population size seemed to be an unsuitable parameter when evaluating the success of AI organizations, e.g. counting the number of bulls in a common top list as pointed out by Grandke and Simianer (1998) and confirmed by the current study. Analysis of variance revealed no significant impact at $P < 0.05$ of the population size on SR. On the contrary, the opposite trend was found. Least Square means for SR in RZG were slightly higher for smaller populations below 50,000 cows and in a non directional order for RZM and RZE, respectively (Figure 9). Lowest success rates for all EBV were found for AI organizations representing a medium population size from 50,000 to 100,000 cows.

One successful AI organization belonging to the group below 50,000 cows has implemented several additional tools such as the use of MOET breeding programs and a centralized test of bull dams on station (Swalve et al., 1993; König and Swalve, 2003) in order to increase the genetic level and to be successful among competitive AI organizations. The application of all available breeding tools (e.g. intensive selection of cow sires but also the establishment of a central station test of potential bull dams as well as the utilization of new reproductive technologies) can obviously compensate for disadvantages in scale. However, the objective of AI organizations is to develop proven bulls that are genetically superior to expand the market share of semen sales in national and international markets (Dekkers and Shook, 1990). After evaluating parameters influencing the success of progeny testing programs, as pointed out by Dekkers et al. (1996) or Vierhout et al. (1998), no significant differences were found between German AI organizations (König, 2001). Size parameters including the percentage of young bulls to be progeny tested per year or the numbers of daughters per bull as well as the genetic merit of parents of bulls were very similar.

Additional parameters have to be defined and monitored for a breeding program to be successful in the national and international competition. Selection strategies for cow sires according to the expected selection intensity in the total merit index indicate a well organized breeding program. AI organizations operating in such a manner carefully consider their breeding policies, they select superior sires in most important traits for dairy producers, they increase the genetic merit of the cow population and finally, they will have more bulls in the national top list. Further consolidations of regional AI organizations towards larger and integrated national organizations force the development of controlling and monitoring instruments in several selection steps to evaluate and verify selection decisions. The applied method presented in this study documents the possibility and usefulness of controlling cow sire selection. For practical work of AI organizations, it is strongly recommended to implement a suitable database system based on current data to verify steps of selection as early as possible.

CONCLUSION

The development of controlling instruments is of increasing concern in several fields of agriculture. In the case of dairy cattle breeding programs, controlling instruments are of particular importance to evaluate selection decisions in the short term as well as for sustainable breeding policies. As shown in this study, parameter describing selection decisions for cow sires, e.g. realized and expected selection intensities as well as controlling values, varied widely among traits and German AI organizations. The efficiency of selection was finally related to the success of the AI organizations when evaluating national top lists of bulls for most important indices. Furthermore, the controlling value indicated the presence of additional potential in the improvement of cow sire selection which is essential for the improvement of the genetic level in the whole population. The applied method also allowed the comparison of the importance of different sub-indices in selection decisions of cow sires over a time span of several years. Consolidation of AI organizations, incorporation of new traits and information sources such as claw disorders or molecular data make breeding policies more complex and difficult. Other tasks beyond the maximization of the total merit index such as control of inbreeding will also play an important role in future dairy cattle breeding programs. Guidelines for optimal selection should be developed and evaluated in defined intervals. Practical selection based on such guidelines or controlling values will ensure more efficiency or at least minimize errors in the practical breeding program. Even the presence of bulls in top lists for indices determining the market share can be increased when applying well defined controlling parameters as shown in this study.

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CHAPTER VIII

GENERAL DISCUSSION

GENERAL DISCUSSION

Statistical models and genetic parameters

Binary traits

Since the key paper by Robertson and Lerner (1949), there have been several discussions about the application of proper statistical models for the analysis of categorical traits. The main question was focused on the advantage of threshold methodology versus linear models. The general concept for the analysis of categorical data (Gianola and Foulley, 1983) as outlined in CHAPTER I, was later on implemented in several computer programs using different frameworks for solving the mixed model equations, e.g. Bayesian analysis or GLMM technique with a probit link function. Another possibility among the used members of the family of GLMMs in the case of binary dependent variables is the logit link funcition (see CHAPTER I). However, for same problems different link functions are possible. For example Greene (1997) concluded his discussion of the issue probit versus logit with the statement “in most applications, it seems not to make much difference”. This advice is frequently given in other fields of research, too (e.g. Powers and Xie, 2000; Fahrmeier and Tutz, 2001).

Table 1 gives an overview of the heritabilities found for claw disorders when applying GLMMs (logit link function, results from CHAPTER II) and for the threshold as well as for standard linear models in the Bayesian framework (results from CHAPTER III). Apart from sole ulcer, heritabilities were generally highest when applying the Bayesian threshold models, especially for disorders showing low incidences lower than 10% such as wall disorders or interdigital hyperplasia. Higher heritabilities on the liability scale obtained from threshold models compared to results from standard linear models is what theory for analysis of categorical traits leads one to expect (Dempster and Lerner, 1950). This was also found in other studies analyzing categorical data with different models (e.g. Weller and Ron, 1992; Andersen-Ranberg et al., 2005). Theoretically, nonlinear models are more appropriate for statistical analysis of categorical traits than linear methods (Thompson, 1979; Gianola, 1982). This was also confirmed in the study in CHAPTER III, where linear and threshold models were compared using the Bayesian Information Criterion (BIC; Schwarz, 1978).

Table 1. Heritabilities for 4 different claw disorders applying GLMM-logit, and threshold and linear models in a Bayesian framework (Results from CHAPTER II and CHAPTER III)

Model	Claw and foot disorder			
	Sole ulcer	D. Digitalis	Wall disorder	Interdigital hyperplasia
GLMM-logit	0.086	0.073	0.104	0.115
Bayesian-linear	0.077	0.100	0.101	0.112
Bayesian-threshold	0.088	0.134	0.136	0.186

Differences in estimated heritabilities form the logit model and the probit (= Bayesian threshold) model could be due to the data or due to due other differences in the statistical model. The data for the logistic model were recorded in 2003 and an animal model was applied. Claw disorders for the Bayesian threshold analysis were collected in 2005 and analyzed via a sire model. The difference in heritabilities seemed mainly to be associated with the data structure. In ongoing studies, König and Swalve (2006a) merged the claw databases from their projects and they estimated heritabilities for laminitis applying threshold-animal and threshold-sire models. Results were nearly identical. However, some simulation studies with threshold animal models did not converge properly when using Gibbs sampling (e.g. Hoeschele and Tier, 1995; Luo et al. 2001). This problem is defined as the 'extreme data category problem', which occurs when all observations within a level of an effect are in the same category. It turned out that sire threshold models are more reliable than animal threshold models.

Relatively new in the field of dairy cattle breeding is the application of recursive or even recursive threshold models as shown in CHAPTER III. Because of the increased importance of functional traits in dairy cattle programs, the implementation of recursive or simultaneous models as described in theory by Gianola and Sorensen (2004) will be continued. In the past, mixed models have been used to infer genetic and environmental correlations between production (mainly milk yield) and functional traits (fertility or SCS). These models, however, ignore direct relationships between the two phenotypes. High milk yield may increase liability to any specific disease and, in turn, the disease may affect milk yield adversely. The possible complexity of such structural equation models is clearly described by de los Campos et al. (2006). In the case of claw disorders and milk production in dairy cows (CHAPTER III), a two-way causal path was postulated (test day milk yield ➔ claw disorder ➔ test day milk yield).

Recursive linear and recursive threshold model were compared with standard linear and threshold models using BIC. In conclusion, the best model was the recursive threshold model and estimates for heritabilities were lesser lower compared to 'usual' threshold models. Ongoing discussions for the improvement of genetic evaluation of production traits, i.e. if to correct production test day records or account statistical models for pregnancy of cows or not, should also evaluate such recursive or simultaneous possibilities. Based on the results in Chapter III and based on results from other recently conducted studies (e.g. Lopez de Maturana et al., 2007; Wu et al., 2007), the real nature among phenotypes in dairy cattle breeding can be depicted much more accurate when considering recursive models.

Counted traits

In the field of animal breeding, Poisson models for counted data have been proposed by Foulley et al. (1987). Some applications in the context of animal breeding were done in sheep, (e.g. Olesen et al., 1994) for the genetic analysis of the number of born lambs, or by Kadarmideen et al. (2004) when counting osteochondrosis lesions in pigs. For disease traits, there is the possibility to apply threshold models or either to count the disease within a predefined interval and to apply Poisson models. A briefly review of the methodological development of GLMM for the analysis of count data is given by Tempelman (1998). However, in the case of traits related to embryo transfer in dairy cattle (e.g. number of flushed ovas, transferable embryos, unfertilized oocytes, and degenerated embryos; CHAPTER IV), threshold models for categorical traits are not appropriate. The distribution of these traits ranges from 0 to greater than 50. Hence, the application of a Poisson model seemed to be the only sensible choice for genetic analysis and delivered, even for complex models considering several genetic groups, reasonable results (CHAPTER IV). However, when dealing with counts, especially for these traits related to ET, the number of observed zeros is larger than what could be expected under a distribution such Poisson. An extension could be the application of a zero inflated Poisson (ZIP) model. Gianola (2006) presented the general idea of a ZIP-model for animal breeding objectives. An application of this idea was recently developed by Rodrigues-Motta et al. (2007) via Bayesian analysis and MCMC of a ZIP model for the number of mastitis episodes in Norwegian dairy cattle. A further extension could be the application of a negative binomial mixed model (Tempelman and Gianola, 1999) which allows for overdispersion, i.e. for the variance being greater than the mean.

Another important part in this study in CHAPTER IV beyond the specification of the distribution was the estimation of genetic covariances for same traits among involved genotypes. Analyzed ET traits either resulted from highly selected donor cows (pre-selection mainly on production) or from for fertility pre-selected recipients. However, estimates for genetic covariances, especially for the final success in pregnancy, revealed the complexity for interactions of genotypes when analyzing fertility. The moderate antagonism between the direct effect of the recipient and the effect of the transmitted embryo ($r_g = -0.21$) clearly suggests the magnitude of physiological components contributing to pregnancy. The direct effect of the recipient seemed to be more associated with the intrauterine environment, whereas the effect of the embryo describes his own vitality. Apart from ET, same interactions for pregnancy after common artificial insemination (AI) can be anticipated. However, in this case, to distinguish between the genetic impact of the genetic mother, the genetic father, and the direct effect of the embryo in a synergistic context (Wilham, 1963) seemed to be much more difficult when compared to ET data. The development of statistical models for fertility traits mainly depends on the structure of the data. Hence, Wilham's ideas for the extension of genetic models were mostly discussed in the context of pig breeding. In pig breeding, e.g. for litter size, maternal genetic effects models have a long tradition (e.g. Southwood and Kennedy, 1990) and even selection strategies were suggested based on negative correlations found between maternal and direct effects (Roehe and Kennedy, 1993).

Data quality

Several methodologies for the genetic analysis of functional traits were applied and discussed in CHAPTERS II, III, IV, and V. Despite minor differences in estimated genetic parameters, the best model should be used for genetic evaluations to obtain most reliable breeding values. For example based on the BIC, the recursive-threshold model gave a better fit to the data compared to a linear model (CHAPTER III). Or in CHAPTER V, the definition of a specific AR(1) covariance structure for repeated measure analysis was superior compared to the CS structure when calculating AIC values. The application of the best model will ensure most selection response, but the most important part is the availability of reliable data for recorded traits. In the case of pregnancy (CHAPTER IV), the direct heritability of the recipient was 5.8%

and therefore generally higher than heritabilities for non-return rates reported in the literature. It can be anticipated that the recorded status of pregnancy from rectal palpation done by veterinarians is much more informative than official non-return rates which are biased due to cullings of cows or due to the impact of natural service bulls. Also the data from the new electronic recording system for claw disorders delivered reliable results and enabled the application of extended statistical models (CHAPTER II and CHAPTER III). The guideline for classification of individual claw disorders was developed by the German Agricultural Society, and trimmers are routinely trained for a uniform identification of traits. The electronic recording system allows a combination with data form herd management programs and with information on test day records, which allows further applications for the estimation of genetic covariances among a variety of traits. Finally, objective and electronic recorded traits for animal behavior, such as the voluntary visits of cows in an automatic milking system (CHAPTER V) can easily implemented in a routine genetic evaluation and EBVs are not biased due to subjective impressions of investigators.

Genetic correlations among traits

All correlations carried out in CHAPTERS II, III, and IV among test day milk yield and claw disorders as well as among lactation milk yield and fertility were antagonistic. For illustration, some results are summarized in Table 2. Minor differences in genetic correlations were found for same traits when applying different methods for the genetic analysis, but the trend of results is always the same. Selection pressure given on milk yield will increase the incidence of claw disorders, will increase somatic cell count and will decrease the success in traits related to fertility such as the number of transferable embryos of donor cows. The antagonistic genetic relationship among production and fertility or correlations close to zero was also shown in several previous studies (e.g. Thaller, 1997).

Another important finding, mainly outlined in Chapter II, is the fact that most genetic correlations among disorders were large and positive. This result suggests that cows genetically susceptible to some type of health problems are likely to be susceptible to other health problems as well. Other examples are the genetic correlations between claw disorders an SCS in the range from 0.15 to 0.28 (CHAPTER II), or the negative genetic correlation between SCS and the number of transferable embryos. The latter correlation indicates a genetically positive association between udder health and fertility and this was also found in another study by König et al. (2006).

Table 2. Genetic correlations (r_g) among milk yield and functional traits. Results are from CHAPTER II, CHAPTER III and CHAPTER IV)

Trait combination	r_g	Description of the model
ATDM[1] : Sole ulcer	0.06	GLMM, binary distribution, logit link
ATDM[1] : D. dermatitis	0.24	GLMM, binary distribution, logit link
ATDM[1] : Wall disorder	0.27	GLMM, binary distribution, logit link
ATDM[1] : I. hyperplasia	0.34	GLMM, binary distribution, logit link
ATDM[1] : ATDSCS[2]	0.20	Linear model
STDM[3] : Sole ulcer	0.22	Recursive threshold model, Bayesian analysis
STDM[3] : D. Dermatitis	0.28	Recursive threshold model, Bayesian analysis
STDM[3] : Wall disorder	0.30	Recursive threshold model, Bayesian analysis
STDM[3] : I.hyperplasia	0.18	Recursive threshold model, Bayesian analysis
305-d-MY[4] : Transferable embryos	-0.27	GLMM, poisson distribution, log link

[1] ATDM = average amount in milk yield form test day 1 and test day 2 after calving

[2] ATDM = average somatic cell score form test day 1 and test day 2 after calving

[3] STDM = Single test day observation in milk yield within 100 days in milk

[4] 305-d-MY = 305 day lactation milk yield

Genetic correlations among claw disorders and conformation traits (CHAPTER II) were approximated from correlations among estimated breeding values applying the formula by Calo et al. (1973). However, pre-assuming large numbers of daughters per bull, this formula provides reliable estimates for genetic correlations and is still used in several investigations where measurements are not available from the same animal (e.g. Harder et al., 2006). For practical applications, it is important to know that improved quality of feet and legs, e.g. better conformation scores for traits such as hocks, foot angle, rear leg rear view, and rear leg side view, is genetically associated with fewer incidences of claw disorders. There was a slight negative correlation between angularity, stature, and body strength with claw disorders supporting some findings by Buenger et al. (2001) when analyzing relationships between conformation traits and longevity.

Several genetic correlations among binary distributed traits (CHAPTER II, CHAPTER IV) were obtained from a GLMM using an appropriate logit or probit link function which is implemented in the package ASReml (Gilmour, 1998). In a bivariate analysis for the estimation of genetic correlations between two categorical traits, ASReml treats one of these traits in the linear sense. However, there was a general proof given by Vinson and Kluwer (1976), showing that genetic correlations are the same; regardless if the specific trait is treated as a real binary trait or as Gaussian. Recently, multivariate threshold models in animal breeding were developed in a Bayesian framework. Heringstad et al. (2004) used a multivariate threshold model for the analysis of clinical mastitis in Norwegian dairy cattle. In this study, a 12-variate liability threshold model was applied. Clinical mastitis was treated as different traits in 12 created intervals within and across lactations. Details for the algorithm used in this study and in an ongoing research project in German Holstein cattle for fertility and milk urea nitrogen (Goergens, 2007) are explained in detail by Chang (2002).

Assessment of breeding strategies

Direct selection on health traits

Involuntary cullings of cows due to feet and leg disorders have nearly the same magnitude compared to fertility or mastitis. Conventional German dairy cattle breeding programs only include a selection for improved claw health via indirect selection on EBVs of four different conformation traits. These conformation traits are foot angle, rear legs rear view, rear legs side view, and the quality of the hocks. As shown in CHAPTER II and III, genetic parameters of various claw disorders enable the possibility for direct selection strategies on these traits. These scenarios shown in CHAPTER II for the calculation of selection response for different selection strategies were extended by König and Swalve (2006b). The aim of their study was to quantify the relative importance of different index traits with respect to selection response for the trait laminitis resistance. A substantial part of laminitis measurements were from the cows used in CHAPTER II. Hence, applying selection index theory, the trait in the breeding goal was laminitis and index sources for EBVs of bulls in laminitis were laminitis observations and linear scores for hock quality of daughters and one claw measure of the bull (hardness of the dorsal wall). Genetic and phenotypic parameters used in this study are shown in Table 3.

Table 3. Heritabilities (diagonal), genetic (above diagonal) and phenotypic correlations (below diagonal) for index traits (König and Swalve, 2006b)

	Laminitis	Hocks	Hardness of dorsal wall
Laminitis	0.14	-0.41	-0.44
Hocks	-0.09	0.16	0.29
Hardness of dorsal wall	-0.05	0.11	0.12

For example the genetic correlation of -0.41 between hocks and laminitis indicates that a better quality of hocks (higher scores) is associated with less incidences in laminitis. In addition to the hocks, genetic correlations among other type scores and claw disorders were calculated in Chapter II. However, the highest correlation was calcualted when using the quality of the hocks. The harder the dorsal wall of the bull, the better the quality of the hocks of the daughters (r_g = 0.29). There are some more claw measurements of young bulls available (Distl, 1995), but among all pairs of genetic correlations estimated in the study by König and Swalve (2006b), the hardness measurement of the dorsal wall was the best predictor for laminitis of cows. Phenotypic as well genetic correlations between laminitis and other claw measurements of young bulls were near zero.

Utilizing these parameters from Table 3, selection response in laminitis resistance per generation and the correlation between the index and the aggregate genotype were calculated for different amount of index sources (Table 4). Selection response in laminitis resistance per generation and accuracy of EBVs of bulls in laminits could be more then doubled when laminitis observations of 50 daughters were included as index traits (scenarios B4, C1, C2, C3, C4) compared with scenario A1. Strategy A1 is the one currently used in Germany: about 50 daughters per bull are routinely scored for conformation traits. The impact of the own performance of the bull (hardness measurement of his claw; scenarios B1-B4 and C2-C4) is of minor importance when focusing on selection response in laminitis. Finally, the correlations among conformation traits and claw disorders are not large enough to achieve a substantial reduction of laminitis or of other claw disorders within the dairy cattle population via indirect selection on conformation traits. Similar results were found in scenarios applied in CHAPTER II.

Table 4. Correlation between index and aggregate genotype (r_{TI}) and selection response (ΔG) per generation under different information scenarios for the target trait "resistance against laminitis" (modified from König and Swalve, 2006b)

			Number of information sources		
Scenario	r_{TI}	ΔG (in %)	Young bull hardness of claw	Daughters hocks	Daughters laminitis
A1	0.34	5.7	-	50	-
A2	0.37	6.3	-	100	-
B1	0.36	6.2	1	50	-
B2	0.58	9.9	1	50	10
B3	0.68	11.7	1	50	20
B4	0.81	13.9	1	50	50
C1	0.80	13.8	-	0	50
C2	0.81	13.8	1	0	50
C3	0.81	13.9	1	20	50
C4	0.82	14.0	1	100	50

When including health traits such as claw disorders in a combined breeding goal, economic weights for all these traits have to be known. The objective of a current dairy cow profitability project by König et al. (2007) is to simulate the individual variability of cows in 212 different traits. Changes during life in production, growth, feed intake and some type traits were modelled through random regression coefficients. The influence of management practices and environmental effects on all these traits and diseases and their interactions in combination with prices and costs over the whole cow's lifespan was used to determine net returns per cow and day. Net returns per cow and day were regressed on their true breeding values to determine relative economic values for each trait. This method also allows the derivation of economic weights for "new traits" like claw disorders, assuming that genetic parameters are available. Hence, genetic parameters estimated for functional traits (CHAPTER II, III, IV, V) will be used in this dairy cow simulation project.

Long term selection strategies

All efforts towards more functionality in dairy cattle breeding programs, such as data collection or the optimization of methods for genetic evaluations, will be eroded in the long term if current breeding policies don't change. This assumption is based on the relatively high genetic relationship (6.19%) between potential bull sires and bull dams (CHAPTER VI) and the detrimental effects of inbreeding on functional traits (e.g Hoeschele, 1991). Mating programs for the selection of cow sires offered by several AI companies, focusing on inbreeding coefficients of individual sires, can address inbreeding concerns on the farms in the short term. However, a straightforward selection on animals with lowest inbreeding coefficients makes no sense for controlling relationships in the long term (Simianer and König, 2003). For example, the mating of a low inbred sire with low inbred cows will produce a large number of half sibs highly related among each other.

Long-term control of inbreeding is mainly determined by the selection of bull dams and bull sires. As discussed in CHAPTER VI, there are several possibilities to find a balance between inbreeding and selection response in the long term, but the current method of choice is the application of the optimum genetic contribution (OGC) theory. In dairy cattle, breeding programs in the United States (Weigel and Lin, 1992) or in the United Kingdom (Kearny et al., 2004) focused their investigations on OGC, but efforts in Germany were limited. König et al. (2003) clearly documented the feasibility and superiority of OGC when applying the extended version accounting for overlapping generations (Meuwissen and Sonesson, 1998) for a pig breeding program. In German dairy cattle (CHAPTER VI), OGC theory has the potential to increase genetic gain under the same constraint for the increase of average relationship by 13.1%. Selection schemes in the past ignoring inbreeding and using only a few outstanding bull sires (CHAPTER VI) caused some economic loss, especially when thinking about the expensive clean up program against CVM-carriers. The advantage of OGC should be used and OGC can easily be implemented in the routine work of a dairy cattle breeding program when selecting bull dams and bull sires. A central element for OGC application is the additive-genetic relationship matrix among selection candidates, and the inverse A^{-1} has to be computed. For a large number of animals, this could be a problem. An alternative method to compute relationships among animals was presented by Hinrichs et al. (2006). However, in dairy cattle breeding programs, bull dams and bull sires are highly pre-selected for a magnitude of traits (König, 2001). For this small number of elite animals, the application of OGC as implemented in the Gencont-program

(Meuwissen, 2000) plus the application of the concrete mating strategy as developed by Sonesson and Meuwissen (2000) delivers reliable results for practical selection strategies in acceptable time.

Scheme of a breeding program

All important steps for the development of a dairy cattle breeding program, beginning with the collecting of data, the genetic evaluation, the application of selection strategies up to possible controlling tools were covered in CHAPTERS II to VII. Especially the implementation of controlling instruments to verify cow sire selection (CHAPTER VII) revealed some potential for the improvement of dairy cow profitability towards more functionality without causing additional costs for breeding organizations. Functional traits will play an important role in the future, enforced through the development in German agriculture. Large-scale dairy farms, mainly located in Eastern Germany, will also be the dominant farm type in the Western part in the next years. In large-scale farms with in average 500 cows, variance componets (König et al., 2005) as well as cow sire selection strategies (CHAPTER VII) were different compared to Western Germany. The larger the farm, the more important is functionality and health, i.e. causing less costs and less labor.

The idea of a breeding program for functional traits based on the results in the previous CHAPTERS is outlined in Figure 1. An essential step for the successful implementation of new recording systems is the establishment of co-operator herds for progeny testing (PT). The strong need for highly accurate phenotyping of additional functional or health traits such as claw disorders is impossible to conduct across an entire population. Potential bull dams are pre-selected for all available traits, which imply a selection among cows located in co-operator herds. Potential bull dams perform an on-station test within their first lactation and they are heavily used for ET or alternatively for ovum pick up. Optimum genetic contribution theory is used to specify the mating design for best bull sires word wide and these bull dams. The main intention of the on-station test is to avoid preferential treatment. The results from ET can be included in an overall breeding goal for bull dams. Male calves from the best bull dams (highest index) are used as young bulls for PT, producing at least 100 daughters in milk. PT of these bulls is restricted to the co-operator herds. Based on the PT information for all traits (also health and measurements for behavior), EBVs for young bulls are computed. For these magnitude of functional or health traits included, recursive models should be applied for genetic evaluations. A net merit index combining the magnitude of traits has to be developed. Selection of cow sires is done by the breeding organizations and due to the substantial impact of cows sires on the whole dairy cattle population, controlling is really important in this step of selection. Also a small fraction of international available sires is used for AI, indicated by the dashed arrows in Figure 1.

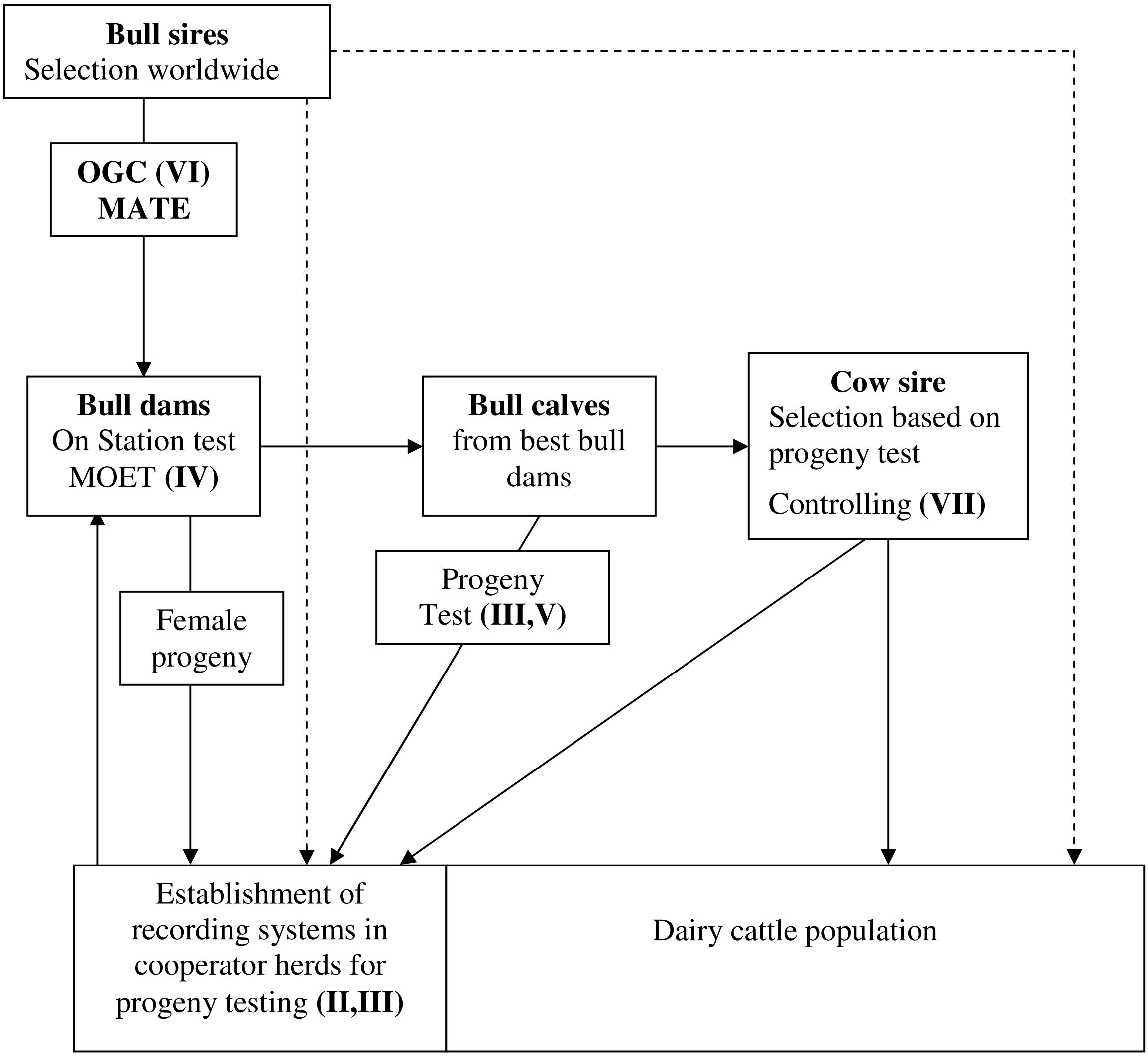

Figure 1. Dairy cattle breeding program for the improvement of functional traits (Latin numbers in brackes are indicating the different CHAPTERS where the specific topic is explained)

Marker- and gene assisted selection: Prospects and concerns

Additional gain or efficiency in dairy cattle breeding programs due to marker assisted selection was mainly proposed for traits with low heritabilities (all functional and health traits), or for traits which can only be recorded late in life such as survival (Lande and Thompson, 1990). However, from the statistical point of view, the probability to find quantitative trait loci (QTL) is lower for these low heritable traits. In addition, for health traits reliable phenotypes from well established recording systems were rare. Kathkar et al. (2003) gave an extensive review for QTL mapping in dairy cattle. Most of the reviewed publications (45 of 55) reported significant QTL for production traits, but relatively few studies have been reported for functional traits such as mastitis, fertility, and health. In addition, most of the found QTL in dairy cattle had small effects of less than 5% in terms of the phenotypic variance for the respective trait (Hayes and Goddard, 2001). Quantitative trait loci mapping of functional traits in the German Holstein population (Kuehn et al., 2003) revealed significant QLT for the maternal effect of dystocia and SCC, as well as for some further putative QTL for the direct effect of dystocia, for paternal and maternal non-return rates, and for functional herd life. Kuehn et al. (2003) also summarized the significant QTL for functional traits found in other dairy cattle populations, e.g. for US Holstein dairy cattle reported by Ashwell et al. (1998).

The marker set used in these QTL mapping studies mostly circumvented about 250 microsattelite markers. The linked markers were in general in population-wide equilibrium with the QTL (= LE-markers; Dekkers, 2004). These LE markers require within family-family analysis and selection. For each application of marker assisted selection (MAS), the linkage pahse between marker and QTL has to be known and verified within families. Hence, for the pratical application in dairy cattle breeding programs, the bottom up desing (Mackinnon and Georges, 1997) was suggested to increase the effecieny of young bull selection before entering the progeny testing scheme. Bottom up can only be applied in cases were the bull sire is heterozygous for the marker genotype, and the linkage phase between marker and QTL has to be identified within each family through the cost-intensive genotyping of the daughters. A significant contrast in daughter yield deviations between marker-genotypes of daughters within sire enables the pre-selection of young bulls based on the valuable marker-genotyp. However, this system was never applied in practical breeding programs. Due to the variety of traits considered in dairy cattle breeding goals and due to the ‘unkwon QTL’ inherited from the bull dam, only the marker assisted pre-selection among of full sibs was suggested. Hence, the use of reproductive technologies on the bull dam pathway is imperative to increase genetic gain based on within-family MAS (Spelman and Garrick, 1998).

Loci that are in population-wide linkage disquilibrium with the functional mutation (LD markers) can be used for selection strategies across the population (Dekkers, 2004). However, Dekkers (2004) gave examples of gene tests used in commercial breeding programs for different species, but in dairy cattle, none LD markers were applied. Even the identification of the direct mutation, e.g. in dairy cattle the DGAT-gene (Winter et al., 2002), is limited for pratical applications. The allele variante increasing milk yield decreases the protein percentage, and for a combined breeding goal in production traits (RZM), the impact of the different allele variants is close to zero.

Actually, dense marker maps based on single nucleotide polymorphisms (SNPs) are available. In dairy cattle, micoarrays with more than 10,000 SNPs can be used. Hence, the entire genome can be covered with SNPs located no more than 1 cM apart. Meuwissen et al. (2001) suggested the estimation of genomic breeding values and the application of genome wide selection using those genome-wide dense marker maps. In their simulation study, the highest correlation between genomic breeding values and true breeding values was 0.85. Based on this study, Schaeffer (2006) developed a strategy for genome-wide selection in dairy cattle which is applicable for all traits. Due to the reduction in the generation interval, the costs compared to a conventional Canadian dairy cattle progeny testing program were reduced by 92%, and genetic gain was doubled. However, problems still remain to solve the linear system of equations for more than 10,000 SNPs and a few genotyped animals. The idea of genomic selection sounds promising, but when following the history in moleculargenetics and the limited practical applications, also genomic selection should be handeled with care. The structure of the breeding program as developed in Figure 1, i.e. the implementation of co-operator herds for high data quality and the extensive use of outstanding bull dams through ET, is a prerequisite for all types of reliable selection strategies, even when focussing on genomic selection.

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ZUSAMNENFASSUNG

Der Inhalt und das Ziel der vorliegenden Habilitationsschrift ist mit dem Titel beschrieben: "*Evaluation of genetic analyses and selection strategies for the improvement of functional traits in dairy cattle*". Die Habilitationsschrift ist in acht Kapitel gegliedert.

KAPITEL I gibt einen allgemeinen Überblick zur Bedeutung und zum gegenwärtigen Status von funktionalen Merkmalen in Zuchtprogrammen beim Milchrind. Möglichkeiten zur statistischen Analyse von kategorialen und longitudinalen Daten werden ebenso angesprochen wie die nachhaltige Implementierung von funktionalen Merkmalen in praktische Zuchtprogramme beim Milchrind.

In **KAPITEL II** wurden „generalized linear mixed models“ (GLMMs) mit einer Logit-Linkfunktion zur Varianzkomponenten- und Zuchtwertschätzung von vier verschiedenen Klauenerkrankungen angewendet. Schätzwerte für die Heritabilitäten lagen im Bereich von 7,3% bis 11,5%. Die Klauenerkrankungen waren untereinander deutlich positiv korreliert. Die genetischen Korrelationen zwischen Testtagsgemelken (Milch-kg) und den Klauen-erkrankungen im Bereich von 0,06 bis 0,37 weisen auf einen genetischen Antagonismus zwischen Gesundheits- und Produktionsmerkmalen hin. Klauenerkrankungen waren aus züchterischer Sicht positiv mit den linearen Merkmalen des Fundaments korreliert. Eine substantielle Verringerung der Klauenerkrankungen in der Population kann allerdings nur dann erreicht werden, wenn direkt auf diese Gesundheitsmerkmale selektiert wird. Hierzu wurden Beispiele anhand von Selektionsindexkalkulationen gegeben.

Heritabilitäten für diese Klauenerkrankungen und genetische Korrelationen zur Milchmenge wurden in **KAPITEL III** mittels Schwellenwertmodellen und linearen Modellen in einem Bayesian-Ansatz geschätzt. Die genetischen Parameter waren recht einheitlich, aber letztendlich sollte doch, basierend auf dem BIC – Informationskriterium, das Schwellenwert-modell zur Auswertung kategorialer Daten verwendet werden. Die Beziehung zwischen den verschiedenen Klauenerkrankungen und der Testtagsmilchmenge wurde weitergehend unter Anwendung rekursiver Modelle untersucht. Hierbei wurde der Einfluss des vorigen Testtagsgemelk auf eine Klauenerkrankung als auch der anschliessende Effekt einer Klauenerkrankung auf das folgende Probegemelk modelliert. Mittels rekursiver Schwellenwertmodell auf der zugrundeliegenden Anfälligkeitsskala geschätzte Heritabilitäten waren geringfügig höher als im rekursiv linearen Modell. Genetische Korrelationen zwischen der

Testtagsmilchmenge und der Inzidenz für Klauenerkrankungen lagen im Bereich von 0,16 bis 0,43. Zucht auf erhöhte Milchmenge erhöht somit die Anfälligkeit für Klauenerkrankungen. „Structural coefficients“ im rekursiven „structural equation model“ beschreiben den Zusammenhang zwischen Milchmenge und Klauenerkrankung auf phänotypischer Ebene. Die Wahrscheinlichkeit des Auftretens einer Klauenerkrankung je kg Milchleistungssteigerung lag im Bereich von 0,003 bis 0,024. „Structural coefficients“ in der Grössenordnung von –0,12 bis -0,67 bedeuten, dass der Anstieg der Krankheitsanfälligkeit um eine Einheit mit einer Leistungsreduktion bis zu 0,67 kg Milch pro Tag einhergeht.

Genetische Analysen von Fruchtbarkeitsmerkmalen waren Gegenstand von **KAPITEL IV**. GLMM-Poisson Modelle wurden für die Auswertung von Merkmalen des Embryo-transfers (ET) von Spenderkühen („Zählvariablen“) verwendet, während für das Binärmerkmerkmal „Trächtigkeit der Empfängertiere“ ein Schwellenwertmodell zur Anwendung kam. Mehere vorangegangene Modellkalkulationen favorisierten sogenannte MOET – Zuchtprogramme, aber der letztendliche Erfolg blieb durch die geringe Anzahl an Nachkommen je Spenderkuh versagt. In der vorliegenden Arbeit gefundene Heritabilitätsschätzwerte (z.B. 0,23 für das Merkmal „gespülte Eizellen“) ermöglichen aber eine grundsätzliche züchterische Bearbeitung und die Berücksichtigung in einem Gesamtzuchtwert für potenzielle Bullenmütter. Analog zu den Klauenerkrankungen wurde ein genetischer Antagonismus zwischen funktionalen Merkmalen (z.B. dem Merkmal „taugliche Embryonen“) und Produktionsmerkmalen (305-Tage-Laktationsleistung für Milch-kg) festgestellt. Mittels synergistischer Modelle wurde der Einfluss mehrerer Genotypen simultan betrachtet. Die direkte Heritabilität (Effekt des Rezipienten) für das Merkmal „Trächtigkeit nach ET“ betrug 0,06, während der Einfluss der genetischen Eltern, welcher zur Vitlität des Embryo beiträgt, weniger als 1% der Totalvarianz ausmachte. Die genetische Korrelation zwischen dem direkten Effekt des Rezepienten und dem Vater des Embryos betrug –0,32 und die genetische Korrelation zwischen Donorkuh und Rezepient –0,14. Dieses Ergebnis macht deutlich, dass Bullen mit positiven Zuchtwerten für Trächtigkeitsmerkmale der Empfängertiere nicht unbedingt die besten sind, wenn die Vitalität von Embryonen verbessert werden soll.

Die Berücksichtigung von Merkmalen des Verhaltens und des Temperaments in Zuchtprogrammen kann zur Verbesserung der Arbeitseffizienz beitragen. Immer mehr Betriebe in Deutschland stellen auf automatische Melksysteme (AMS) um, was solche Tiere verlangt, die freiwillig die Melkbox aufsuchen. 15 Betriebe aus Nordwestdeutschland mit gleichem Bautyp des AMS wurden für die Untersuchung in **KAPITEL V** ausgewählt, um genetische Parameter für das Mermale „freiwillige Besuche im AMS = Melkfrequenz pro Kuh und Tag“ zu schätzen. Wiederholte Beobachtungen waren die durchschnittlichen Besuche pro Kuh und Tag im AMS an verschiedenen Testtagen. Entsprechend des Laktationsstadiums wurde die Analyse stratifiziert nach Laktationsabschnitten durchgeführt: Abschnitt 1 = Abkalbung bis Tag 100, Abschnitt 2 von Tag 101 bis Tag 200 und Abschnitt 3 von Tag 201 bis Tag 300). Genetische Parameter wurden unter Berücksichtigung verschiedener Kovarianzstrukturen für die wiederholten Messungen geschätzt. Basierend auf dem Akaike-Informationskriterium (AIC) wurde die autoregressive Kovarianzstruktur der Resteffekte favorisiert. Heritabilitäten für das Merkmal „Melkfrequenz pro Tag“ lagen für die einzelnen Laktationsabschnitte im Bereich von 0,16 bis 0,22. Diese moderaten Heritabilitäten von objektiven Beurteilungen erlauben eine generelle züchterische Bearbeitung dieses Verhaltensmerkmals.

Im konventionellen Besamungszuchtprogramm beim Milchrind wird der Inzuchtminimierung im Rahmen der Anpaarung von Bullenmüttern mit Bullenvätern nur wenig Bedeutung beigemessen. Der Anstieg des Inzuchtgrades in der deutschen Holsteinpopulation, wie in **KAPITEL VI** beschrieben, kann zu den erhöhten unfreiwilligen Merzungen wegen Unfruchtbarkeit, Mastitis oder Klauenerkrankungen beitragen. Die „optimum genetic contribution“ (OGC) Methodik wurde daher exemplarisch für die Selektion von Bullenvätern und Bullenmüttern einer deutschen Zuchtorganisation angewendet. Für ein gleiches tolerierbares Maß der verwandtschaftlichen Beziehungen zwischen Bullenvätern und Bullenmüttern konnte durch die Anwendung von OGC 13,1% mehr Zuchtfortschritt verglichen mit der aktuellen Selektionsstrategie erzielt werden. Mittels eines „simulated annealing algorithm“ für konkrete Anpaarungen war es möglich, den Inzuchtkoeffizient in der nächsten Generation verglichen mit Zufallspaarung um 66,3% zu reduzieren. Die Implementierung der OGC – Methoddik in praktische Rinderzuchtprogramme wurde somit nachhaltig empfohlen.

Der Einsatz von Controllingmechanismen ist von zunehmender Bedeutung im gesamten landwirtschaftlichen Sektor. In **KAPITEL VII** wurde ein „Controlling Value“ für Kuhväter entwickelt, der das Verhältnis der realisierten zur tatsächlichen Selektionsintensität beschreibt. Dieser „Controlling Value“ kann eingesetzt werden, um für verschiedene Merkmale die Effizienz der Kuhvaterselektion zu überprüfen. Insbesondere für die funktionalen Merkmale der Nutzungsdauer, des somatischen Zellgehaltes und des gesamten Fruchtbarkeitskomplex wurde zusätzliches Potenzial zur Effizienzsteigerung deutlich. Mehr als 60% aller Besamungen resultieren von Kuhvätern des eigenen Zuchtprogramms. Somit kommt der Selektion der Kuhväter aus dem Pool der Testbullen eine entscheidende Bedeutung zu, wenn es darum geht, das genetische Potenzial in der gesamten Population für funktionale Merkmale zu verbessern.

Eine abschliessende allgemeine Dikussion, fokussiert auf die Resultate der vorliegenden Arbeit und den angewandten statistischen Methoden, ist Gegenstand von **Kapitel VIII.** Desweiteren werden Möglichkeiten der marker- oder genunterstützen Selektion evaluiert. Wie in mehreren Abschnitten der Habilitationsschrift deutlich wurde, besteht zusätzliches Potenzial zur Zucht auf mehr Funktionalität in der deutschen Holsteinpopulation. Die Grundvoraussetzung hierfür ist die Etablierung von Datenerfassungssystemen, die Anwendung geeigneter statistischer Auswertungsmethoden und letztendlich die Definition einer optimalen Zuchtstrategie unter Anwendung von Controllinginstrumenten. Es ist aber auch zu konstatieren, dass ca. 95% in der Gesamtvarianz für Fruchtbarkeitsmerkmale, ca. 90% in der Gesamtvarianz für Gesundheitsmerkmale und ca. 80% der Gesamtvarianz für Merkmale des Verhaltens durch Umwelteinflüsse determiniert wird. Dem Herdenmanagement muss daher trotz allen züchertischen Möglichkeiten zur Verbesserung von funktionalen Merkmalen eine vorangige Stellung eingeräumt werden.

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