Optimization of a genomic breeding program for a moderately sized dairy cattle population

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ABSTRACT

Although it now standard practice to genotype thousands of female calves, genotyping of bull calves is generally limited to progeny of elite cows. In addition to genotyping costs, increasing the pool of candidate sires requires purchase, isolation, and identification of calves until selection decisions are made. We economically optimized via simulation a genomic breeding program for a population of approximately 120,000 milk-recorded cows, corresponding to the Israeli Holstein population. All 30,000 heifers and 60,000 older cows of parities 1 to 3 were potential bull dams. Animals were assumed to have genetic evaluations for a trait with heritability of 0.25 derived by an animal model evaluation of the population. Only bull calves were assumed to be genotyped. A pseudo-phenotype corresponding to each animal's genetic evaluation was generated, consisting of the animal's genetic value plus a residual with variance set to obtain the assumed reliability for each group of animals. Between 4 and 15 bulls and between 200 and 27,000 cows with the highest pseudo-phenotypes were selected as candidate bull parents. For all progeny of the founder animals, genetic values were simulated as the mean of the parental values plus a Mendelian sampling effect with variance of 0.5. A probability of 0.3 for a healthy bull calf per mating, and a genomic reliability of 0.43 were assumed. The 40 bull calves with the highest genomic evaluations were selected for general service for 1 yr. Costs included genotyping of candidate bulls and their dams, purchase of the calves from the farmers, and identification. Costs of raising culled calves were partially recovered by resale for beef. Annual costs were estimated as $10,922 + $305 × candidate bulls. Nominal profit per cow per genetic standard deviation was $106. Economic optimum with a discount rate of 5%, first returns after 4 yr, and a profit horizon of 15 yr were obtained with genotyping 1,620 to 1,750 calves for all numbers of bull sires. However, 95% of the optimal profit can be achieved with only 240 to 300 calves. The higher reliabilities achieved through addition of genomic information to the selection process contribute not only in obtaining higher genetic gain, but also in obtaining higher absolute profits. In addition, the optimal profits are obtained for a lower number of calves born in each generation. Inbreeding, as allowed within genomic selection for the Israeli herd, had virtually no effect on genetic gain or on profits, when compared with the case of exclusion of all matings that generate inbreeding. Annual response to selection ranged from 0.35 to 0.4 genetic standard deviation for 4 to 15 bull sires, as compared with 0.25 to 0.3 for a comparable half-sib design without genomic selection.
Key words: genomic selection, economic optimization, genetic gain, herd simulation, inbreeding

INTRODUCTION

Genomic selection of young bulls can improve genetic gain by reducing generation interval and increasing accuracy of evaluations (Goddard, 2009; Börner et al., 2012; Schefers and Weigel, 2012). Genomic selection also enables identification of individuals of new bloodlines that would not be tracked by selection based on parents' average (reviewed by Weller, 2016). As genotyping costs have decreased, large numbers of both males and females are routinely genotyped. In the United States alone, more than one million Holsteins have been genotyped since 2009 through mid-2016, of which over 180,000 are males (https://www.cdcb.us/Genotype/cur_density.html). Recently, 2 studies have attempted to estimate the economically optimum level of female genotyping for various scenarios. Thomasen et al. (2016) investigated the advantage in monetary genetic gain of combining genomic selection of females with reproductive technologies. Calus et al. (2015) studied the economic effect of different cow replacement strategies using genomic selection, yielding formulas for calculating break-even genotyping costs. As genotyping costs decline, the economically optimum number

of bulls calves selected for genotyping should also increase. Unlike genotyping of female calves, in which generating the genotype is the only additional cost to the farmer, increasing the number of potential AI bull calves results in additional costs, as these calves must be isolated at special farms designated for this purpose.

Recently interest has increased in application of genomic selection to moderately sized dairy populations, reviewed by Pryce and Daetwyler (2012), Calus (2016), Lund et al. (2016), and Schöpke and Swalve (2016). For highly organized moderately sized populations, virtually all male calves born can be considered potential AI bulls. Although several studies have attempted to optimize genomic schemes with respect to the number of cows genotyped, no studies have attempted to economically optimize genomic schemes with respect to the number of male calves genotyped. Thomasen et al. (2014) varied the number of young bulls genotyped, but did not attempt to find the optimum. Our study is based on the simulation of a commercial cow population of approximately 120,000 cows, similar to the Israeli Holstein population. We assume that there is essentially no limitation on males available for selection, as assumed in the simulation study of Wensch-Dorendorf et al. (2011) and Calus et al. (2015). Because the young bulls are selected from progeny of selected sires and dams, the Mendelian sampling is the source of more than 50% of the young bulls' genetic variability. Furthermore, we consider accuracy as defined for the case of selection of bulls out of an already selected population, thereby preventing biases in the calculated genetic gain (see details in Calus et al., 2015). Economic optimization was based on maximizing long-term profit for the entire dairy industry from a single generation of selection as a function of the number of bull calves genotyped. The genomic selection scheme was compared with a standard half-sib selection scheme without genomic evaluation. The half-sib design was used because of its similarity with the genomic selection program, even though this design is not used in practice. Theoretical studies have shown that expected genetic gain is almost equal to the progeny test scheme (Weller, 2016). We compared the genetic gain and economic profit achieved by each selection strategies, varying across reliability values, allowing or disallowing inbreeding when matching parents.

MATERIALS AND METHODS

Breeding Program

The 2 basic breeding programs with and without genomics are illustrated in Figure 1. Both are half-sib designs. That is, young bulls are selected for general service at the age of 1 yr without a progeny test. In Figure 1a, without genomic evaluation, the bulls are selected based on pedigree. In Figure 1b, with genomic selection, a larger number of candidate bulls is first selected in the first stage based on pedigree, and then selected in the second stage based on their genomic genetic evaluations. Cow genotypes are not considered, and only bulls with genetic evaluations based on daughter records are used as bull sires. One generation of selection was simulated for each scenario. Genetic gain was calculated in units of the genetic standard deviation.

Herd Simulation

Parents. The parent herd population was simulated by sampling genetic values from a normal distribution with variance, $\sigma_g^2 = 1$. The dam population, including 90,000 cows, was stratified into 4 age groups based on parities: heifers, and parities 1 through 3. The group sizes were set to 30,000, 25,000, 20,000, and 15,000 for heifer calves and 3 parities, respectively. (Cows with parity >3 were not considered as potential bull dams.) The corresponding genetic means were set to 0, −0.2, −0.4, and −0.6, under the assumption of an annual genetic gain of 0.2 genetic standard deviations per year. The μ_d, the weighted average of the additive genetic mean effects across the dams' age groups, = −0.244. Let G_d denote the additive genetic values for dams, and G_s the additive genetic values for sires. In the first generation, G_s are sampled from a normal distribution with $N\left(0, \sigma_{gs}^2\right)$, where the variance $\sigma_{gs}^2 = \sigma_g^2 = 1$. Within each age group, the genetic values of the dams are also samples from a normal distribution with a variance of 1.

Defining each animal's phenotypic value as its estimated breeding value, let the phenotypic values for dams and sires be denoted by Y_d and Y_s, respectively, and computed as

$$Y_d = G_d + E_d \text{ and } Y_s = G_s + E_s, \qquad [1]$$

where E_d and E_s denote nongenetic effects included in the estimated breeding values for dams and sires, respectively, and $E_d \sim N\left(0, \sigma_{ed}^2\right)$, $E_s \sim N\left(0, \sigma_{es}^2\right)$. The σ_{ed}^2 and σ_{es}^2 are calculated by

$$\sigma_{es}^2 = \frac{\sigma_g^2 - r_s^2 \sigma_{gs}^2}{r_s^2} \text{ and } \sigma_{ed}^2 = \frac{\sigma_g^2 - r_d^2 \sigma_{gd}^2}{r_d^2}, \qquad [2]$$
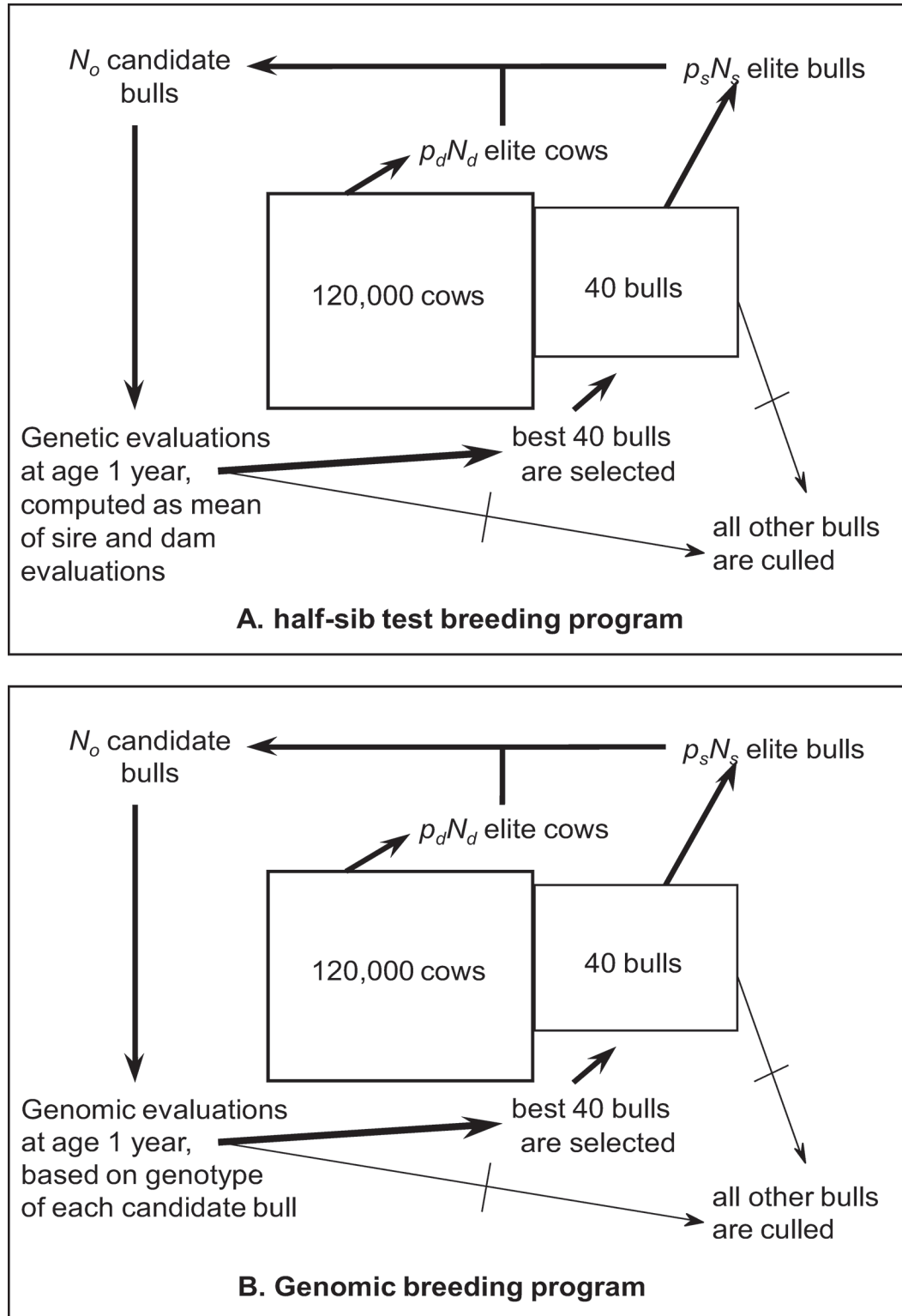
Figure 1. A. The half-sib selection scheme without genomic evaluation. B. The half-sib selection scheme with genomic selection. N_s and N_d are the total numbers of potential sires and dams in the population, and p_s and p_d are the fractions of sires and dams selected as candidate bull sires, respectively. The number of candidate bulls is computed as $N_o = 0.3 p_d N_d$.

where r_d^2 is the age-group weighted reliability of the dams, with reliabilities of 0.3275, 0.46, 0.52, and 0.54 for calves and parities 1, 2, and 3, respectively. Because genomic selection will favor heifers (female calves), their reliability may rise to the level of the bull calves, set here to 0.43, according to the explanation below. This will affect the generation interval for the dam-to-son track and thus will not keep it arbitrarily fixed. The r_s^2 is the sire reliability, which was set to 0.9, under the assumption that each sire has a genetic evaluation based on several hundred progeny. Lower values are also used because this may not always be the case, and to assess the effect of this parameter.

    Offspring. Let the additive genetic effect of the offspring be denoted by G_o and defined by the sum of G_p, the parents' average genetic effect, and G_m, the genetic effect due to Mendelian sampling,

$$G_o = \frac{(G_s + G_d)}{2} + G_m = G_p + G_m, \qquad [3]$$

where $G_m \sim N\left(0, \sigma_m^2\right)$ with $\sigma_m^2 = \frac{\sigma_g^2}{2}$, and σ_{go}^2 is the variance of G_o. Note that $\sigma_{go}^2 < \sigma_g^2$ because of selection of parents; thus, σ_{go}^2 is estimated empirically.

    Let Y_{oG} denote the phenotypic value for offspring selected by genomic evaluation. In this case the Mendelian sampling effect can be estimated. Then Y_{oG} is defined by

$$Y_{oG} = G_p + G_m + E_o, \qquad [4]$$

where E_o denotes the nongenetic effect (including error) for offspring. Then $E_o \sim N\left(0, \sigma_{eo}^2\right)$, and σ_{eo}^2 is calculated by

$$\sigma_{eo}^2 = \frac{\sigma_{go}^2 - r_{oG}^2\left(\sigma_{go}^2\right)}{r_{oG}^2}, \qquad [5]$$

where r_{oG}^2 is the reliability for offspring with genomic evaluations. Weller et al. (2015) obtained the estimate of 0.43 for r_{oG}^2 as follows. For the Israeli index, a correlation of 0.59 was found between young bulls with genomic evaluations, and their evaluations based on daughter records 4 yr later. This gives a coefficient of determination of $0.59^2 = 0.3481$. Dividing it by 0.81, the mean reliability of bulls with daughter evaluations, gives 0.43.

    Let Y_o denote the phenotypic value for offspring selected without using genomic evaluation. Define Y_o by

$$Y_o = \frac{(G_s + G_d)}{2} + X_o,$$

where X_o is composed of the (unknown) genetic effect due to Mendelian sampling and the nongenetic effect (including error) for offspring. Let $X_o \sim N\left(0, \sigma_{xo}^2\right)$, and σ_{xo}^2, which is the sum of σ_m^2 and σ_{eo}^2, is calculated by

$$\sigma_{xo}^2 = \frac{\sigma_{gp}^2 - r_o^2\left(\sigma_{gp}^2\right)}{r_o^2}, \qquad [6]$$

where σ_{gp}^2 is the variance of the parents' average additive genetic effect, $\frac{(G_s + G_d)}{2}$. With no selection of dams, it would equal 0.5; however, dams are selected based on their genetic effects, so σ_{gp}^2 was estimated empirically. The r_o^2 is the reliability of the offspring without genomic evaluations, given by

$$r_o^2 = \frac{r_s^2 + r_d^2}{4}.$$

The Selection Procedure

    Let N_s and N_d equal the total numbers of dams and sires, and let p_s and p_d equal the fraction of dams and sires selected as parents of sire for the next generation. The top ranking $p_s N_s$ sires and the top ranking $p_d N_d$ dams were selected to be parents based on their phenotypic performance. During each year, a dam is mated only once, whereas sires are mated to multiple dams. Assuming that the probability of obtaining a healthy male calf suitable to be an AI bull from each mating is 0.3, then the number of candidate bulls produced, N_o, can be computed as follows:

$$N_o = 0.3 p_d N_d.$$

Sire-dam matches were randomly generated, and offspring genotypic and phenotypic values were obtained by Equations [3], [4], and [6], and the top ranking $N_{o,selected} = 40$ offspring were selected.

    Because the number of bulls selected as sires of bull calves is small, it is possible that a large fraction of the candidate bulls could be progeny of a single sire. Therefore, a limitation was introduced as to the maximum number of candidate bull progeny from each sire. Let p_{lim} be the maximal proportion allowed for a single sire to father bulls, among all $N_{o,selected}$ selected young bulls.

    Define the excess use for sire i by

$$\Delta_i = p_i - p_{lim}, \qquad [7]$$

where $p_i = \dfrac{N_i}{N_{o,selected}}$ is the actual proportion for sire i, with N_i the actual number of selected offspring for that sire.

A limitation for each sire was imposed as follows:

1. For each sire with excess use, namely $\Delta_i > 0$, eliminate from its selected offspring list all those corresponding to the lowest $N_{i,del} = \Delta_i N_{o,selected}$ phenotypes.
2. For each sire i with no excess use, $N_{i,add} = abs(\Delta_i) N_{o,selected}$ is the maximal number of offspring that can be added for that sire so that the sire will not be used in excess of the imposed limitation.
3. For each sire i with no excess use, mark its non-selected offspring corresponding to the highest $N_{i,add}$ phenotypes.
4. Combine the marked nonselected offspring of all sires and rank them together.
5. Use the offspring in the ranked list corresponding to the highest $N_{i,del}$ phenotypes to replace the deleted offspring.

Genetic Gain Evaluation

Let R denote the expected annual response,

$$R = \frac{R_{ss} + R_{sd} + R_{ds} + R_{dd}}{L_{ss} + L_{sd} + L_{ds} + L_{dd}}, \qquad [8]$$

with R_{ss}, R_{sd}, R_{ds}, R_{dd} denoting genetic gain per generation for the paths sire-to-son, sire-to-daughter, dam-to-son, and dam-to-daughter, respectively. L_{ss}, L_{sd}, L_{ds}, L_{dd} denote the generation intervals for the sire-to-son, sire-to-daughter, dam-to-son, and dam-to-daughter paths, respectively. Here $R_{sd} = 0$ because all selected sires are assumed to produce an equal number of daughters, and R_{dd} is fixed to 0.21, as given in Table 3.1 in Weller (2016). Thus, no genomic selection is assumed on this path. The gains from parents to sons, R_{ss} and R_{ds}, are the differences between the mean genetic value of the offspring after selection and the average of the parent mean genetic value. Thus,

$$R_{ss} = G_o - G_s \text{ and } R_{sd} = G_o - G_d, \qquad [9]$$

and the genetic gain for dams, G_d, is the mean gain weighted by the age group proportions of cows used as bull dams.

From Table 3.1 in Weller (2016), $L_{sd} = 2.5$ and $L_{dd} = 4$. L_{ds} is the weighted average generation intervals across the sire dams' age, where $L_{ds,calves} = 2$, $L_{ds,parity1} = 3$, $L_{ds,parity2} = 4$, $L_{ds,parity3} = 5$, and the weights are the relative sample sizes for each age group among the selected dams.

Number and Conditions of Simulations. The N_o was varied from 60 to 3,000. The number of sires of sons was varied from 4 to 15. In all cases the simulation were run without limitation on the number of sons selected from a specific sire, and with the number of sons limited to one-third of all sons selected. All simulations were run with and without genomic selection. All genetic gain estimates were generated by averaging over 10,000 simulations for each set of conditions. For each parameter configuration, σ_{go}^2 and σ_p^2 were estimated based on 100 simulations.

Response Curve Estimation. For each number of sires of sons, R as a function of N_o could be approximated by the following function.

$$R = \beta_0 + \beta_1 N_0 + \beta_2/N_0 + \beta_3\sqrt{N_0} + \varepsilon, \qquad [10]$$

where the β terms are the regression coefficients, and ε is the random residual.

Accounting for Inbreeding

The effect of inbreeding on the genetic gain and the economic optimum was assessed as well, as inbreeding is typically allowed to some extent within parental matching. A second generation of young bulls was generated, and inbreeding was accounted for when choosing from all possible matches between the selected sires and selected dams.

For the second generation, the sire population was the 40 selected young bulls of the first generation. The dam population was re-generated in the same way as for the first generation, only its mean was now adjusted for the genetic gain across a generation, based on the assumed annual genetic gain and the generation interval from dam to daughter. Thus the adjustment was by $0.2L_{dd} = 0.8$.

Next, as in the first generation, the top ranking $p_s N_s$ sires and the top ranking $p_d N_d$ dams were selected to be parents based on their phenotypic performance. The number of all possible matches between the selected parents, denoted by N_{match}, is equal to $p_s N_s p_d N_d$.

If inbreeding was not restricted, N_o parental matches were selected at random to produce offspring. If inbreeding was restricted, the selection accounted for the level of inbreeding for the given match, as follows: N_{match} inbreeding scores were sampled from a $\chi_{(1)}^2$ distribution,

and the scores were standardized to have a standard deviation of 1 and then shifted to have a mean of 2.5. These values are based on the accumulated Israeli herd data since 2010. The N_o parental matches with the lowest scores were selected to produce offspring. For both schemes, $N_{o,selected}$ offspring were selected as in the first generation.

Economic Evaluation

Profit Evaluation. Let V denote the nominal profit per year for the population, and let T denote the profit horizon (in years). In addition, assume t years until profit occurs and an interest rate of d. Then, from Hill (1971), the cumulative discounted returns are

$$RET = V\left[\frac{r^t - r^{T+1}}{\left(1-r\right)^2} - \frac{\left(T-t+1\right)r^{T+1}}{1-r}\right], \quad [11]$$

where $r = \dfrac{1}{1+d}$. Let P denote the profit per unit gain in the selection objective per cow. As noted previously, the unit used to compute genetic gain is the genetic standard deviation of the index. Units of the Israeli breeding index are approximately equal to kilograms of milk. The genetic standard deviation of the index is 708 units. Profit per kilogram = $0.15, thus $P = \$0.15(708)$ = \$106.2 per unit of the genetic standard deviation. Denote by $\hat{R}$ the expected annual response predicted by the regression model in Equation [10], and denoting the total number of cows in the population as N, V can then be computed as follows:

$$V = \hat{R}PN. \quad [12]$$

Let C_c denote the nominal annual cost of the breeding program. Then, from Hill (1971), the cumulative discounted costs are

$$C = C_c\left[\frac{r\left(1-r^T\right)}{1-r}\right]. \quad [13]$$

A nominal cost function was constructed based on all costs generated by raising the bull calves and obtaining genomic evaluations. The following unit costs were assumed (based on exchange rate of ~3.9 Israel Shekels per \$1, as of June 26, 2016): \$95 for a genomic chip, \$1.5 for ear tagging, additional purchase cost of \$153 for a calf that was kept by the Sion Artificial Insemination Institute (Shikmim, Israel) and \$64 for a calf that

was sold for beef, \$90 for a DHL Express (Airport City, Israel) shipment of 12 samples, \$164 for a labor costs per day. Each group of 10 calves was assumed to generate an additional day of labor. Shipping and tagging were insignificant relative to the other costs and thus are ignored. Costs are summarized in Table 1. Finally, total cumulative profit is obtained by subtracting the total cumulative costs (Equation [13]) from the total cumulative returns (Equation [11]).

Maximum Profit Determination. The cumulative profit as a function of N_o was approximated by subtracting the cumulative cost curve from the profit curve. The N_o yielding maximal profit, and the numbers of calves at which 90, 95, and 99% of maximal profit are obtained are extracted from this curve.

RESULTS

Cost Analysis

Nominal cost (\$) as a function of N_o is given in Figure 2 for the individual cost elements and for total costs. Linear regression on the total cost as a function of N_o can be approximated by the following equation:

$$C_c = 10{,}922 + 305N_o, \quad [14]$$

and the coefficient of the determination was 0.99.

Table 1. Values of parameters and variables used in the simulations

| Variable	Value
Total number of cows in the population	120,000
Number of heifers	30,000
Number of parity 1 cows	25,000
Number of parity 2 cows	20,000
Number of parity 3 cows	15,000
Heifer reliability	0.3275
Reliability of parity 1 cows	0.46
Reliability of parity 2 cows	0.52
Reliability of parity 3 cows	0.54
Reliability of bull sires	0.9
Number of bulls for general service each year	40
Number of bull sires	4–15
Number of bull dams	120–10,000
Probability of obtaining a healthy male calf from each bull dam	0.3
Genetic standard deviation in trait units	708
Economic value of one trait unit (\$)	0.15
Price of genomic evaluation per animal (\$)	95
Price of ear tag (\$)	1.5
Purchase cost of male calf from farmer (\$)	153
Recovery cost for male calf sold for beef (\$)	64
DNA sample shipment costs for 12 samples (\$)	90
Number of days additional labor per calf	0.1
Cost of labor per day (\$)	164
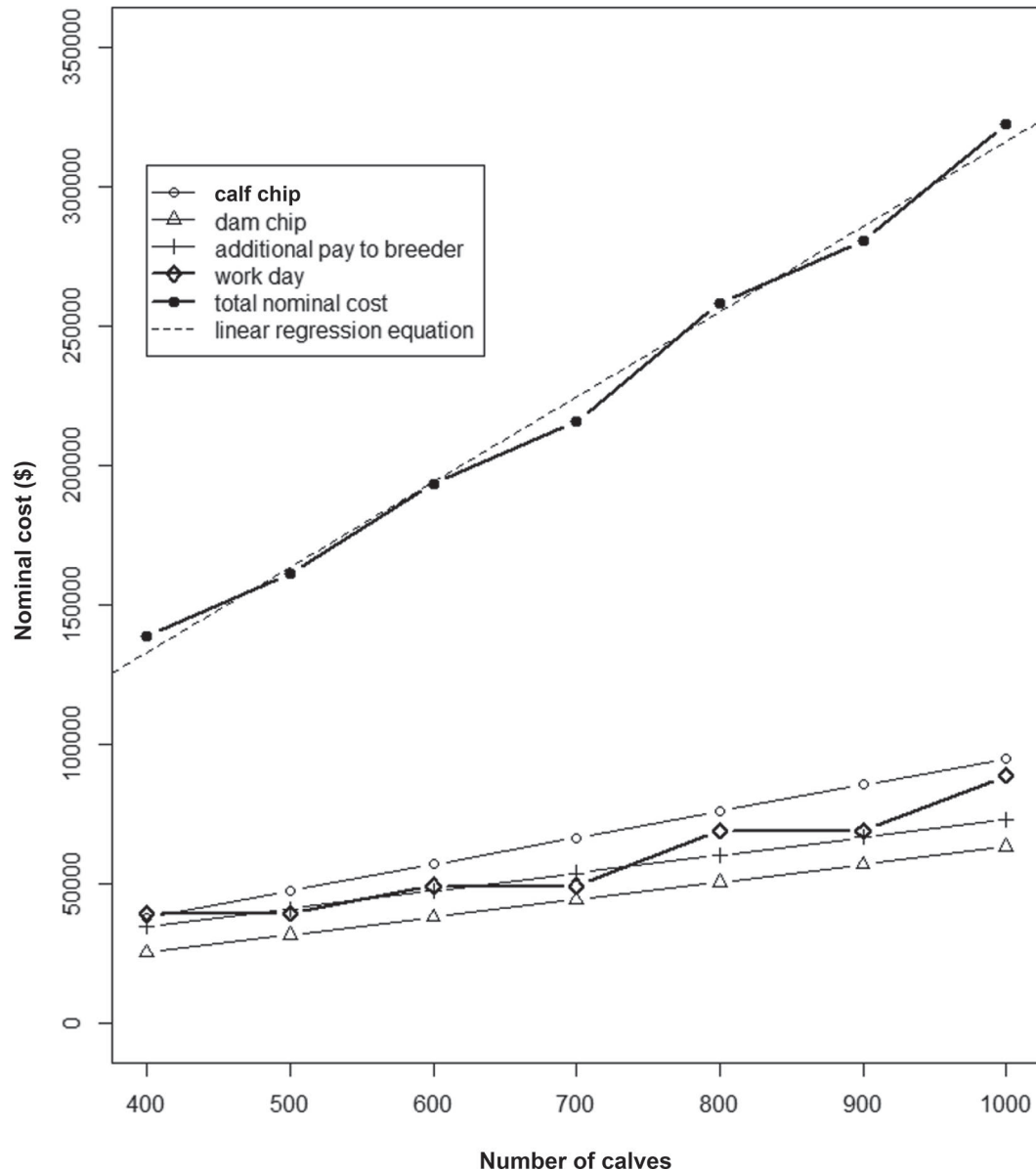
Figure 2. Nominal cost ($) versus number of calves for genetic selection involving genomic evaluation. The following unit costs were assumed (based on exchange rate of ~3.9 Israel Shekels per $1, as of June 26, 2016): $95 for a genomic chip, $1.5 for ear tagging, additional cost of $153 for a calf that was kept by the Sion Artificial Insemination Institute (Shikmim, Israel) and $64 for a calf that was sold for beef (summing both with the calf numbers as weights generates the total additional pay to the breeder), $90 for a DHL Express (Airport City, Israel) shipment of 12 samples, and $164 for labor costs per day. Each additional 10 calves required one additional day of labor. Shipment and tagging are not included in the plot due to their relatively small costs. The nominal cost linear prediction is given by Equation [14].

Genetic Gain

The R as a function of N_o for 4, 8, and 15 sires of sons are plotted in Figure 3 for both genomic and pedigree selection, with and without limitation on the maximum number of sons per sire. The economically optimum value for N_o computed as described previously is also shown. The maximal expected annual response ranged between 0.35 and 0.4 units of the genetic standard deviation for selection with genomic evaluation, compared with 0.25 to 0.28 for selection without genomic evaluation. The response rapidly increased with increase in N_o up to 400, and then started to level off. The slight decrease in genetic gain without genomic evaluation for $N_o > 400$ is somewhat surprising, and may be due to the 2-step nature of the selection scheme. That is,
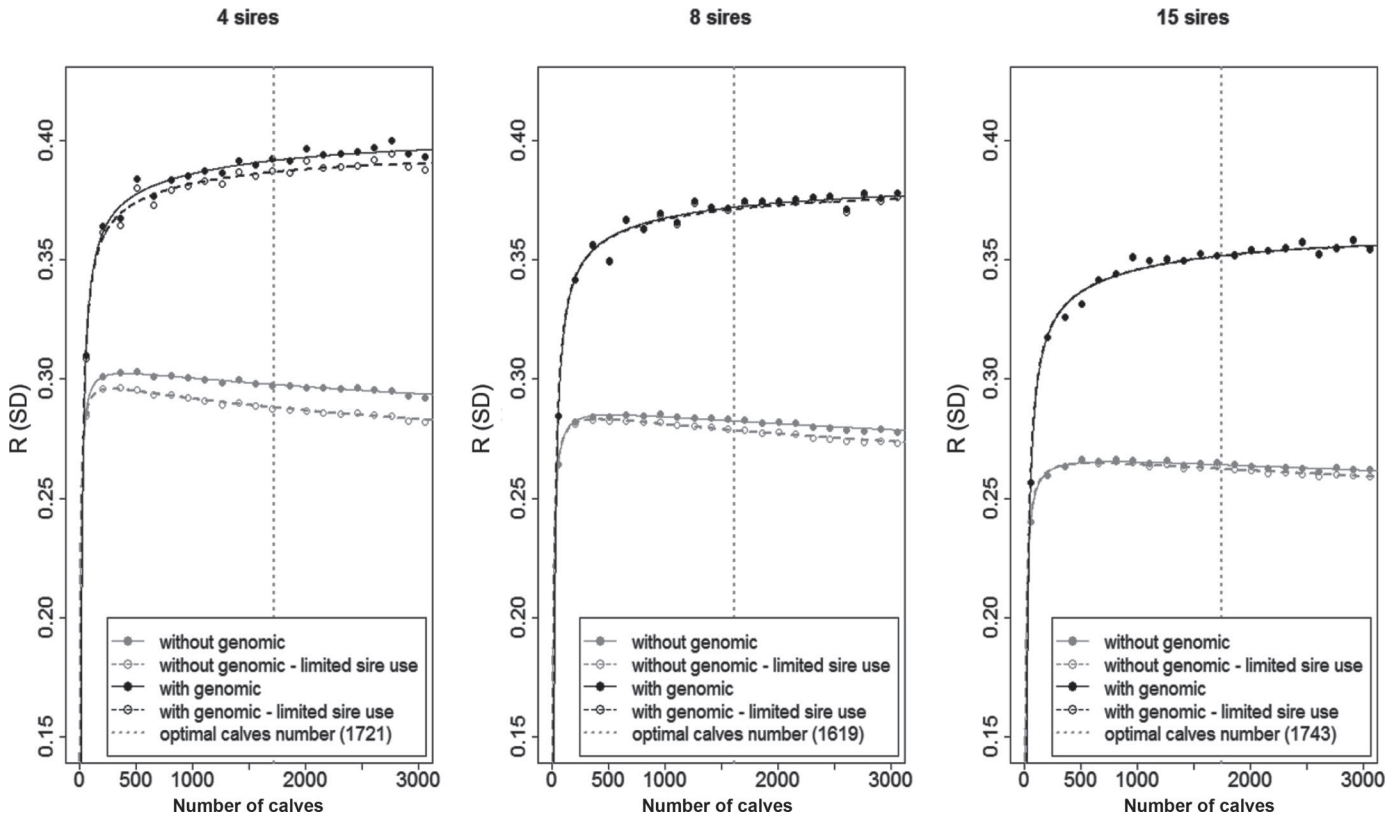
Figure 3. Expected annual response (R) with 3 numbers of bull sires, as a function of the number of bull calves, in units of the genetic standard deviation. Results are given for selection strategies involving or not involving genomic evaluation and with or without sire use limitation. The vertical dashed line marks the optimal number of calves with genomic evaluations, corresponding to the maximal profit (see Figure 6). Estimates are based on 10,000 repeated simulations (SE <0.00035). Limit for sire use is 33%.

first bull dams were selected based on their own genetic evaluations, and then progeny were selected based on the mean of their sire and dam evaluations.

As expected, response decreases as a function of the number of bull sires because the sires' mean genetic value decreases when lower ranking sires are included. However, change in the number of bull sires had virtually no effect on the economically optimal value for N_o, which was in the range of 1,650 to 1,850 for all scenarios. Limiting the percentage of use of a single inseminating sire has only a minor effect on the response, but may have a significant effect on reducing inbreeding over the long term. As expected, the reduction diminishes as the number of inseminating sires increases because the share of each sire tends to be smaller.

The individual gains along the sire-to-son and dam-to-son paths with and without genomic selection are given in Figure 4. Corresponding to the results in Figure 3, the gains are higher when selection is based on genomic evaluation. For selection without genomic evaluation, the maximal gain is reached with ~200 calves, whereas genomic evaluation can increase the gain considerably up to 1,500 calves for both paths.

Generation intervals for the dam-to-son path are given in Figure 5. At the economic optimum, generation intervals with only 4 sires of bulls were almost 1 yr greater with genomic selection. Without genomic evaluation, young bulls are selected based only on parent average, and due to the genetic trend in the population, selection of bull dams is skewed toward younger dams. With genomic information, a larger fraction of sons of older cows is likely to be selected, based on their Mendelian sampling effect, which is independent of the genetic trend. The standard deviation among the pseudo-phenotypes is increased, which diminishes the advantage of younger dams due to pedigree.

Profit ($) as a function of the number of calves (in $\log_2$ scale) for the genomic selection scheme is plotted in Figure 6 for 4, 8, and 15 sires. Profit is positive with 60 calves, which is the minimum number tested. It then increases relatively slowly until it reaches its maximum. Consequently, as can be seen in Figure 6, even though the maximal profit is obtained for roughly 1,600 calves with 8 inseminating sires, to roughly 1,750 calves with 15 inseminating sires, 99% of the profit can be obtained with only between 700 and 800 calves, and 95% with
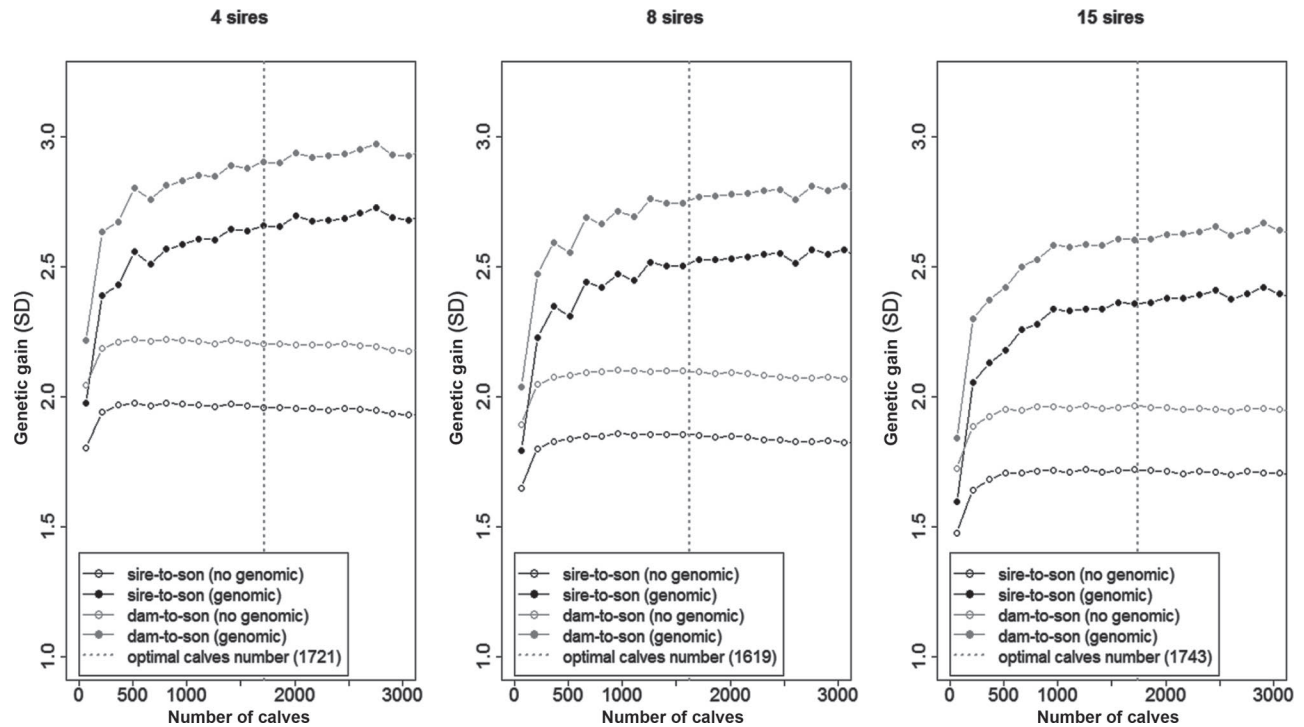
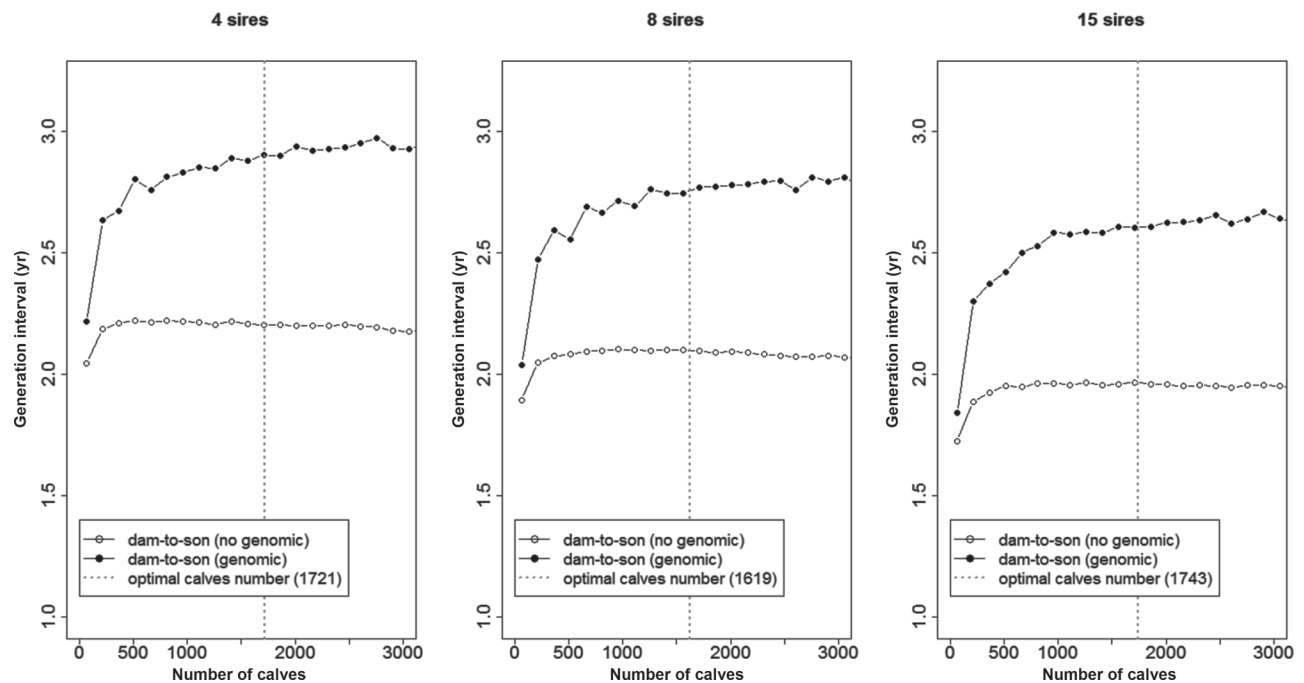**Figure 4.** Genetic gain for sire-to-son and dam-to-son paths, with 3 number of bull sires as a function of the number of bull calves, in units of the genetic standard deviation. Results are given for selection strategies involving or not involving genomic evaluation and sire use limitation. The vertical dashed line marks the optimal number of calves with genomic evaluations, corresponding to the maximal profit (see Figure 6). Estimates are based on 10,000 repeated simulations (SE <0.0027). Results are shown for no restriction on sire use, but similar results were obtained with restricted use.


Figure 5. Generation interval for dam-to-son path, with 3 number of bull sires as a function of the number of bull calves in units of the genetic standard deviation. Results are given for selection strategies involving or not involving genomic evaluation. The vertical dashed lines mark the optimal number of calves with genomic evaluations, corresponding to the maximal profit (see Figure 6). Estimates are based on 10,000 repeated simulations (SE <0.0016). Results are shown for no restriction on sire use, but similar results were obtained with restricted use.
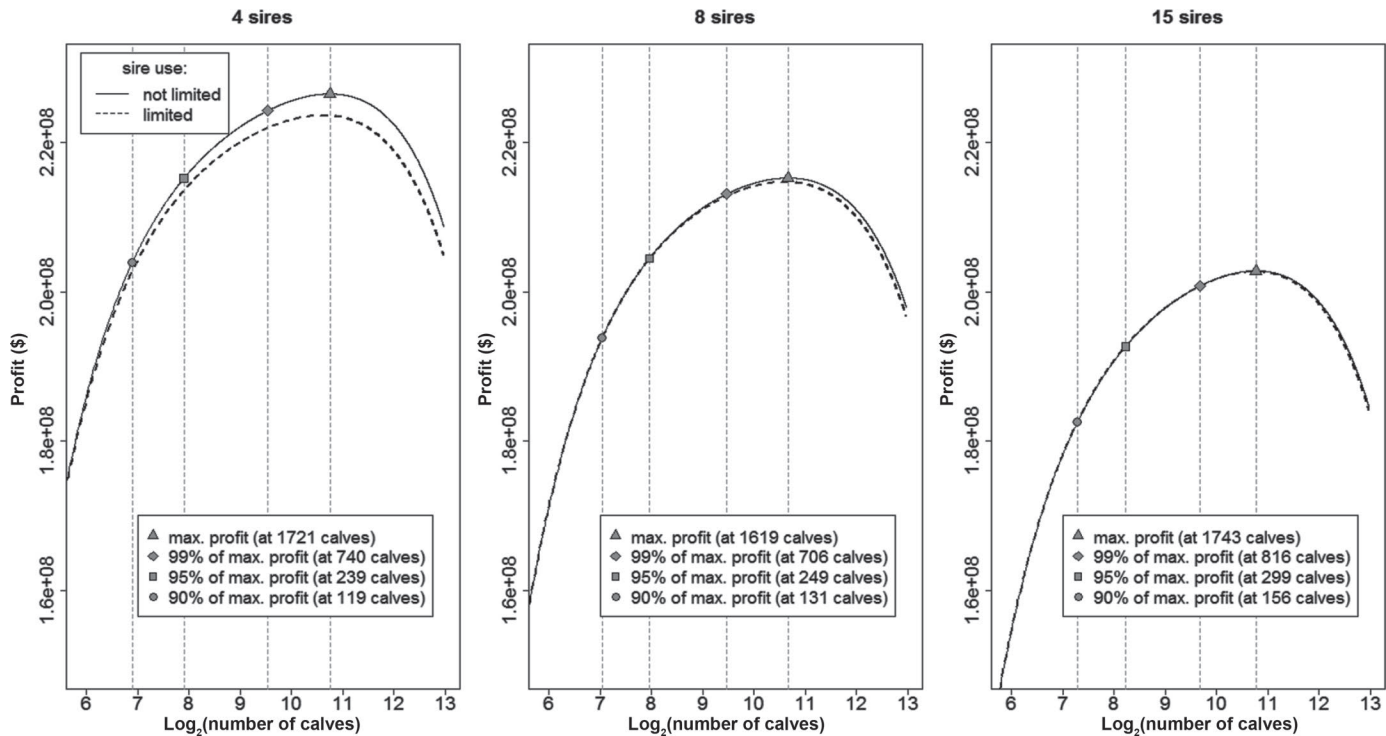
Figure 6. Profit ($) as a function of the number of calves (in $\log_2$ scale) for the genomic selection scheme with and without limited sire use. The curve starts at 5.9, which equals the $\log_2$ of 60: the minimal number of calves used. The vertical dashed lines mark the optimal number of calves, corresponding to the maximal (max.) profit (triangle), and the numbers of calves that result in 90 (circles), 95 (squares), and 99% (diamonds) of maximal profit. The profit curves are based on the expenses and response curves given in Figures 2 and 3. Profits are calculated assuming a 15-yr profit horizon, 4 yr until profit, 5% discount rate, profit of $106.2 per unit of the genetic standard deviation, and with nominal cost assumed to be approximately linear in the number of calves, as shown in Figure 2. Limit for sire use is 33%.

only ~250 calves. Considering uncertainties and risk inherent in long-term calculations, increasing the number of genotyped male calves above 300 cannot be justified.

Effects of Reliability

As reliabilities for sire and female calves increase, genetic gain increases as well, as can be seen in the response curves presented in Figures 7a and 8a. As reliability increases, the absolute profits increase, and the maximal profit is obtained for a lower number of calves born in each generation, as can be seen in Figures 7b and 8b. Yet the large general effect of genomic information on the achieved response, compared with selection without using genomic information, is preserved. In addition, as reliability increases, the maximal profit obtained when using genomic selection increases as well and is obtained for a lower number of calves born in each generation.

Effects of Inbreeding

Restricting inbreeding had virtually no effect, as compared with the scenario of no restriction on inbreeding.

This can be seen for genetic gain in Figure 9 and for the absolute profits and their optimum, in Figure 10.

DISCUSSION

Our study showed a substantial advantage in genetic gain due to use of genomic evaluation, and demonstrated the relationship between annual genetic gain and the number of calves genotyped. We used stochastic simulation techniques to construct the population and to employ the selection strategies. We fitted an expected annual response curve to each scenario. Profit prediction was based on a deterministic economic formulation. Thus, we were able to offer a procedure for determining the optimal selection path for a given herd population and economic parameters.

Selection based on parents' average is highly influenced by genetic relationships, and therefore tends to increase inbreeding and reduces the effective number of males selected as parents. As noted by Boichard et al. (2015), using a large number of bulls as service sires and bull sires both can increase genetic trends and reduce inbreeding. Genomic selection entails a higher chance of identifying males from new blood lines and
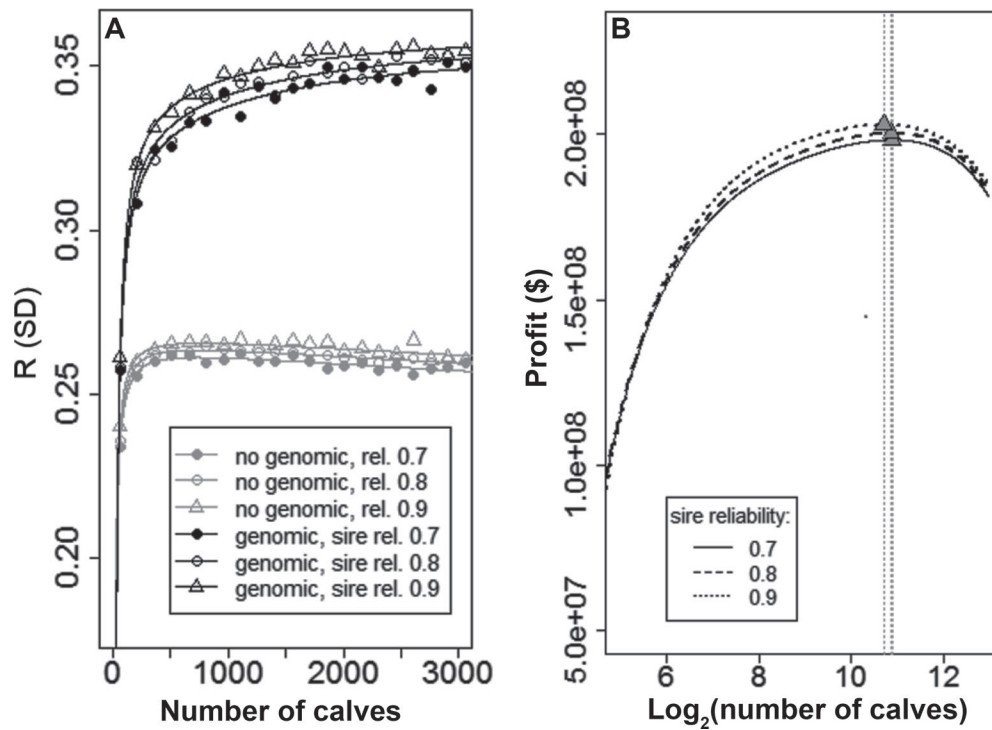
Figure 7. Response (R; A) and profit (B) curves with genomic evaluations varied by sire reliability (rel.), ranging between 0.7 and 0.9, where 0.9 is the assumed value for the Israeli herd if genomic genotyping is available. The vertical dotted lines mark the optimal number of calves with genomic evaluations, corresponding to the maximal profit, and the triangles mark maximum profit at each reliability value.
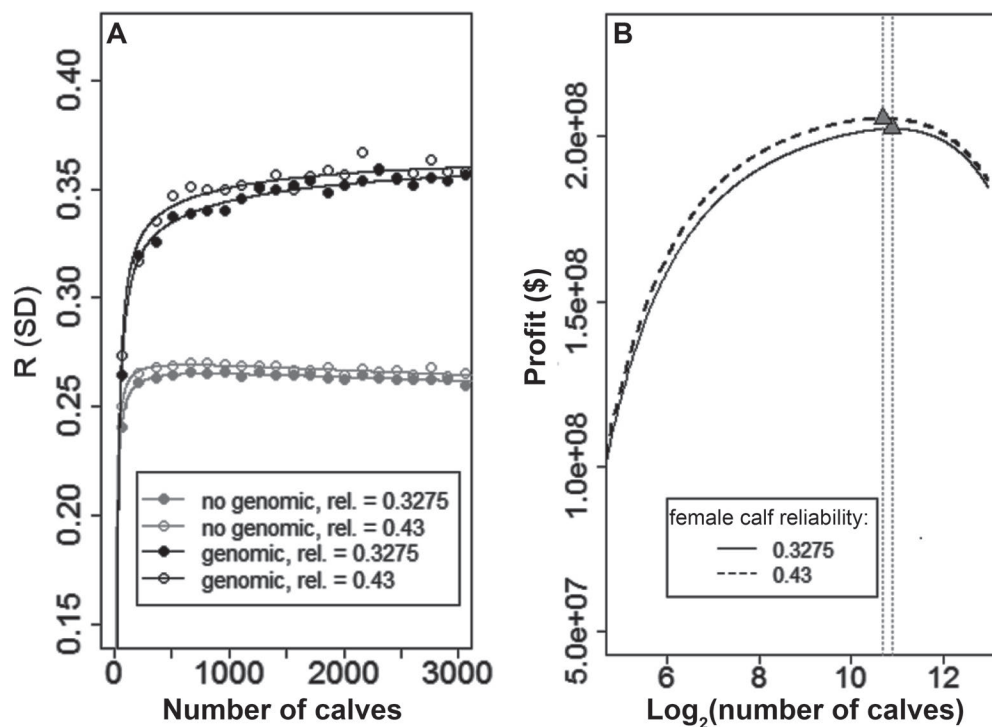

Figure 8. Response (R; A) and profit (B) curves with genomic evaluations varied by female calf reliability (rel.), using the values of 0.3275, assumed for the Israeli herd, and 0.43, potentially achieved if calves are genotyped. The vertical dotted lines mark the optimal number of calves with genomic evaluations, corresponding to the maximal profit, and the triangles mark maximum profit at each reliability value.
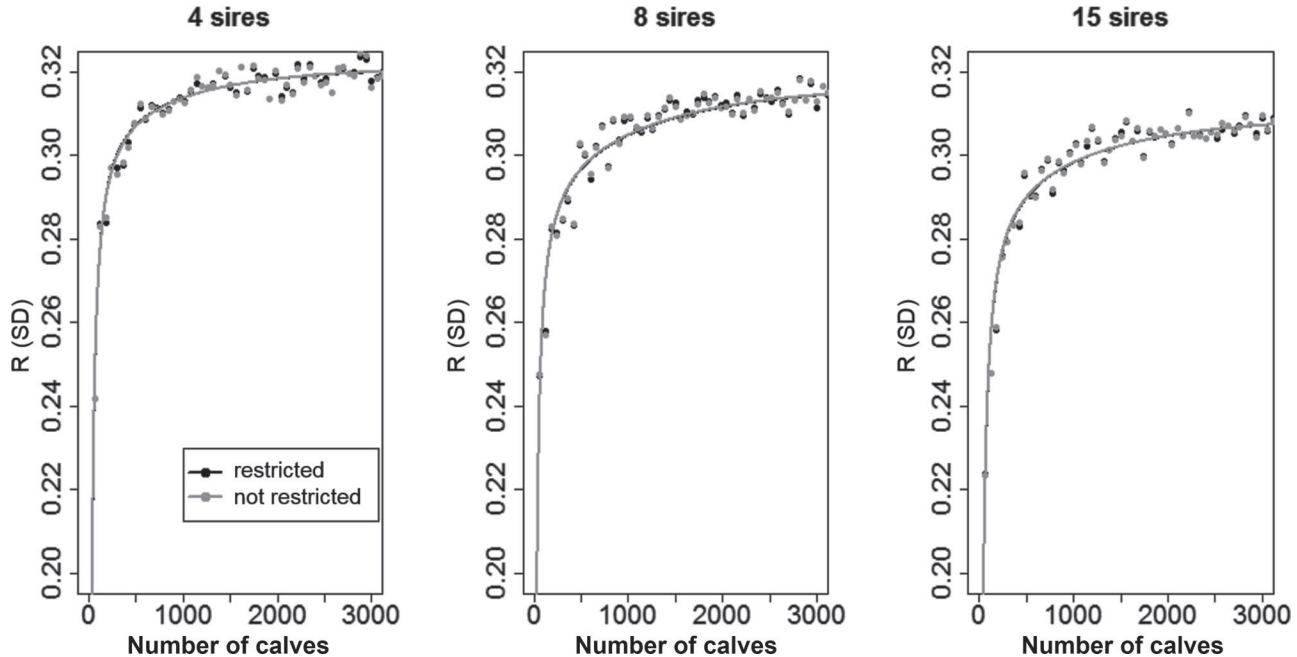
Figure 9. Expected annual response (R) with 3 numbers of bull sires, as a function of the number of bull calves, in units of the genetic standard deviation. Results are given for selection involving genomic evaluation and with or without restriction of inbreeding between the matched parents. Estimates are based on 1,000 repeated simulations (SE <0.0011). Limit for sire use is 33%.
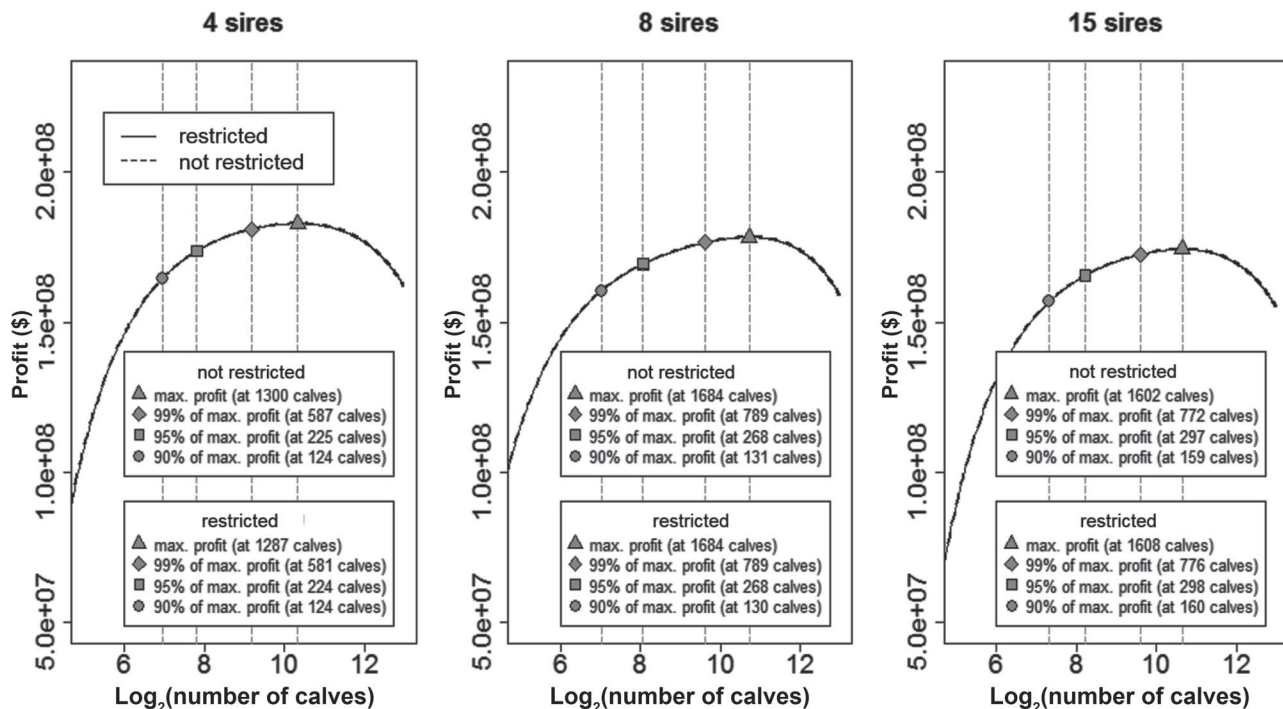

Figure 10. Profit ($) as a function of the number of calves (in $\log_2$ scale) for the genomic selection scheme with or without restriction on inbreeding between the matched parents. The curve starts at 5.9, which equals the $\log_2$ of 60: the minimal number of calves used. The vertical dashed lines mark the optimal number of calves, corresponding to the maximal (max.) profit (triangle). The profit curves are based on the expenses and response curves given in Figures 2 and 9. Profits are calculated assuming a 15-yr profit horizon, 4 yr until profit, 5% discount rate, profit of $106.2 per unit of the genetic standard deviation, and with nominal cost assumed to be linear in the number of calves, as shown in Figure 2. Limit for sire use is 33%.

thus may reduce inbreeding. Investigating its long-term implications across several generations is of interest. Here, we showed that inbreeding, as restricted in the selection strategy for the Israeli herd, had virtually no effect on the genetic gain and the profits achieved by genomic selection.

Averaged over the entire population, the additional cost due to genomic evaluation is relatively inexpensive compared with reproductive technologies, such as multiple ovulation and embryo transfer and ovum pickup, as well as sexed semen (Schaeffer, 2006; Schefers and Weigel, 2012). However, genetic gain and profit can be enhanced by application of both genomic evaluation and reproductive technologies. A study comparing the genetic and economic performances combining all these alternatives using similar tools as in this paper may be of high value for the farmers and breeders in their decisions to invest in each strategy.

CONCLUSIONS

Between 4 and 15 bulls and between 200 and 27,000 cows with the highest pseudo-phenotypes were selected as candidate bull parents. Annual costs were estimated as $10,922 + $305 × candidate bulls. Economic optimum with a discount rate of 5%, first returns after 4 yr, and a profit horizon of 15 yr was obtained with genotyping 1,620 to 1,750 calves for all numbers of bull sires. However, 95% of the optimal profit can be achieved with only 240 to 300 calves. Considering uncertainties and risk inherent in long-term calculations, increasing the number of genotyped male calves above 300 cannot be justified. Annual response to selection ranged from 0.35 to 0.4 genetic standard deviation for 4 to 15 bull sires, as compared with 0.25 to 0.3 for a comparable half-sib design without genomic selection. The increased reliabilities achieved by adding genomic evaluation to the selection process contribute not only in increasing the absolute profits, but also in lowering the economically optimum number of male calves genotyped. Inbreeding, as restricted within the selection strategy for the Israeli herd, had virtually no effect on the genetic gain and the profits achieved by genomic selection. This result was obtained based on inbreeding effective after one additional generation of selection, beyond the initial simulated parents and their offspring. In the medium and long term, the effect of inbreeding may vary and have a more complicated pattern.

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