Contract Herds for Progeny Testing: Selection Strategies, Prospects and Concerns

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Introduction

Since the implementation of artificial insemination (AI), the structure of dairy cattle breeding programs as suggested by Skjervold and Langholz (1964) was implemented via practical progeny testing (PT) programs. Progeny testing in general is characterized by a random mating system of young bulls in the whole population. This system works very well and enables relatively high selection intensities, especially on the bull sire, bull dam, and cow sire path of selection, associated with a sustainable increase in selection response for traits being under intensive selection pressure (König et al. (2007)). However, nowadays several reasonable arguments from the practical as well as from the scientific point of view focus on a general modification of a population wide PT scheme towards PT in selected contract herds. These arguments can be stratified into the following three topics:

i) The optimal test environment: genetic evaluation of production traits

ii) New health traits for genetic evaluation: data recording systems and breeding strategies

iii) Genome wide selection: Logistics, and further modifications of the breeding scheme

The optimal test environment. In Germany, AI stations (= breeding organizations) operate regionally. This means that PT is performed within distinct regions, but estimated breeding values (EBV) of bulls are published in one single national list. Hence, success of a breeding program is defined as the number of own regionally tested bulls in the national top-list. Dekkers et al. (1996) considered economical aspects and gave general recommendations for a breeding organization to be competitive, e.g. via the optimization of the number of test bulls per year, or the optimal size of progeny groups. Despite these optimization criteria for the general design of a breeding program, the impact of heterogeneous variances across regions or herds on results of breeding value estimation and selection has been extensively discussed in several studies (e.g. Van Vleck (1963); Garrick and Van Vleck (1987)). Van Vleck (1963) found higher additive genetic variances with an increasing production level in herds, and he suggested ignoring daughter records from low production level herds when estimating breeding values of bulls. Simulation studies by Garrick and Van Vleck (1987) showed an increase of EBVs with increasing intra-herd variances. The optimisation of husbandry and feeding strategies (Padilla and Keown (1990)), the milking technology and herd size (Weigel et al. (1993)), or the knowledge of herdsmen (Short et al. (1990)) were given as possible reasons for increased intra-herd variances. Final success of an AI station, defined as the number of top bulls in a common national list, may not be the most important goal from a scientific point of view in the context of heterogeneous variances across regions.

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Instead, the paramount goal of each breeding program must always be the accurate identification of genetically superior animals among the total pool of test candidates. This goal can be achieved through selecting superior environments for PT (Hammond (1947)), so that animals can express their true genetic potential.

New health traits for genetic evaluation. As indicated by Miglior et al. (2005), breeding objectives nowadays gradually shift from production towards functionality. However, the main problem is the lack of appropriate data for the genetic evaluation of functional traits which are mainly based on indirect measurements. 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 20 years. The Scandinavian countries have a unique position in registration and collection of information about functional traits. 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). Simianer and König (2002) identified a substantial advantage in selection response for udder health for the Scandinavian countries due to the direct recording and selection against mastitis. Modern technology offers new recording opportunities for new functional traits (Mark (2004)). However, when transferring those ideas to German Holsteins including almost 1.5 Mio. registered cows kept in almost 15,000 farms, the ultimate question is: how to collect sufficiently reliable daughter records for health traits when focusing on all herds in a population wide perspective?

Genome wide selection. Schaeffer (2006) was the first who compared a genomic and a conventional PT breeding program in terms of selection response derived from the general 4-pathway model (Robertson and Rendel (1950)). However, when thinking about detailed modifications in existing breeding programs in the genomic era, e.g. modifying the size of progeny groups, or modifying established schemes of a central station test for potential bull dams, the magnitude of the correlation between the true breeding value and the genomic estimated breeding value (GEBV) is of crucial interest. In fact, this correlation, also referred to as the accuracy of GEBVs (r_{mg}), may determine to what extent genomic selection will be applied on the different pathways of selection in future breeding programs in dairy cattle. This accuracy of GEBV is different for different traits (e.g. van Raden et al. (2009)). Especially in the context of recording functional traits in contract herds for genetic evaluation, the no. of required contract herds mainly depends on the no. of daughters per genotyped sire to achieve a sufficient reliability (r_{TI}) for a sire EBV combining both phenotypic and genomic information.

Concerns and questions. Setting up a system of contract herds for PT implies the exclusion of a large number of farms. Exclusion from the PT program is associated with limited access to relatively cheap semen from young sires. From the practical point of view, the other main question is: which criteria or which approach should be used to select those contract herds? According to Hammond (1947), herds used for PT should be characterized by a superior herd management, so that animals can express their true genetic potential. Possible measurements for the expression of genetic potential could be an intra-herd variance, or an intra-herd heritability, which was also negatively correlated with sire misidentification rates (Dechow et al. (2008)). Selecting superior herds for PT, and later on using superior sires in the whole population, leads to the topic of genotype x environment interactions. Genotype x

environment interaction is present when different genotypes are not equally affected by different environments (Falconer and Mackay (1960)). This results in unequal differences between genotypes across environments or even in a re-ranking of genotypes for different environments. Interactions can be detected via the estimation of genetic correlations between environments under an animal model based on data comprising genetic links between the strata. This was done in a multitude of studies where data was stratified according to country borders or production systems (e.g. König et al. (2005)).

The aim of the present paper is to examine the above topics i), ii), and iii). The content of these topics is based on previous studies, but focus on the German Holstein breed in particular. Selection strategies for contract herds are discussed in the context of phenotypic expression of genetic potential (i), claw and foot disorders from data recording up to the evaluation of breeding plans are used as an example for new health traits (ii), and selection index calculations were applied to specify the framework for genomic (PT) breeding programs (iii).

Material and methods

The optimal test environment – **selection strategies.** Three selection strategies were investigated in two different projects for two different breeding organizations in Germany. These were: 1. Estimation of variance components within herds; 2. Cluster analyses, and 3. utilizing of yield deviations (YD). Estimation of variance components and cluster analyses was based on the same dataset. The total data set comprised 605,765 first lactation test day production records of 65,833 Holstein cows located in one region within Eastern Germany recorded between 1998 and 2003. Stratification of data in three different subsets within strata (table 1) was done according to herd size, average protein yield, and average age at first calving (AFC).

Table 1:	ble 1: Descriptive statistics of strata as used for estimation of variance components								
Subset	Strata		No. of		Mean within herds				
_		Test days	HTD	Cows	Prot. yield (kg)	AFC (d)	Herd size		
	Herd size								
1	50 - 252	177,843	23,806	21,878	766±184	886±106	126±61		
2	253 - 392	197,967	7,400	21,584	787±194	871±99	309±138		
3	393 - 1168	209,954	3,363	22,371	818±209	850±84	621±178		
	Protein yield								
4	520 - 759	190,552	14,976	22,072	702±163	882(±104)	198±156		
5	760 - 833	199,195	9,830	22,100	783±193	866(±94)	230±185		
6	833 - 1247	198,238	9,483	20,851	889±201	854(±92)	234±200		
	AFC								
7	743 - 846	206,677	9,301	21,299	806±205	815(±75)	267±200		
8	847 - 889	198,569	10,470	21,605	789±196	867(±78)	223±190		
9	889 - 1350	182,950	14,629	19,419	778±191	928(±106)	183±143		

 Table 1: Descriptive statistics of strata as used for estimation of variance components

For protein yield, a random regression test day model (RRTDM) was applied to 24-hour test day yields from first lactation. Each subset was analysed separately using the REML procedure, and using relationships among animals traced back to 1920. In total, nine different variance component estimation runs were performed. The RRTDM was identical to the model defined by Reinhardt et al. (2002). In a second approach, cluster analysis was used to identify herds for PT combining desired effects of herd size, average protein yield, and AFC (= components describing herd management). The goal of a cluster analysis is to choose cluster membership that will minimize the variability within the clusters, and maximize the difference between clusters.

For the YD selection strategy, 9,739 first-crop daughters of 98 young test bulls from one breeding organization located in North West Germany, and representing relatively small family farms were grouped in four classes within sire according to the magnitude of their YD. When grading daughters, poor and high YDs within sires were ranked equally, because we wanted to identify those daughters with extreme genetic contributions. Rank 1 was for the 10% highest and 10% poorest daughters within each sire, rank 2 was for the 10%- 20% as well as for the 80%- 90% group, rank 3 for the 30%- 40% as well as for the 70%- 80% group, and rank 4 for the remaining group of "neutral" daughter contributions. First-crop daughters were assigned to herd-calving years for computing mean ranks within herds. Data from additional 167,985 contemporary comparisons were used to calculate mean herd characteristics with regard to production level, genetic level, and AFC.

New health traits: claw and foot disorders. This joint venture in Germany including University of Göttingen and University of Halle started with data recording in the field, continued with the estimation of variance components, and was completed with the evaluation of breeding strategies for claw health improvement. The overall aim of this project was to quantify the relative importance of different phenotypic information sources with respect to selection response for the trait laminitis resistance. Information sources for EBVs of bulls were laminitis observations and linear scores for hock quality (HQ) of in total 5,593 daughters, and one claw measurement (hardness of the dorsal wall = HDW) of the bull. The generalized linear mixed model with a logit link function used for the estimation of genetic parameters for the binary health trait "laminitis" included the random effects of the animal, the random permanent environmental effect, and fixed effects of farm, parity, and classes for days in milk. Genetic parameters for HDW were adopted from Reinhardt et al. (2005). For the evaluation of different breeding strategies in terms of reliabilities and genetic gain, selection index procedures were applied.

Assessment of genomic breeding strategies. For answering the last question, i.e. the no. of required daughters of a genotyped sire to achieve a pre-defined reliability of an aggregate genotype including both phenotypic and SNP information, again selection index calculations were applied. Selection index methodology was proven as a valid approach for calculation of selection response for different genomic selection criteria in the theoretical study by Dekkers (2007), or by Lande and Thompson (1990) for marker assisted selection. In the present approach, this method was extended to specific scenarios relevant in current dairy cattle breeding programs when including SNP information.

Results and discussion

The optimal test environment – selection strategies. Increasing additive genetic variances and increasing heritabilities were found with increasing herd size, increasing production level, and decreasing AFC (figure 1). Especially in the middle and the end of lactation, differences in genetic parameters for different strata were substantial.

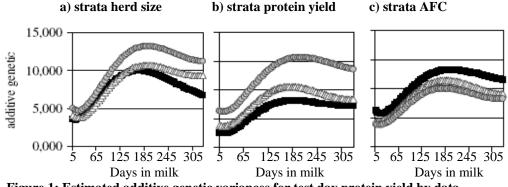


Figure 1: Estimated additive genetic variances for test day protein yield by data stratification. a) herd size: black squares = subset 1, white triangles = subset 2, grey circles = subset 3 b) protein yield: black squares = subset 4, white triangles = subset 5, grey circles = subset 6 c) AFC: black squares = subset 7, white triangles = subset 8, grey circles = subset 9

An explanation for the increase of additive genetic variances (and also of heritabilities, not shown) is an anticipated correlation between investigated herd parameters and farm management. All available management tools are applied to treat cows according to their genetic potential on modern large scale dairy farms. Brügemann (2008) estimated intra herd heritabilities for a specific selection of contract herds. However, the efficiency of this approach is questionable due to tremendous computing time and relatively high standard errors of estimated genetic parameters. Cluster analysis was less time consuming, and can be used to detect superior herds combining desired effects of low AFC, high protein yield, and large herd sizes (= cluster 1, table 2). Additive genetic variances and heritabilities were also highest in cluster 1 (not shown).

		Parameters for characterizing herds					
		AFC (days)		Protein yield (kg)		Herd size (cows)	
Cluster	No. of herds	Mean	SD	Mean	SD	Mean	SD
1	44	852.67	54.46	0.82	0.08	638.56	193.18
2	208	860.54	33.59	0.75	0.05	194.43	98.59
3	100	876.17	50.69	0.89	0.04	161.40	94.58
4	92	995.60	79.62	0.72	0.06	131.45	90.84

 Table 2: No. of herds, means and standard deviations (SD) for herd parameters stratified by clusters.

A further alternative to identify informative herds for genetic differentiation is the suggested YD approach. Methodology does not require additional computing time, is also suitable for small herds as prevalent in West Germany, and can be incorporated in the process of routine national genetic evaluation. More extreme YD were found with increased herd production levels, and were associated with higher SD of cow EBVs within herds (table 3).

Table 3: Means and SD for protein yield (mean of first three test days) and for SD of	
cow RZM (production index) by herd calving years (HCY) with different ranks	

		HCY parameters				
		Protei	n yield	Standard deviation for RZM		
Mean HCY-rank ^{α}	No. of HCY	Mean	SD	Mean	SD	
1 - 2	1911	0.876	0.116	11.354	1.549	
> 2 - 3	2630	0.869	0.119	10.009	1.452	
> 3 - 4	1635	0.822	0.117	8.602	1.491	

^{α}The lower the HCY-rank, the higher the percentage of daughters of young bulls having extreme YD within HCY (positive YD as well as negative YD).

New health traits: claw and foot disorders. Heritability for laminitis was 0.14 and therefore in the range of heritabilities for claw disorders as found in previous projects when applying threshold models, or threshold models in recursive systems (König et al. (2008)). Table 4 depicts the matrix of parameters as used for selection index calculations.

Table 4: Heritabilities (diagonals), genetic (above diagonal) and phenotypic correlations (below diagonal) for index traits.

	Laminitis	Hock quality	Hardness of dorsal wall
Laminitis	0.14	0.41	0.44
Hock quality	0.09	0.16	0.29
Hardness of dorsal wall	0.05	0.11	0.12

Results in terms of selection response (= reduction of laminitis incidence per generation) for different breeding strategies is depicted in figure 2.

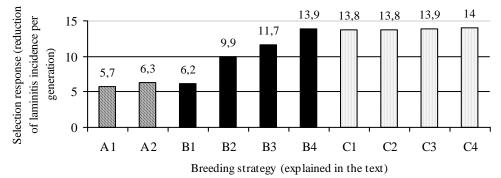


Figure 2: Selection response per generation in laminitis for different breeding strategies

Index sources in strategies A1 and A2 were 50 and 100 daughter records for HQ, respectively. Strategies B generally include the bull observation for HDW, 50 daughter records for HQ, and a gradual increase of daughter records for laminitis: 0, 10, 20, and 50 daughter records for B1, B2, B3, and B4, respectively. Scenarios C generally considered 50 daughter records for laminitis, and varied in HDW and HQ. Selection response in laminitis resistance per generation could be doubled when laminitis observations of 50 daughters were included as index traits (comparison of breeding strategies B4, C1, C2, C3, or C4 with A1 or A2). The necessity of scoring conformation traits (e.g. HQ) and the claw measurements of young bulls (e.g. HDW) is questionable with regard to improvement of laminitis resistance.

Assessment of genomic breeding strategies. The precise size of progeny groups for sires to achieve desired values of r_{TI} were calculated by altering heritabilities and r_{mg} (table 5). Additional daughter records for genotyped sires are not necessary for optimal scenarios where $r_{mg} \ge r_{TI}$, i.e. $r_{mg}=0.9$, and $r_{TI}=0.80$. Following the results from the most recent studies for estimating SNP effects (e.g. van Raden et al. (2009)), an interpretation should focus on scenarios with $r_{mg}=0.5$, and $r_{mg}=0.7$. For these moderate correlations and low heritability functional traits, there is still a necessity for phenotypic daughter records to ensure a desired r_{TI} . Consider as an example a trait with a low heritability of 0.01 and $r_{mg}=0.5$. The critical value for breeder acceptance of genomic information is $r_{TI}=0.80$ (König et al. (2009)), and 581 daughters are needed to achieve this value in this scenario, which is 129 less than in a conventional breeding program

Table 5: Required number of daughters per genotyped sire to achieve pre-defined correlations between index and aggregate genotype (r_{TI}) for different heritabilities and different correlations between GEBV and true EBV (r_{mg}) .

	r _{mg} =.50		$r_{mg}=.70$		r _{mg} =.90		Without genomic information	
h^2	r _{TI} =.80	$r_{T I} = .95$	$r_{TI}=.80$	$r_{TI} = .95$	$r_{\rm TI} = .80$	$r_{TI} = .95$	$r_{TI}=.80$	$r_{TI}=.95$
.01	581	3561	330	3310	0	1993	710	3694
.05	115	705	65	656	0	395	141	732
.10	57	348	32	324	0	195	70	361
.15	38	230	21	213	0	129	46	238
.20	28	170	16	158	0	95	34	176

Conclusion

Criteria when selecting herds for PT should focus on two tasks: First, the accurate genetic differentiation of animals in superior environments, and second to establish a system of herds and motivated farmers within these environments for the recording of new health traits. Methods for selecting herds or environments were suggested for large-scale as well as for small family farms. However, when distinguishing between test and production environment, GxI is an important topic which needs to be carefully evaluated. The estimates of genetic correlations between two environments for different strata within Germany were generally higher than the critical value of 0.8 (König et al., (2005)). The no. of required contract herds strongly depends on the herd size, the no. of cows used for matings with young bulls, and

accuracies of GEBVs in the genomic era. This paper did not discuss further logistic advantages (possibly even for DNA sampling of test bull daughters), or the cost component in terms of reduction of financial support from the government for performance testing in the whole population. All together, modifications of existing PT schemes after 50 years are an inevitable challenge for the near future. It was Schaeffer (2006) who suggested establishing a system of co-operator herds as a substantial pre-requisite for generating accurate phenotypes and genotypes, which could be financed by the savings generated using his genome-wide selection strategy.

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