



## Genomic selection strategies in a small dairy cattle population evaluated for genetic gain and profit

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### ABSTRACT

The objective of this study was to evaluate a genomic breeding scheme in a small dairy cattle population that was intermediate in terms of using both young bulls (YB) and progeny-tested bulls (PB). This scheme was compared with a conventional progeny testing program without use of genomic information and, as the extreme case, a juvenile scheme with genomic information, where all bulls were used before progeny information was available. The population structure, cost, and breeding plan parameters were chosen to reflect the Danish Jersey cattle population, being representative for a small dairy cattle population. The population consisted of 68,000 registered cows. Annually, 1,500 bull dams were screened to produce the 500 genotyped bull calves from which 60 YB were selected to be progeny tested. Two unfavorably correlated traits were included in the breeding goal, a production trait ( $h^2 = 0.30$ ) and a functional trait ( $h^2 = 0.04$ ). An increase in reliability of 5 percentage points for each trait was used in the default genomic scenario. A deterministic approach was used to model the different breeding programs, where the primary evaluation criterion was annual monetary genetic gain (AMGG). Discounted profit was used as an indicator of the economic outcome. We investigated the effect of varying the following parameters: (1) increase in reliability due to genomic information, (2) number of genotyped bull calves, (3) proportion of bull dam sires that are young bulls, and (4) proportion of cow sires that are young bulls. The genomic breeding scheme was both genetically and economically superior to the conventional breeding scheme, even in a small dairy cattle population where genomic information causes a relatively low increase in reliability of breeding values. Assuming low reliabilities of genomic predictions, the

optimal breeding scheme according to AMGG was characterized by mixed use of YB and PB as bull sires. Exclusive use of YB for production cows increased AMGG up to 3 percentage points. The results from this study supported our hypothesis that strong interaction effects exist. The strongest interaction effects were obtained between increased reliabilities of genomic estimated breeding values and more intensive use of YB. The juvenile scheme was genetically inferior when the increase in reliability was low (5 percentage points), but became genetically superior at higher reliabilities of genomic estimated breeding values. The juvenile scheme was always superior according to discounted profit because of the shorter generation interval and minimizing costs for housing and feeding waiting bulls.

**Key words:** genomic selection, genomic breeding scheme, dairy cattle, small population

### INTRODUCTION

Combining information from pedigree and SNP markers leads to increased reliabilities of genomic EBV (**GEBV**) compared with parent average estimates (Hayes et al., 2009b). With increased reliability, young bulls (**YB**) become more competitive relative to progeny-tested bulls (**PB**) in populations with considerable genetic gain. Thus, several studies have shown that higher genetic gain can be achieved if young males without progeny performance are used as parents for the next generation (de Roos et al., 2011; Buch et al., 2012). In the pre-genomic era, conventional breeding schemes were characterized by long generation intervals. Now, cattle breeding organizations move toward breeding schemes with more intensive use of YB as bull sires and for inseminations of cows, partly because of higher reliability of genomic predictions and partly because of reduced cost when keeping fewer waiting bulls. Furthermore, the cost of genotyping has decreased, which has made it even more feasible to genotype more selection candidates followed by increased selection intensity for the YB selection pathway.

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The number of genotyped reference bulls with daughter proofs is the most important factor in determining reliabilities of genomic predictions for selection candidates (Goddard and Hayes, 2009). However, for small dairy cattle populations, the number of potential reference bulls is limited. Hence, the gain from using genomic information is low (Pryce et al., 2011). A gain in reliability of 4 percentage points was estimated in the Danish Jersey breed (Thomassen et al., 2012) based on a reference population of 1,000 bulls, whereas a gain of 20 percentage points was obtained in the Nordic Holstein breed (Lund et al., 2011) based on a larger European Holstein reference population consisting of nearly 20,000 bulls.

Most of the simulation studies on genomic selection published to date have focused on optimization of genomic breeding schemes in larger cattle populations (for a review, see Pryce and Daetwyler, 2012). Because genomic information adds less to reliabilities in smaller populations, we expect that conclusions from studies for larger populations might not apply to smaller populations. For example, annual genetic gain increases more with intensive use of YB because the reliability of genomic predictions increases (Buch et al., 2012). Hence, a key design parameter for such a small breeding scheme is what proportion of YB is optimal to maximize annual genetic gain, as we expect PB to remain competitive with YB.

The main objective of this paper was to evaluate different genomic selection schemes by changing the proportion of genomically selected YB among both bull sires and cow sires with different amounts of genomic information. We hypothesized that increased genomic information in the form of higher reliabilities of genomic predictions would interact positively with more widespread use of YB in the genomic breeding scheme. The second objective was to compare the default genomic breeding scheme to the conventional breeding scheme. The primary evaluation criterion for the comparison of the breeding schemes was annual monetary genetic gain (AMGG), and discounted profit (DP) was used as an indicator of the economic outcome of the breeding scheme. Furthermore, the balance of AMGG for a production trait and a functional trait is presented.

## MATERIALS AND METHODS

### *Experimental Design*

Three overall breeding designs were compared: (1) a progeny testing scheme without use of genomic information (conventional scheme), (2) a juvenile scheme with genomic information where bulls are used before progeny information is available (turbo scheme), and

(3) a scheme that is intermediate in terms of using both young and progeny tested bulls (hybrid scheme).

The main objective was investigated by varying parameters affecting annual genetic gain in the hybrid scheme: (1) increase in reliability due to genomic information, (2) number of genotyped bull calves, (3) proportion of bull dams mated with YB, and (4) proportion of cows mated with YB.

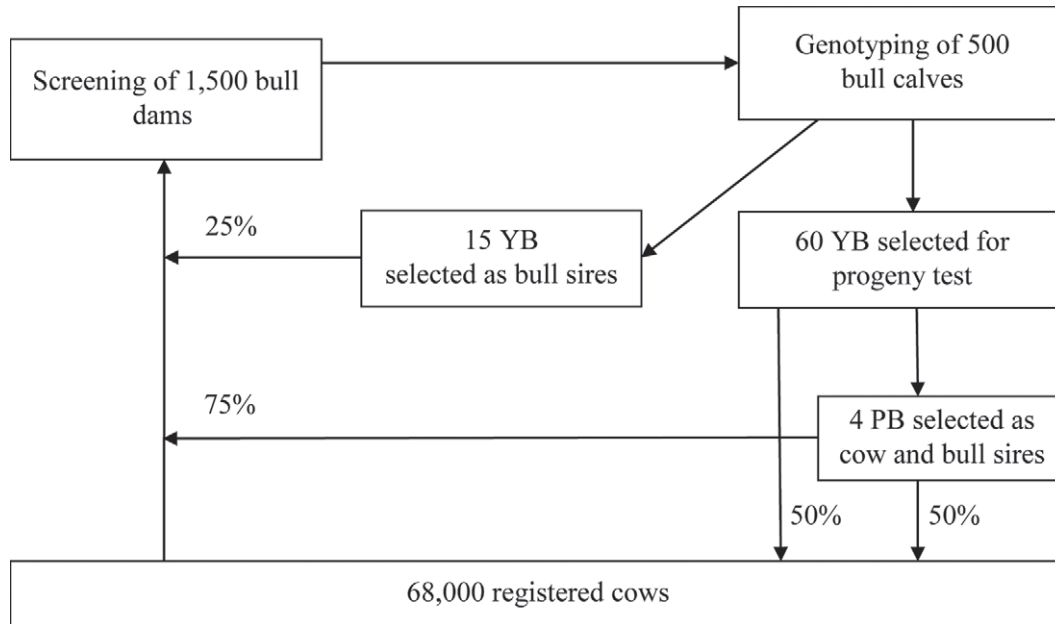
The population structure, parameters, and breeding schemes were chosen to mimic practically feasible options for the Danish Jersey cattle population, being representative of a small dairy cattle population.

### *Hybrid Scheme*

The hybrid breeding scheme reflected the current breeding scheme with use of genomic information as carried out in the Danish Jersey breed. The general structure of the hybrid breeding scheme is illustrated in Figure 1. The population consisted of 68,000 cows with records. The 1,500 cows with the highest EBV according to the breeding goal were screened as bull dam candidates. It was assumed that these cows were inseminated with relevant bull sires to produce the 500 bull calves that would be genotyped. Sixty YB were selected for progeny testing according to their GEBV. These YB were randomly used for 50% of inseminations in the cow population. This corresponds to Danish Jersey farmers' current use of YB for insemination of cows. The 15 YB with the highest GEBV were selected as bull sires and mated to 25% of the bull dams. Finally, 4 PB were selected both for use as bull sires, contributing 75% of the inseminations, and for inseminations in the cow population, contributing 50% of the inseminations. These PB were available because a waiting bull system is run until their daughter proofs are available. For this breeding scheme, 4 key parameters were varied, as follows.

***Increase in Reliability of GEBV.*** The value of genomic information was measured by the increase of reliability of genomic predictions compared with the reliability of the parent average. An increase in reliability of 5 percentage points was used in the reference scenario. This is approximately the current gain observed by including the genomic information in Danish Jersey (Thomassen et al., 2012). The reliability was increased in steps of 5 percentage points up to the level of the reliability of a progeny-tested bull, which was obtained by adding 40 percentage points to the reliability of the parent average. In this study, the EBV for the PB only included the information from daughter records and no genomic information.

***Number of Genotyped YB.*** The number of genotyped bull calves was varied from 500 to 2,000 to evaluate the effect of increasing the selection intensity of bull



**Figure 1.** Illustration of selection steps in the genomic hybrid breeding scheme. Proportion of inseminations of bull dams and production cows by young bulls (YB) and proven bulls (PB) refers to the reference hybrid breeding scheme.

calves that go into progeny testing. A price of €100 was connected to each SNP typing (Table 1). When increasing the number of genotyped bull calves, the number of bull dams was increased to maintain a fixed ratio of 3 bull dams per genotyped bull calf. In the reference scenario of the hybrid scheme, 500 bull calves out of 1,500 bull dams were genotyped yearly (Table 1), which is the current number of bull calves genotyped in the Danish Jersey breeding program. The experience is that 1,500 screened bull dams inseminated with relevant bull sires are required to obtain 500 bull calves that fulfill the criteria for genotyping (P. G. Larson, VikingGenetics, Randers, Denmark, personal communication). No costs are incurred due to the increase in reliability.

**Proportion of Bull Dams Mated with YB.** The proportion of bull dams mated with YB was varied from 0 to 1, investigating the values 0, 0.25, 0.50, 0.75, and 1. In the reference scenario, a proportion of 0.25 was used. The remaining bull dams were inseminated with PB.

**Proportion of Cows Mated with YB.** The proportion of cows mated with YB was determined by the farmers. The proportion was varied from 0.25 to 1, investigating the values 0.25, 0.50, 0.75, and 1.

For testing interaction effects between the mentioned parameters, all 2-way combinations of the 4 parameters were investigated.

### **Turbo Scheme**

An extreme breeding scheme was studied. This scheme maximized the use of genomic information.

Only YB were used as bull sires and as sires of dams. Thereby, the generation interval was minimized. It also reduced the cost of the breeding plan because YB were slaughtered as soon as enough semen had been produced.

### **Conventional Scheme**

A conventional progeny testing breeding program without use of genomic information was investigated. We used the same breeding plan parameters as used in the Danish Jersey breeding scheme before genomic selection was introduced. This breeding program had a lower proportion of cows mated with YB (Table 1) compared with the hybrid scheme and an exclusive use of PB as sires of sons. In this breeding scheme, 5 PB were selected yearly compared with 4 in the hybrid breeding scheme. The numbers of YB and bull dams were the same as in the reference hybrid scheme.

### **Method and Evaluation Criteria**

A deterministic approach was used to simulate and evaluate the different breeding strategies. The software ZPLAN (Willam et al., 2008) was used. It allows evaluation of selection strategies mainly based on the gene flow method (Hill, 1974) combined with a selection index procedure for predicting reliabilities. With ZPLAN, it is possible to evaluate both the genetic and the economic consequences of the different breeding strategies for a given investment horizon. We used 2

**Table 1.** Essential input parameters used for modeling Danish Jersey breeding schemes: the conventional breeding scheme without use of genomic information, the hybrid breeding scheme with a combined use of genomic selected young bulls and progeny-tested bulls, and the turbo breeding scheme only with use of young bulls

Parameter	Conventional	Hybrid <sup>1</sup>	Turbo
Population parameters: varied			
Proportion of cows mated with young bulls	0.3	<b>0.5</b>	1.0
Proportion of bull dams mated with young bulls	0	<b>0.25</b>	1.0
No. of genotyped bull calves	0	<b>500</b>	500
Increased reliability of genomic EBV (percentage points)	0	<b>+5</b>	+5
Population parameters: fixed			
No. of cows in population	68,000	68,000	68,000
No. of young bulls mated with cows	60	60	60
No. of proven bulls selected per year	5	4	—
No. of young bulls mated with bull dams	0	15	15
No. of selected bull dams per genotyped bull calf	—	3	—
No. of selected bull dams per year	1,500	—	1,500
Biological coefficients			
Average calving interval (yr)	1.1	1.1	1.1
Inseminations per pregnancy	2.2	2.2	2.2
Inseminations per first-lactation record	10	10	10
Rearing percentage for heifers and bull calves	0.9	0.9	0.9
Calving percentage	0.9	0.9	0.9
Survival rate for cows	0.8	0.8	0.8
Survival rates for waiting bulls	0.95	0.95	0.95
Use of proven bulls (yr)	2.0	2.0	—
Use of young bulls (yr)	0.3	0.3	0.6
Generation interval for bull dams	2.4	2.4	2.4
Generation interval for production cows	3.2	3.2	3.2
Variable cost parameters (€)			
Inspection of bull dams (per bull dam)	5	5	5
Inspection of bull calves (per genotyped calf)	—	40	40
Costs for SNP typing per genotyped calf	—	100	100
Variable costs covering feeding and labor (per test bull per year)	2,500	2,500	2,500
Interest rate for return/costs (%)	6/4	6/4	6/4
Investment period (yr)	15	15	15

<sup>1</sup>Values in bold are varied in the hybrid breeding scheme.

criteria to compare the value of the different breeding strategies: (1) AMGG was used as the genetic evaluation criterion, and was defined as the average increase per year in monetary superiority of the progeny of the selected animals after one round of selection; and (2) DP for the economic evaluation, defined as the discounted monetary profit based on the genetic superiority and expressed as the improved profit per animal in the total population over the given investment period. In this study, we used an investment period of 15 yr. The interest rates for returns and costs were 6 and 4%, respectively.

In this study, AMGG was the primary evaluation criterion mainly used to compare schemes of approximately equal costs. In addition to AMGG, DP was used when comparing schemes with different costs over time. However, using DP as an evaluation criterion is more unreliable than AMGG because more assumptions are made for calculating DP according to long-term cost levels and interest rates.

The ZPLAN software requires population, biological, and cost parameters, which are given in Table 1.

The biological parameters were obtained partly from the official milk recording statistics (Lauritsen, 2012) and partly from an analysis of bull statistics for Danish Jersey in VikingGenetics (P. G. Larson, VikingGenetics, Randers, Denmark, personal communication). The included cost parameters exclusively reflected the variable costs related to the breeding program (Table 1), whereas fixed costs were ignored. All results for AMGG and DP were expressed as relative values referring to the values of the reference scenario of the hybrid scheme, which were set to 100.

The ZPLAN program does not provide estimates of inbreeding rates. As increase in inbreeding is a consequence of selection, breeding schemes should, in general, be compared only at similar rates of inbreeding. Lillehammer et al. (2011) simulated a small dairy cattle population with use of genomic selection. We used that study as a reference for adapting the number of active bulls to ensure approximately the same levels of inbreeding across the different breeding schemes. In schemes where YB are used as sires of sons, more sires of sons need to be used to balance the effect of lower selec-



tion accuracy (Daetwyler et al., 2007). In Lillehammer et al. (2011), similar rates of inbreeding were obtained by using 12 PB in the conventional breeding scheme and 20 genomic-selected bulls in the genomic breeding scheme. To compensate for the lower reliabilities of genomic breeding values in our study, the number of genomic selected bulls was further increased. Overall, the number of bulls was increased from 5 PB in the conventional scheme to 15 genomic-selected bull sires in the turbo scheme (Table 1). For these reasons, more PB and YB were selected than were actually needed for producing the required amount of semen for supplying the Jersey cow population.

### **Breeding Goal and Traits**

The breeding goal was a weighted sum of 2 traits. The first trait represented milk production traits ( $h^2 = 0.30$ ) and the second trait represented functional traits ( $h^2 = 0.04$ ). An unfavorable genetic correlation of  $-0.30$  between the 2 traits was assumed, and the residuals were assumed uncorrelated. The economic values were set to €83 for the milk production trait (**PT**) and €82 for the functional trait (**FT**) per additive genetic standard deviation. These economic values ensured that the correlation between milk production and breeding goal was the same as in the Nordic total merit index (Buch et al., 2012). All animals were selected for the overall breeding goal.

### **Reliability of EBV**

The ZPLAN program calculated the reliability of the index for each selection group separately. The index used was constructed as a selection index including the information sources own performance, maternal and paternal half-sibs, half-sibs of sire and dam and progeny. Each YB had 113 daughter records for the production trait and 104 daughter records for the functional trait. This is the current average daughter group size in Danish Jersey.

The reliability of genomic prediction is influenced by the level of linkage disequilibrium between SNP markers and QTL. Another factor is family relationship information (Habier et al., 2007). In this study, the linkage disequilibrium was assumed to persist over generations, with frequent re-estimation of the SNP effects. The reliability due to family relationship depends on the candidates' relationship to the reference population.

The increase in reliability of GEBV for YB relative to reliability of parent average was modeled by adding the gain in reliability for each index trait separately. It was assumed that the gain in reliability due to genomic information was independent of the heritability of the

trait, as found by Thomassen et al. (2012) in the Danish Jersey population. As the parent average reliability is different for PT and FT due to differences in heritabilities, the marginal value of adding 5 percentage points to each index trait expressed in number of effective daughters differed. For the PT, the value calculated in ZPLAN was 1 effective daughter and for the FT, 10 effective daughters. Adding these daughter equivalents increased the reliability of the multi-trait selection index from 25 to 29%. Adding 40 percentage points (maximum level used in this study) to each trait separately increased the reliability of the selection index to 64%, which was approximately the same reliability as that of the daughter-based breeding value for the PB (67%). This reliability is in line with the reliability of the Nordic total merit index for a PB.

In a breeding scheme where YB are used as bull sires, the reliability of GEBV is lower compared with a breeding scheme where PB are used as bull sires. We modeled this reduction in reliability of GEBV by removing the paternal half-sib information for the proportion of YB that were used as bull sires.

The reliabilities of the multi-trait indices were 29, 67, and 35% for YB, PB, and cows, respectively, in the conventional breeding scheme. In the turbo scheme, the reliabilities of YB were lowered to 21% because the bull sires do not have daughter information when their sons are selection candidates. In the hybrid breeding scheme, the reliabilities of the YB were 29%, which is the same as in the conventional breeding scheme. However, this reliability resulted from adding 5 percentage points to the parent average due to genomic information and reducing the paternal half-sib information for the proportion (0.25) of the YB having a YB as bull sire.

## **RESULTS**

### **Comparison of Breeding Schemes with Default Parameters**

Table 2 shows the results when comparing the 3 default breeding schemes. The levels of AMGG and DP for the hybrid scheme were set to 100. For AMGG, the hybrid scheme was 6.8% superior compared with the conventional breeding scheme. This difference was mainly due to a shorter generation interval in the hybrid scheme compared with the conventional scheme (3.58 vs. 4.14 yr). This reduction in generation interval more than compensated for the lower reliability of YB compared with PB. The hybrid scheme was also superior for AMGG compared with the turbo scheme (3.9%).

In contrast, among the 3 breeding schemes with default parameters, the turbo scheme yielded the highest

**Table 2.** Comparison of the 3 default breeding schemes: conventional, hybrid, and turbo<sup>1</sup>

Item	Conventional	Hybrid	Turbo
AMGG (%)	93.2	100	96.1
Discounted profit (%)	88.7	100	120.5
Generation interval (yr)	4.14	3.58	2.48
AMGG from PT vs. FT	67.2/32.8	66.3/33.7	63.8/36.2

<sup>1</sup>Breeding schemes are evaluated for annual monetary genetic gain (AMGG), discounted profit, generation interval, and proportion of AMGG from production trait (PT) and functional trait (FT). Value of AMGG and discounted profit for the hybrid scheme is standardized to 100.

DP, resulting in a 20.5% higher DP than the hybrid scheme. The hybrid scheme had 11.3% higher DP than the conventional scheme. The FT had the highest contribution to AMGG in the turbo plan (36.2%), which was 3.4 percentage points higher than in the conventional scheme.

**Effect of Increasing Reliability of Genomic Prediction**

The value of increasing reliability of GEBV of YB compared with reliability of parent average is shown in Table 3. Increasing the reliability of GEBV from +5 to +10 percentage points increased AMGG by just 1.1%. Increasing the reliability up to +40 percentage points, which was equivalent to assuming that the genomic information yielded the same reliability as daughter proofs, increased AMGG by 7.5% and DP by 13%. The increase in DP only expresses the discounted return because no cost was attached to increased reliability.

**Effect of Increasing the Number of Genotyped YB**

Doubling the number of genotyped YB from 500 to 1,000 increased AMGG by 3% (Table 4). The marginal effect on AMGG was lower (2.2%) when the number of genotypings was increased from 1,000 to 2,000 bull calves. Increasing the number of genotypings increased the cost of the breeding scheme. In addition to extra genotyping cost, extra costs were incurred as more bull dams have to be inspected (Table 1). Taking this variable cost into account, DP increased by 4.4% when increasing the number of bull calves from 500 to 1,000.

**Effect of Alternative Strategies Using YB**

The use of YB was varied around the default values, independently for inseminations of bull dams (Table 5) and inseminations of cows (Table 6). In the hybrid breeding scheme, the default proportion of bull dams inseminated with YB was 25%. This value resulted in the highest AMGG. A higher proportion of bull dams inseminated with YB gave, in general, a marginally lower AMGG (down to -1.8%) but a higher DP (up to 6.5%). A genomic preselection scheme exclusively using PB for insemination of bull dams reduced AMGG by 0.5% and DP by 2.1%. The proportion of AMGG that originated from PT was reduced from 66.3 to 65%.

Using only YB for insemination of cows resulted in the highest AMGG (+3.1%), highest DP (12.7%), and largest contribution of FT to AMGG (36.5%), given default values for the other parameters in the hybrid scheme.

**Interaction Effects of Breeding Scheme Parameters**

The strongest interaction effect was observed between increased reliability of GEBV and a more intensive use of YB for inseminating bull dams both for AMGG (Figure 2) and DP (Figure 3). With a gain in reliability for GEBV of +5 percentage points compared with reliability of parent average, the optimal proportion of bull dams inseminated with YB was 0.25 when schemes were evaluated for AMGG (Figure 2). For higher levels of gain in reliability of GEBV, the optimum shifted toward using only YB as bull sires. For

**Table 3.** Effect of increasing reliability of genomic EBV on annual monetary genetic gain (AMGG), discounted profit, generation interval, and proportion of AMGG from production trait (PT) and functional trait (FT) for the hybrid breeding scheme

Item	Increase in reliability (percentage points)				
	+5 <sup>1</sup>	+10	+20	+30	+40
AMGG (%)	100	101.1	103.4	105.5	107.5
Discounted profit (%)	100	102.1	105.9	109.5	113.0
Generation interval (yr)	3.58	3.58	3.58	3.58	3.58
AMGG from PT vs. FT	66.3/33.7	66.2/33.8	65.8/34.2	65.4/34.6	65.2/34.8

<sup>1</sup>Reference scenario of hybrid scheme.

**Table 4.** Effect of increasing number of genotyped young bulls on annual monetary genetic gain (AMGG), discounted profit, generation interval, and proportion of AMGG from production trait (PT) and functional trait (FT) for the hybrid breeding scheme

Item	No. of genotyped young bulls				
	500 <sup>1</sup>	750	1,000	1,500	2,000
AMGG (%)	100	101.9	103.0	104.6	105.2
Discounted profit (%)	100	102.8	104.4	106.3	107.1
Generation interval (yr)	3.58	3.58	3.58	3.58	3.58
AMGG from PT vs. FT	66.3/33.7	66.0/34.0	65.8/34.2	65.6/34.4	65.4/34.6

<sup>1</sup>Reference scenario of hybrid scheme.

a gain in reliability of +40 percentage points, AMGG increased relatively by 23.8% by increasing the use of YB for inseminating bull dams from 25 to 100%. For all levels of gain in reliability, the highest DP was obtained when exclusively YB were used as bull sires (Figure 3).

In general, the strongest interaction effects were observed for all parameters related to increased gain in reliability of GEBV (results not shown). The marginal value of extra genotypings was also larger with greater gains in reliability of GEBV. Furthermore, higher marginal gains in AMGG and DP were obtained by genotyping more bull calves, when YB were used more intensively in the population (results not shown).

Optimal use of YB as bull sires with regard to AMGG depends on the use of YB in the population (Figure 4). If farmers decide to exclusively use YB for inseminating cows, the highest AMGG is obtained for a breeding scheme using only PB as bull sires. The optimal breeding scheme shifted toward using a higher percentage of bull dams inseminated with YB, when fewer cows (<75%) were inseminated with YB. In a breeding scheme only using YB as bull sires, all levels of using YB in the population resulted nearly in the same level of AMGG (96.1 to 98.2). Using DP as the evaluation criterion, the interaction between the use of YB in the population and the use of YB for inseminating bull dams disappeared (Figure 5). Exclusive use of YB in the population was superior for all levels of use of YB as bull sires, and exclusive use of YB as bull sires was superior for all levels of use of YB in the population.

## DISCUSSION

This study showed that a genomic breeding scheme is superior to a conventional breeding scheme even in small dairy cattle populations, even though genomic information provides a relatively small increase in reliability. Given the farmers' current strategy for inseminations in the cow population of 50% inseminations with YB, the optimal breeding scheme as measured by AMGG is characterized by mixed use of YB and PB as bull sires. Strong interaction effects exist between increased reliabilities of GEBV and a more intensive use of YB as bull sires. As a result, the turbo scheme only becomes genetically superior when sufficiently high reliabilities of GEBV can be obtained. The turbo scheme is always preferable when DP is used as an indicator of economic outcome.

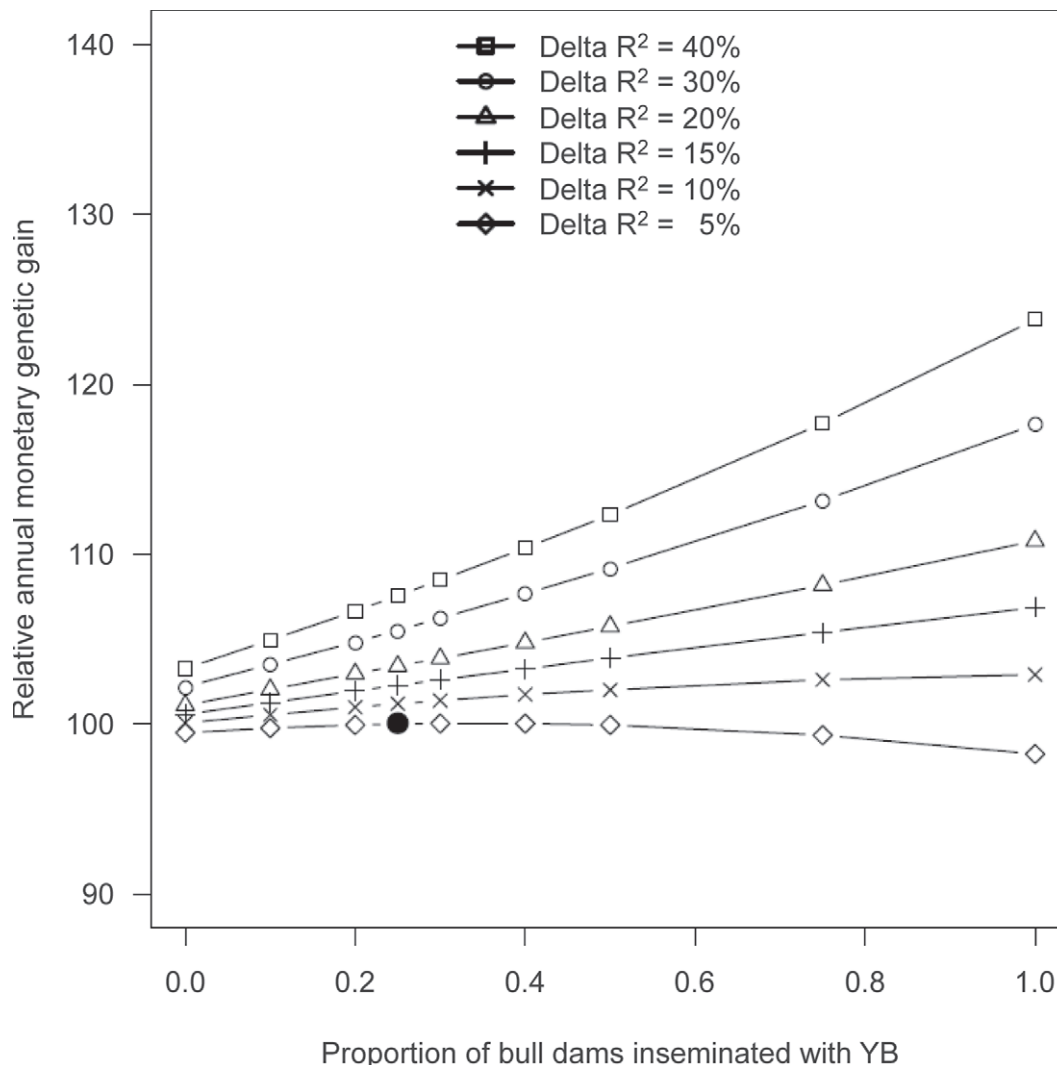
### *Optimal Breeding Scheme for a Small Dairy Cattle Population*

All genomic breeding schemes tested yielded higher AMGG than the conventional scheme. However, as expected, the genetic superiority found in the default genomic selection scheme was lower than that found in other studies, which are based on larger population sizes and hence larger reference populations. In a review study, Pryce and Daetwyler (2012) found 12 to 16% higher annual genetic gain, which is 5 to 9 percentage points higher than improvements in our study. These

**Table 5.** Effect of proportion of bull dams mated with young bulls on annual monetary genetic gain (AMGG), discounted profit, generation interval, and proportion of AMGG from production trait (PT) and functional trait (FT) for the hybrid breeding scheme

Item	Proportion of bull dams mated with young bulls				
	0	0.25 <sup>1</sup>	0.50	0.75	1
AMGG (%)	99.5	100	99.9	99.3	98.2
Discounted profit (%)	97.9	100	102.1	104.1	106.5
Generation interval (yr)	3.79	3.58	3.37	3.15	2.94
AMGG from PT vs. FT	66.7/33.3	66.3/33.7	65.9/34.1	65.4/34.6	65.0/35.0

<sup>1</sup>Reference scenario of hybrid scheme.



**Figure 2.** Annual monetary genetic gain as a function of increased proportion of bull dams inseminated with young bulls (YB) for different levels of increase in reliability (Delta R<sup>2</sup>) due to added value of genomic information. The relative value of the reference scenario is set to 100 (●).

studies were based on larger reference populations and higher selection intensities of YB. The reliabilities of GEBV were around 60% in these studies, considerably higher than the reliabilities of GEBV (29%) in our default hybrid scheme.

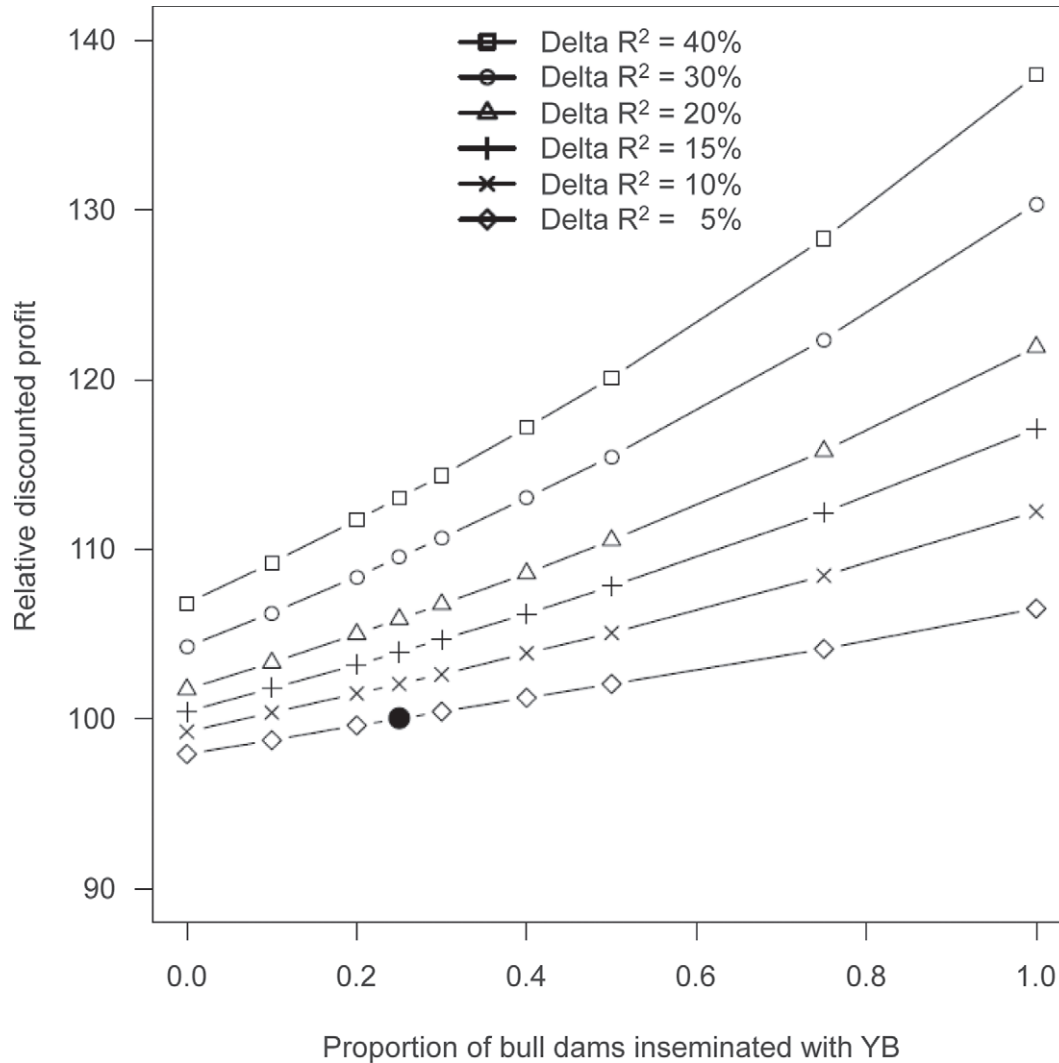
Lillehammer et al. (2011) is the most relevant study for a small dairy cattle population. They modeled the Norwegian Red cattle population consisting of 120,000 cows, 750 genotyped bull calves, 60 PB, and reliabilities of GEBV of 46% ( $h^2 = 0.15$ ) in a preselection scheme.

**Table 6.** Effect of proportion of cows mated with young bulls on annual monetary genetic gain (AMGG), discounted profit, generation interval, and proportion of AMGG from production trait (PT) and functional trait (FT) for the hybrid breeding scheme

Item	Proportion of cows mated with young bulls			
	0.25	0.50 <sup>1</sup>	0.75	1
AMGG (%)	95.4	100	102.1	103.1
Discounted profit (%)	91.0	100	106.7	112.7
Generation interval (yr)	3.82	3.58	3.33	3.09
AMGG from PT vs. FT	69.5/30.5	66.3/33.7	64.5/35.5	63.5/36.5

<sup>1</sup>Reference scenario of hybrid scheme.





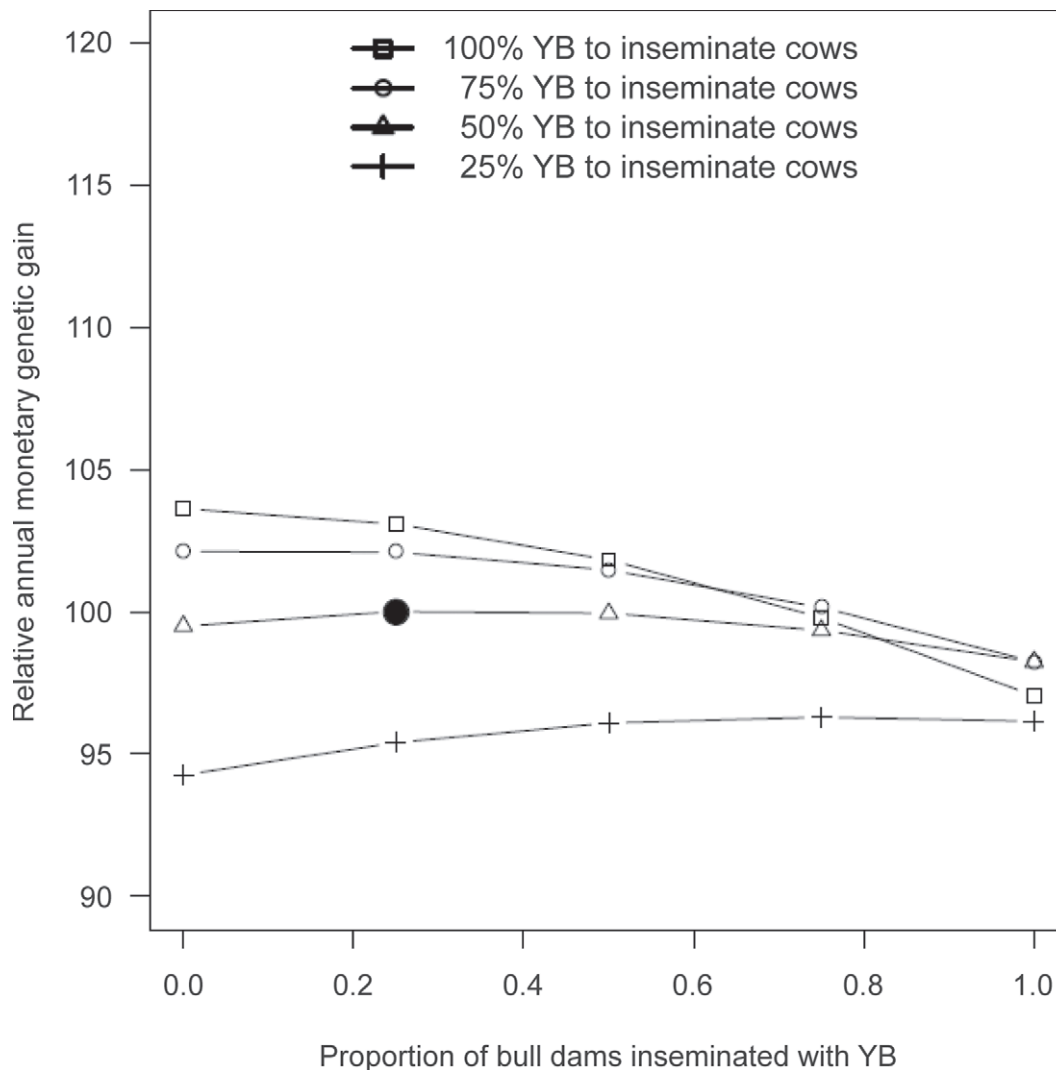
**Figure 3.** Discounted profit as a function of increased proportion of bull dams inseminated with young bulls (YB) for different levels of increase in reliability (Delta R<sup>2</sup>) due to added value of genomic information. The relative value of the reference scenario is set to 100 (●).

They found that the annual genetic gain increased by 12% compared with that in a conventional breeding scheme. Their annual genetic gain was twice the gain in our study, but was obtained for a reference population consisting of 3 times the number of bulls and marginally higher selection intensities. To achieve a comparable genetic gain in our study, we had to assume an increase in reliability of 15 percentage points compared with reliability of parent average and exclusive use of YB as bull sires (Figure 2).

We found that the turbo scheme, for an increase in reliability of 5 percentage points, was genetically inferior to the hybrid scheme with mixed use of YB and PB. This is in contrast to several studies in which turbo schemes provide consistently higher annual genetic gains (König et al., 2009; Pryce and Daetwyler, 2012). The main reason is that the YB in our study were

selected with a lower reliability of genomic breeding values, which was not compensated by the shortened generation interval in the turbo scheme. In the turbo scheme, the sires of genotyped bull calves have not yet obtained a progeny test. As part of the reliability arises from family information (Habier et al., 2007, 2010; Wientjes et al., 2012), a reduction of the value of this information source has a large effect on the reliability of GEBV of YB when the value of the genomic information is low. However, with increased reliabilities of GEBV, we also found that schemes using only YB as bull sires became genetically superior compared with the hybrid scheme.

The turbo scheme, however, was superior when evaluated on DP instead of AMGG, for 2 main reasons. First, in the turbo scheme, YB were slaughtered as soon as enough semen doses were produced to sup-

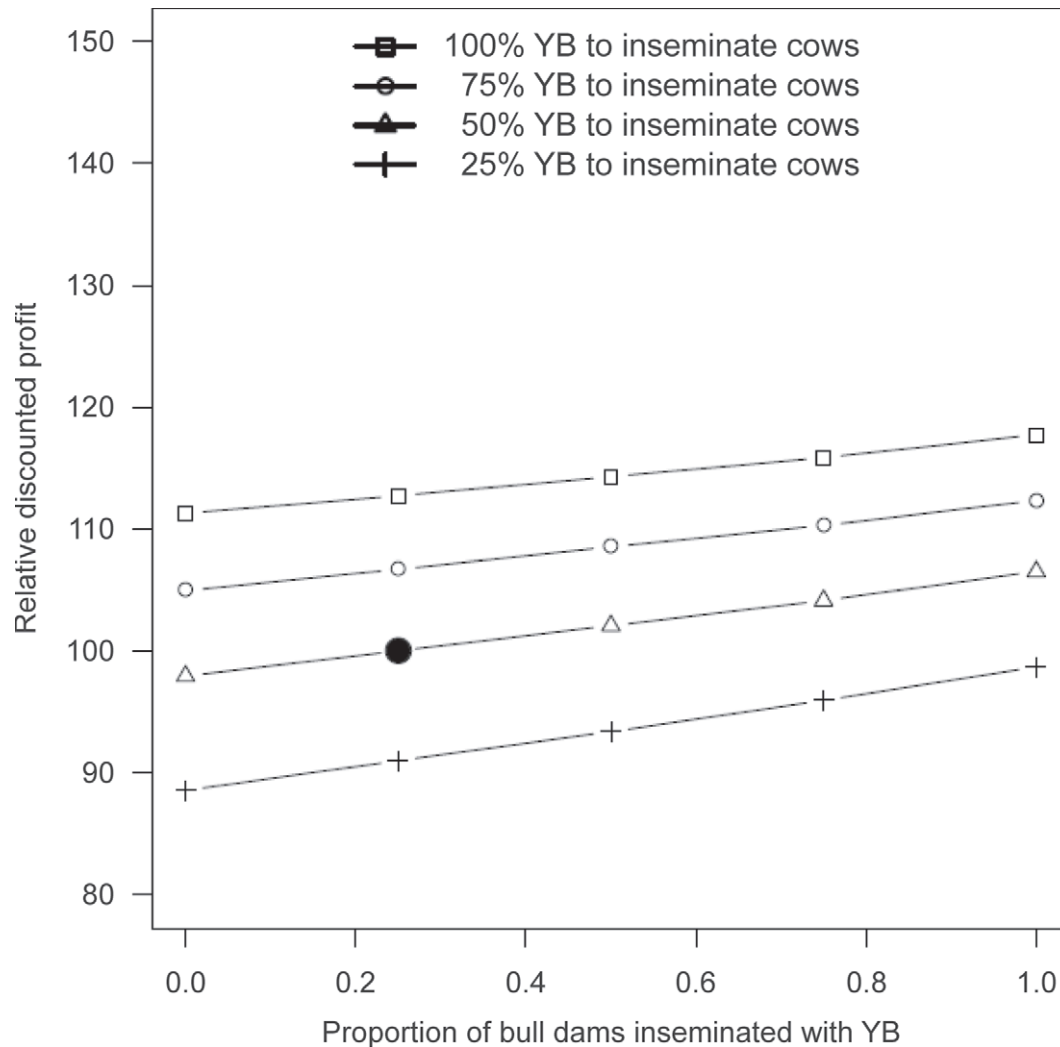


**Figure 4.** Annual monetary genetic gain as a function of proportion of bull dams inseminated with young bulls (YB) for different levels of YB use for inseminations of cows shown for a gain in reliability due to genomic information of 5 percentage points. The relative value of the reference scenario is set to 100 (●).

ply the population. Housing and feeding the bulls in the waiting period is by far the most expensive part of the breeding scheme. In the turbo scheme, this cost is reduced to a minimum. Second, AMG is expressed earlier in the turbo scheme because of a shorter generation interval (from 3.58 to 2.48 yr). The difference in DP between the different breeding schemes depends on the discounting rates used as well as the investment period. However, a sensitivity analysis showed that the turbo scheme still had a superiority of 95% with a reduction of the interest rate for costs and returns to 4 and 2% and extension of the investment horizon to 20 yr. Discounted profit is, however, highly sensitive to the choice of system—in our case, a farmer-owned cooperative with 100% loyalty and unchanged market shares internationally. Therefore, DP can never be used

on its own. However, DP is an indicator for evaluation of future investment strategies in the breeding scheme. Although the turbo scheme in this study showed superiority in DP, it was inferior in AMG. There is a risk that market shares drop in the long term, in which case the predicted DP will be misleading.

Only 2 studies have looked at an evaluation of the economic value of genomic breeding schemes (Schaeffer, 2006; König et al., 2009). Both studies found substantially higher profits for the turbo scheme compared with a conventional breeding scheme. However, those results were obtained for scenarios in which reliabilities of GEBV were assumed to be considerably higher than in the present study. In these studies, they did not model the reduction in reliability of sire information, which may explain part of the difference in reliabilities.



**Figure 5.** Discounted profit as a function of proportion of bull dams inseminated with young bulls (YB) for different levels of YB use for inseminations of cows. The relative value of the reference scenario is set to 100 (●).

In addition, König et al. (2009) used a much higher selection intensity in the YB selection path.

A consequence of moving from conventional to genomic breeding schemes is a shift in the composition of genetic progress toward a relatively larger contribution from the low heritability trait, as the relative gain in reliability for this trait was higher. This effect was more pronounced at higher gains in reliabilities and with more intensive use of genomic information in selection decisions; that is, selection of bulls before progeny information is available.

#### **Optimal Use of YB for Inseminating Cows**

The proportion of cows inseminated with YB is a decision made by the farmers. In our reference scenario of the hybrid scheme, 50% of the cows were inseminated with

YB, which reflects the actual use in the Danish Jersey population. We have shown that exclusive use of YB can increase AMG by 3.1% (Table 6). It requires, however, that farmers accept the use of YB with a lower reliability than PB. This suggestion was questioned by König et al. (2009), who also recommended a breeding scheme with 50% use of PB for inseminations of cows, even though the scheme resulted in a lower AMG compared with exclusive use of YB. In contrast, we find that similar AMG were obtained regardless of which strategy the farmers had for using YB when only PB were used as bull sires in the breeding scheme (Figure 4).

Exclusive use of YB is always superior, irrespective of other factors, when the evaluation criterion is DP. The reason is that discounting favors breeding schemes, where the return is realized as quickly as possible; that is, when the genetic superiority is disseminated into the

population as quickly as possible. If increased reliability of GEBV can be obtained, it will be more attractive for the farmers to use YB.

### ***Increased Value of Genomic Information in Hybrid Scheme***

In the present study, extra use of genomic information is expressed either through higher reliabilities of GEBV or by additional genotypings of bull calves. The value of increased reliability of GEBV in the YB path was limited (Table 3) provided that all other breeding parameters were kept constant in the hybrid scheme; that is, when PB were used more intensively than YB. Genotyping of 1,000 bull calves provided approximately the same improvement in AMGG as an increase of 20 percentage points in reliability. Doubling the number of genotyped bull calves would also be attractive as DP also increased compared with the reference scenario of the hybrid scheme. Hence, even with the current cost of genotyping, the potential return can pay for the additional genotypings.

With more than 1,000 additional genotypings of bull calves, we observed a diminishing return in terms of AMGG. This finding is supported by other studies (Sørensen and Sørensen, 2009; Henryon et al., 2012). However, the rate at which the return diminished was smaller with increasing reliabilities of GEBV, which was also found by Henryon et al. (2012). With increasing reliabilities, we also observed a diminishing return in terms of DP, which was, however, smaller than that observed for AMGG (results not shown).

In this study, no costs were attached to the increase in reliability. The costs for obtaining a higher reliability might be highly dependent on the information source available. Exchange of already genotyped proven bulls between Jersey populations might be almost free of cost. In contrast, genotyping of cows is far more costly, as many more genotypings are required. The economic aspects of genotyping cows were evaluated by Egger-Danner et al. (2012). Adding 5,000 cows to a reference population consisting of 6,000 bulls increased the DP by nearly 2%, assuming a cost of €100 per genotyping. The predicted gain in reliability was 5 percentage points. For populations with an even smaller reference population than Danish Jersey, the marginal effect of adding genotyped cows to the reference population is likely even larger. However, over time, as the reliability increases, the marginal gain by adding cows will be reduced.

### ***Perspectives for Effective Breeding Schemes in Small Dairy Cattle Populations***

Small dairy cattle populations are challenged by low reliability of genomic predictions. In this study, we

demonstrated that a low reliability sets limitations for moving toward more efficient breeding schemes with more intensive use of YB. This also limits the opportunities to run a more cost-effective breeding scheme with lower housing and feeding costs for waiting bulls. Such savings of cost could be used for genotyping more bull calves to increase selection intensity in the male selection path.

Therefore, the key focus for smaller dairy cattle breeds should be to increase reliabilities of GEBV. Collaboration to exchange SNP information of internationally evaluated bulls has shown to be effective for the Holstein population (Lund et al., 2011). For a small dairy cattle breed such as Danish Jersey with only 1,000 bulls in the reference population, the marginal effect might be even bigger. It requires, however, that strong genetic links exist between the Jersey subpopulations, genotype by environmental interactions are not too pronounced, and reliable EBV are available for all important traits in the breeding goal. The North American Jersey population is the most promising collaborator for the Danish Jersey (Thomassen et al., 2013). Another option is to include genotyped females with their own records in the reference population (McHugh et al., 2011; Egger-Danner et al., 2012). Using reference populations from the larger Holstein populations has so far not been successful for increasing reliabilities of genomic predictions for small dairy cattle populations (Hayes et al., 2009a; Erbe et al., 2012).

No matter which strategy is used, collaboration or genotyping of cows, deliberate action is required, because low reliabilities are the limiting factor for improving genomic selection in small populations.

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