

Investigating the Bias Resulted from Ignoring Bulmer Effect on the Genetic and Economic Output in Progeny Test and Genomic Selection Program

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Abstract

This study aims to investigate the degree of bias resulted from ignoring Bulmer effect during the estimation of genetic and economic progress in progeny test and genomic selection programs. To this end, a deterministic approach based on gene flow method in a time horizon of 70 years was used. In this study, milk production was considered as the selection goal under a four-path selection strategy. In the progeny test, asymptotic genetic variance of sires and dams decreased by 67.59% and 64.97%, respectively. Also, in genomic selection program, asymptotic genetic variance in sires and dams decreased by 68.56% and 63.06%, respectively. The maximum reduction in genetic variance occurred in the first three generations. In the progeny test program, the bias of genetic progress per generation due to ignoring Bulmer effect was four times higher than genomic selection program, but this difference decreased significantly in the results of single round and continuous selection after 20 generations. Bulmer effect resulted in 51.64% and 44.62% reduction in the economic efficiency of progeny test and genomic selection, respectively. According to the results of this study, ignoring Bulmer effect in the investigations concerning comparison between progeny test and genomic selection seems to be unreasonable. Long-term selection has more severe effect on genetic and economic aspects of progeny test in comparison to genomic selection program via decreasing genetic variance.

Keywords: *Bulmer effect, Genomic selection, Bias, Progeny testing, Selection intensity*

Bulmer Etkisinin Gözardı Edilmesinin Projeni Testinde Genetik ve Ekonomik Sonuçları ve Genomik Seleksiyon Programındaki Olumsuz Etkisinin Araştırılması

Özet

Bu çalışmada Bulmer etkisinin göz ardı edilmesinin projeni testinde genetik ve ekonomik sonuçlarının tahmini ile genomik seleksiyon programındaki olumsuz etki derecesinin araştırılması amaçlanmıştır. Bu amaçla, 70 yıla yayılan gen akış metodu temelli belirleyici bir yaklaşım kullanıldı. Çalışmada, 4 yollu seleksiyon stratejisi altında seleksiyon hedefi olarak süt üretimi kullanıldı. Projeni testinde, baba ve annelerin asimtotik genetik varyansı sırasıyla %67.59 ve %64.97 azaltıldı. Genomik seleksiyon programında, baba ve annelerin asimtotik genetik varyansı da sırasıyla %68.56 ve %63.06 azaltıldı. Genetik varyansda maksimum azalma ilk üç nesilde gerçekleşti. Projeni test programında, Bulmer etkisini göz ardı etme sonucu, her nesildeki genetik ilerleme etkisi genomik seleksiyon programından dört kat daha fazlaydı. Ancak bu fark tek tur ve 20 nesil sonrasında devamlı seleksiyon sonuçlarında anlamlı derecede azaldı. Bulmer etkisi, projeni testinin ekonomik verimliliğinde ve genomik seleksiyonda sırasıyla %51.64 ve %44.62 azalmaya neden oldu. Bu çalışmanın sonuçları projeni testi ile genomik seleksiyonun karşılaştırıldığı incelemelerde Bulmer etkisinin göz ardı edilmesinin kabul edilebilir olmadığını göstermiştir. Uzun süreli seleksiyonun genetik varyansı azaltmak suretiyle genetik seleksiyon programı ile karşılaştırıldığında projeni testinin genetik ve ekonomik yönleri üzerine daha ciddi etkileri bulunmaktadır.

Anahtar sözcükler: *Bulmer etkisi, Genomik seleksiyon, Olumsuz Etki, Projeni testi, Seleksiyon yoğunluğu*



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INTRODUCTION

Due to the intensive use of artificial insemination and limited number of superior sires, the existing population of dairy cattle has limited size; its effective size is only 50-100 heads in each country [1]. Therefore, alleles of limited number of ancestors are shared among the population. Reduction in the size of selected population has serious effects on genetic variance of this population [1,2]. The selection not only influences the mean of population, but also affects the genetic variance. The decrease in the genetic variance could affect the economic-genetic progress of the subsequent generations [3]. Truncating a distribution affects both the mean and the variance of the distribution. The effect of selection on genetic variance was first investigated and involved in breeding estimations by Bulmer [4]. Hence, according to the investigations conducted by Bulmer, the effect is often referred to as the "Bulmer Effect".

The group of selected animals represents one tail of non-normal distribution curve and reduction factor of genetic variance depends on selection intensity. The genetic variance of a population prior to selection is partitioned into the parental and Mendelian sampling components. Only the parental contributions to genetic variance are affected by selection [4].

Utilization of IVF and MOET duplicates the effect of the limited number of selected superior individuals on genetic variance [5]. The highest selection intensity often belongs to sire of sire (SS) path. Dam of dam (DD) path has the lowest selection intensity due to high demand for replacement heifers in commercial dairy farms [6]. Correction for Bulmer effect has not been considered in many investigations carried out so far [7-11]. Moreover, nowadays, due to the need for decision-making in the selection of efficient animal breeding programs, many simulations are conducted in order to compare progeny test and genomic selection programs under a variety of strategies. The main point is that the variation in genetic variance using these two selection programs has remained unknown; different degrees of bias due to ignoring Bulmer effect may therefore lead to unreliable inferences in such comparisons. Thus, studying the bias rate of results due to ignoring Bulmer effect in progeny test and genomic selection seems necessary. In this study, the variation of genetic variance due to selection was calculated by simulating progeny test and genomic selection schemes during 20 generations. Then, based on these estimated variations in genetic variance, the genetic and economic progresses resulting from these two selection programs were calculated.

MATERIALS and METHODS

Description of Simulation Condition

A deterministic model based on gene flow method [12] was used to estimate the effect of altering the accuracy

of genomic selection evaluations (AGSE) on economic efficiency (EE) of selection program through time horizon of 70 years. The time horizon of 70 years was chosen to ensure reaching the equilibrium phase for genetic growth [9]. All calculations were undertaken using MATLAB 8.0 programming language [13]. Population statistics, productive, reproductive and economic parameters were based on the Holstein cattle production in Iran. In the present study, the milk yield trait was considered as the selection goal, with genetic standard deviation of 477 kg and heritability of 0.29 based on average estimates offered by Chegini [14] and Ghavi Hossein-Zadeh [15] for Holstein dairy cattle in Iran. Productive and reproductive statistics of Iranian Holstein dairy cattle are shown in Table 1. EE was calculated as the ratio of the revenues to the costs of simulated programs.

Overall Structure of Progeny Test

A four-pathway -including sires of future sires (SS), sires of future dams (SD), dams of future sires (DS), and dams of future dams (DD) pathways- selection program was considered in the simulated progeny test program. The superior dams were selected from breeding population as DS. Also, a proportion of productive cows were inseminated by young bulls (test capacity) and the young bulls were evaluated using the daughters' records.

Revenues were divided into two parts: (1) revenues obtained from genetic progress and (2) non-genetic revenues. The revenues from genetic progress resulting from selection program depend on the economic value of milk trait; the non-genetic revenues, moreover, included the revenues from sale of omitted tested bulls or proven bulls. Generally, the costs were divided into three parts: quarantined costs, proving costs and the costs after proving. The proving costs (C_{prove}) were calculated as follows: (Formula 1)

$$C_{prove} = N_{YB} \left(C_{YB} + (C_{cs} + C_{ps})S_{dose} + C_{in}S_{dose} + \sum_{t=1}^{t=w_{yr}} (C_m + C_f) \left(\frac{1}{1+i_c} \right)^t + (r_c r) \left(\frac{1}{1+i_c} \right)^{(1+w_{yr})} \right)$$

Where r_c is the recording cost per daughters, i_c discounting factor of cost, w_{yr} the number of expected years for testing the young bulls, C_f the feeding cost per young bull in a period of one year and C_m the maintenance cost of each young bull in a period of one year. C_{YB} is the purchase cost of each young bull after quarantine, C_{cs} the collection cost of each sperm dose, C_{ps} the producing cost of each sperm dose, S_{dose} the number of sperm doses resulting from young bulls for inseminating productive population in order to produce daughter progenies, C_{in} insemination cost, and R_c the recording cost of young bull's daughters. Considering the maintenance of proved sires for a period of 4 years, the costs after proving were calculated by the following (Formula 2):

$$CP_{m-f} = \sum_{t=5}^{t=8} \left((C_c + C_{save} + C_m + C_f) \left(\frac{1}{1+i_c} \right)^{w_{yr}+t} \right) n_{SD}$$

Table 1. Productive and reproductive parameters		
Items	Productive and Reproductive Parameters	Values units
Population parameters	Number of productive cows	502400
	Percentage of herd book population	33%
Biological variables	Heritability of milk production ¹	0.18-0.36
	Genetic variance of milk production	477 (kg)
	Proportion of captured genetic variance	0.875
	Twining rate	53.4 (%)
	Abortion rate	62.8 (%)
	Number of needed mothers for producing one YB	6.07
	Alive daughters per cow	40 (%)
	Young cows under milk recording as DS	30 (%)
	Death birth rate	29.3 (%)
	Death rate at 3 month	27.8 (%)
	Insemination number per pregnancy	2.22
	Technical variables	Years of using a proved bull
Quarantine time		6 (month)
Time interval between 2 recalculating haplotype effects		2
Number of individual in training set ²		500-10000
Number of daughters per bulls in training set		100
First calving age		2.13
Open days		397.8
Economic variables	Sperm production per bull	18000 (dose)
	Insemination cost	7 (US\$)
	Cost of buying a YB	1429 (US\$)
	Maintenance and feeding cost in Quarantine/month/YB	157 (US\$)
	Cost of testing for diseases in Quarantine/YB	28 (US\$)
	Cost of collecting each Vial of Sperm	2 (US\$)
	Cost of recording/daughter	2 (US\$)
	Feeding cost/year/YB	1543 (US\$)
	Maintenance cost/year/YB	343 (US\$)
	Price of culled bull	2000 (US\$)
	Genotyping cost ³	50-400 (US\$)
	Discount rate of costs	0.06
	Discount rate of returns	0.08
	Economic value of milk production (US\$)	0.23

1: In the basic scenario number of individuals in training set was 1,000, in the first scenario varied from 500 to 3,500 and in order to produce varied from 500 to 10,000; 2: In the basic scenario the assumed heritability was 0.29 and in the second scenario varied from 0.18 to 0.36; 3: In the basic scenario genotyping cost was 100 US\$ and in the third scenario varied from 50 to 400 US\$

C_c is the collection cost of 18000 sperm dose, C_{save} the costs of production and storing of 18000 sperm dose, C_m the maintenance cost of each proved sire, and C_f the annual feeding cost of each proved sire. Finally, the sum of these costs was considered as the costs resulting

from single round selection based on progeny test.

Structure of Genomic Selection Program

In genomic selection program, all productive cows were inseminated by young bulls, but, in progeny testing program, a proportion of productive cows (P : test capacity) was inseminated by young bulls and the remaining ones were inseminated by proven bulls. In this investigation we tried to consider the required and available numbers of individuals in different paths of genomic selection program, close to that of progeny test program. The accuracy of genetic evaluations was calculated using (Formula 3) [16].

$$r = w \sqrt{\frac{N_p R^2}{N_p R^2 + M_e}}$$

Where w shows the proportion of genetic variance captured by markers, and was assumed to be 0.875 [16]; N_p is the number of individuals in the training set and R^2 is the reliability of breeding values in the sire's population. R^2 was calculated by; $\frac{n}{\frac{4-h^2}{h^2}+n}$

n is the number of daughters of each progeny tested bulls. Also, M_e is the number of independent genome segments. In all paths, except DD, selection was implemented based on genomic information. Accuracy of DD path was assumed to be the square root of heritability.

Estimated effective number (N_e) of Holstein population in Iran is approximately 62.49; based on this N_e , the calculated M_e is 440.07 [17].

We planned the re-calculation of haplotype effects in the training set to be conducted every two years. Hence, it is necessary to keep up recording of sire's daughters in the training set. The cost of proving was calculated as follows: (Formula 4)

$$C_{prove} = N_{YB}(C_{YB} + C_{f-m} + R_c) + (N_{YB} + rr_{DS}N_{DS} + \frac{N_p}{h})G_c$$

Where G_c is the genotyping cost per selection candidate, h the time interval to determine Haplotype effects in training set and G_{cost} the costs of genotyping. The after proving costs were also calculated in a way similar to that of progeny test, except that the 1 to 5 year-old sires were used for insemination of productive population instead of 5 to 8 year-old proven bulls (in progeny test) and the discounting rates regarding these years were used. As well, in this selection method all costs were summated at the end of calculations in order to calculate the cost of performing single round selection.

Consideration of Bulmer Effect in Two Selection Programs

The value of genetic variance affected by selection (Bulmer

effect) was calculated using the method represented by Bulmer [4]. In four-path selection, genetic variance of sires and dams are calculated separately due to the difference in how the parents are selected for producing replacement sires and dams [18]. Hence, the genetic variance in generation t, in sire ($\sigma_{S^*}^2$) and dam ($\sigma_{D^*}^2$) populations was calculated according to the following formulas (5-7) [18]: (Formula 5)

$$\sigma_{S^*}^2 = 0.25(1 - K_{SS}r_{SS^*}^2)\sigma_{S(t-1)}^2 + 0.25(1 - K_{DS}r_{DS^*}^2)\sigma_{D(t-1)}^2 + 0.5\sigma_0^2$$

Where $\sigma_{S(t-1)}^2$ is sire genetic variance in generation t-1, $\sigma_{D(t-1)}^2$ dam genetic variance in generation t-1, K_{SS} the factor by which the variance in SS path is reduced, K_{DS} reduction factor of genetic variance in DS path, $r_{SS^*}^2$ the accuracy of selection in SS path, $r_{DS^*}^2$ the selection accuracy in DS path, and σ_0^2 the variance due to Mendelian sampling. (Formula 6)

$$\sigma_{D^*}^2 = 0.25(1 - K_{SD}r_{SD^*}^2)\sigma_{S(t-1)}^2 + 0.25(1 - K_{DD}r_{DD^*}^2)\sigma_{D(t-1)}^2 + 0.5\sigma_0^2$$

Where K_{SD} is the reduction factor of genetic variance in SD path, K_{DD} the reduction factor of genetic variance in DD path, $r_{SD^*}^2$ the accuracy of selection in generation t in SD path, and $r_{DD^*}^2$ the accuracy of selection in generation t in DD path. Therefore, genetic variance is reduced by factor K which in each selection path (K_{ij}) depends on selection intensity (i_{ij}) and truncation point (X_{ij}) of the path. Given the truncation selection, K is calculated by (Formula 7) [4]:

$$K_{ij} = i_{ij} (i_{ij} - X_{ij})$$

Comparison of Two Selection Programs

In both selection programs, genetic progress per generation was calculated by multiplying the selection intensity, the accuracy of each path and genetic standard deviation of milk trait and genetic progress results from single round and continuous selection, it is the gene flow that estimated by tracking the flow of genes in population through 70- yeartime horizon by the use of gene flow method. When it comes to generations, genetic progress is obtained from single round and continuous selection but in the 70-year time horizon it is obtained using gene flow method. At first, the genetic and economic aspects were investigated during 70 years without considering Bulmer effect and thereafter; all output calculations were conducted by correction for Bulmer effect. The bias was calculated by dividing the corrected value by non-corrected value. The economic efficiency (EE) was obtained as the ratio of total discounted return to total discounted costs.

RESULTS

Genetic variance and heritability of milk production in sire and dam pathways in both cases of taking into account and ignoring the Bulmer effect (during 20 generations of continuous selection) in progeny test and genomic selection program are represented in Table 2. At the asymptotic point, genetic variance of sires and dams decreased by 67.59% and 64.97% and reached 73753.01 and 79695.13 (kg²), respectively. The trend of genetic variance in sires and dams in the progeny test program is represented in Fig. 1. According to this diagram, the maximum reduction in genetic variance of sires and dams occurred in the first three generations and then the slope of variance reduction decreased by time and reached its asymptotic value in generations 14 and 15 in sire and dam pathways, respectively. Hence, in the first three generations after starting selection, a considerable upstream bias would occur in genetic variance due to ignoring the Bulmer effect. Because of higher selection intensities in paths DS and SS compared to that in paths DD and SD, a further reduction in genetic variance of sires was observed. Also, in genomic selection program, the genetic variance in sires and dams reached its asymptotic phase after 12 and 16 generations, respectively. In asymptotic phase, the genetic variance of sires and dams decreased by 68.56% and 63.06% and reached 71532.06 and 84045.22 (kg²), respectively. Fig. 2 shows the trend of genetic variance in selection program based on genomic information. The trend of genetic variance in sires and dams in genomic selection method was similar to progeny test. Also the maximum reduction of genetic standard deviation in genomic selection occurred in the first three generations and due to higher selection intensities in paths DS and SS, the dams resulting from these two paths experienced more reduction in genetic variance. The percentage of reduction in asymptotic genetic variance in sires and dams were approximately similar in both selection methods. The average generation interval through all paths in the progeny test method and genomic selection were 5.29 and 3.25 years, respectively. Hence, because of different generation interval in these selection programs, comparison of the annual variation in genetic

Table 2. Genetic variance and heritability in sire and dam pathways in both cases of ignorance and consideration of Bulmer effect (during 20 generations of continuous selection) in progeny test and genomic selection program

Selection Program	Sire Genetic Variance	Dam Genetic Variance	Sire Heritability	Dam Heritability
PT	227529	227529	0.29	0.29
PT _b	73753.01	79695.13	0.1169	0.1252
GS	227529	227529	0.29	0.29
GS _b	71532.06	84045.21	0.11	0.13

PT= Progeny test program, PT_b= Progeny test in the case of adjustment for Bulmer effect, GS= Genomic selection, GS_b= Genomic selection in the case of adjustment for Bulmer effect

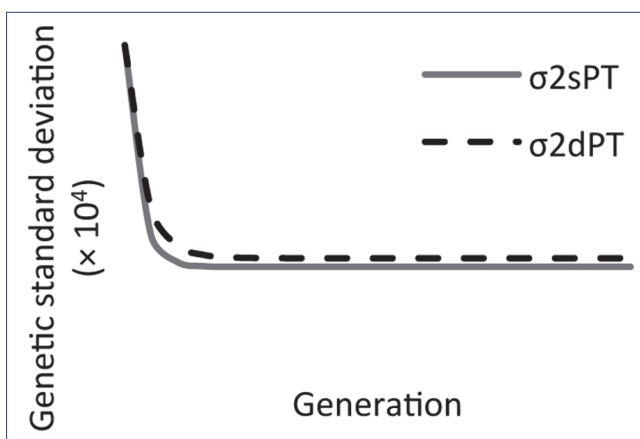


Fig 1. The trend of genetic variance in sires (σ_{2sPT}) and dams (σ_{2dPT}) in progeny test

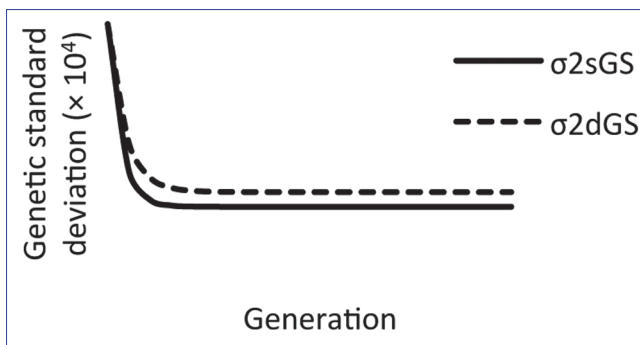


Fig 2. The trend of genetic variance in sires (σ_{2sGS}) and dams (σ_{2dGS}) in genomic selection

variance through 20 generations is not reasonable. The primary value of heritability in both selection methods was assumed to be 29%. According to [Table 2](#), in the progeny test, heritability in sires and dams decreased by 59.69% and 56.83% and reached 0.1169 and 0.1252, respectively. The heritability variations were equal to the variations of genetic variance. According to [Table 3](#), the heritability of sires and dams in genomic selection method was decreased by 60.76% and 54.79%, respectively.

The asymptotic values of heritability in sire and dam pathways were 0.11 and 0.13 (kg^2), respectively. The reduction of genetic variance caused by continuous selection in progeny test resulted in the reduction of the accuracy of genetic evaluations in all the paths. The accuracy of genetic evaluations in paths SD and SS was decreased by 7.99%. The reduction in the accuracy of paths DD and DS was estimated about 34.30% (data not shown). After correction for Bulmer effect in genomic selection, the estimated accuracy of sires in training set changed from 0.8866 to 0.7534 (equal to 14.91%). As a result of the reduction in the accuracy of breeding evaluation of sires in training set, the accuracy of genetic evaluations in paths SS, SD and DS decreased by 3.01%. The reduction in the accuracy of path DD was 32.76%, which was almost

Table 3. Genetic progress per generation (per genetic standard deviation) in sires of future sires (SS), sires of future dams (SD) dams of future sires (DS) and dams of future dams (DD) in the progeny test and genomic selection programs in both cases of ignoring and considering the Bulmer effect

Selection Program	SS	SD	DS	DD
PT	2.23	1.24	1.39	0.19
PT _b	2.05	1.15	0.91	0.12
GS	1.11	1.11	1.84	0.19
GS _b	1.08	1.07	1.78	0.13

PT= Progeny test program, PT_b= Progeny test in the case of adjustment for Bulmer effect, GS= Genomic selection, GS_b= Genomic selection in the case of adjustment for Bulmer effect

the same as the reduction in the accuracy of this path in the progeny test program. Considering the results of this study, in the paths where the selection was based on the genomic information, the accuracy of breeding evaluations was less influenced by Bulmer effect. In path DD, in which the selection was not based on the genomic information, the reduction in the accuracy was higher. In this path the accuracy rapidly decreased in the first three generations and then slight variations were observed until it reached the asymptotic phase. Genetic progress per generation (per genetic standard deviation) in sires of future sires (SS), sires of future dams (SD), dams of future sires (DS) and dams of future dams (DD) in the progeny test and genomic selection programs in both cases of ignoring and considering the Bulmer effect are shown in [Table 3](#). In progeny test program in the case of ignoring Bulmer effect, the biases in genetic progress in SS, DD, DS, and DD paths were equal to 8.15%, 7.56%, 34.30% and 34.05%, respectively. In progeny test program, due to higher reduction in the accuracy of breeding evaluations of dams, the maximum reduction in genetic progress per generation was observed in DS and DD paths. Because of higher selection intensity in path DS, Bulmer effect caused higher reduction in genetic progress per generation in this path. In genomic selection method, in the case of ignoring the Bulmer effect, the biases in genetic progress in paths SS, SD, DS, and DD were about 3.07%, 3.07%, 3.99% and 31.89%. In this selection method, due to higher percentage of reduction in the accuracy of DD path, more depression in genetic progress occurred. Genetic progress per generation (G), genetic progress resulting from single round selection after 70 years (G_0) and continuous selection for 70 years (G_c) in all paths of selection program based on the progeny test and genomic information in both cases of ignoring and considering Bulmer effect are presented in [Table 4](#). In progeny test program, ignoring the Bulmer effect resulted in 16.24% upward bias in the genetic progress per generation. The biases resulted from single round and continuous selections were equal to 51.81% and 51.97%, respectively. In genomic selection, ignoring the Bulmer effect caused 4.48 percent upward bias in the genetic progress per generation. In spite of small bias in estimated

Table 4. Genetic progress per generation (G), genetic progress resulting from single round selection after 70 years (G_o) and continuous selection after 70 years (G_c) in all paths of selection program based on the progeny test and genomic information in both cases of ignoring and considering Bulmer effect

Selection Program	G	G_o	G_c
PT	5.05	113.76	0.02
PT _b	4.23	54.82	0.07
GS	4.24	155.60	0.02
GS _b	4.05	87.79	0.01

PT= Progeny test program, PT_b= Progeny test in the case of adjustment for Bulmer effect, GS= Genomic selection, GS_b= Genomic selection in the case of adjustment for Bulmer effect

Table 5. Discounted cumulative profit and economic efficiency after 70 years continuous selection based on progeny test and genomic information in both cases of ignoring and considering Bulmer effect

Selection Program	Discounted Cumulative Profit	Economic Efficiency
PT	1835	11.00
PT _b	793	5.32
GS	3402	23.89
GS _b	1817	13.23

PT= Progeny test program, PT_b= Progeny test in the case of adjustment for Bulmer effect, GS= Genomic selection, GS_b= Genomic selection in the case of adjustment for Bulmer effect

genetic progress per generation, short generation interval in genomic selection led to higher bias in genetic progress through single round and continuous selection in 70 years, but still it was less than in progeny test (Table 5).

DISCUSSION

In the progeny test program, the bias of genetic progress per generation in the case of ignoring Bulmer effect was four times higher than genomic selection program, while, this difference significantly decreased in the results of selection after 70 years.

Discounted cumulative profit and economic efficiency after the 70-year continuous selection, based on progeny test and genomic information, in both cases of ignoring and considering Bulmer effect is presented in Table 5. In progeny test program, discounted profit per dairy cattle in the case of adjustment for Bulmer effect was 1042\$ less than the non-corrected case (equal to 56.79 percent upstream bias in the case of ignoring Bulmer effect). As mentioned previously, the bias of genetic variance in the sire and dam paths was about 67.59% and 64.97%, respectively. The bias percentage in discounted profit was less than that of genetic variance in sires and dams. Correction for Bulmer effect induced 46.59% reduction in discounted cumulative profit per dairy cattle in genomic selection program (Table

5). According to these results, reduction of profit due to the reduction of genetic variance in progeny test is more serious than in genomic selection. Bulmer effect resulted in 51.64% reduction in economic efficiency of progeny test. In genomic selection, reduction of variance resulted in 44.62% decrease in the economic efficiency. Bijma^[19] explained that ignoring Bulmer effect, leads to over-estimation of response and accuracy of selection.

The results of the current research showed that the overestimation is different for genomic selection and the progeny test. Therefore, ignoring Bulmer effect in the investigations concerning comparison between progeny test and genomic selection (e.g.^[9,20-24]) seems to be unreasonable. The bias in the results of such studies might influence the confidentiality of related results and inferences. Schaeffer^[11] studied the advantages of selecting individuals based on genomic information, and compared it with conventional progeny test. The influence of Bulmer effect on the genetic variance and asymptotic genetic progress in long term was ignored in this study. König et al.^[20] explained that it is not probable to involve Bulmer effect in deterministic simulations concerning selection strategies. Thus, this effect was ignored in their calculations and comparisons. In their study, the progeny test was compared with different strategies of genomic selection. Different levels of accuracies and selection intensities were assumed in their simulations. According to the results of this study, the Bulmer effect is expected to differently influence the results of these comparisons.

The results of the current research showed that the effect of genetic variance reduction, caused by long-term continuous selection, on the economic factors is stronger in progeny test than in genomic selection and would reduce economic factors more rapidly. Börner and Reinsch^[22] compared a progeny test program with different strategies of genomic selection. They assumed that both selection programs would affect the genetic variance in the same way. They suggested that ignoring this effect does not make any changes in the comparison of genomic selection and progeny test because the effect is equally ignored in both programs. According to the results of the current, Bulmer effect differently influences the result of selection, depending on the selection intensity and the type of selection program; therefore, error may occur in the comparisons of these two selection programs.

Through the last decade, genomic selection based on low and high density markers^[25,26] were applied for studying genetic variation and structure of domestic animals populations^[27-29]. Hence, utilization of genetic information allows for the selection of animals which induce more genetic variation. According to the aspects mentioned above and also the results of the current study, the utilization of genomic information could significantly prevent the reduction of genetic variation and its side effects. Genomic prediction has successfully been tested

in large breeds of dairy cattle^[30,31]. Other applications of genomic information in the management of dairy cattle include estimation of family relationship and inbreeding coefficient using single-nucleotide polymorphism^[1,31], homozygosity values^[32] or combination of different information resources^[33]. In genomic selection, the inbreeding rate can be much lower than in traditional BLUP or mass selection because Mendelian sampling effects can be estimated more accurately in genomic predictions, which leads to better differentiation within families and reduce the co-selection of sibs^[34,35].

However, the accuracy of genomic EBV has a diminishing-return relationship with the size of the reference population. As a consequence, when GS schemes have a moderate decrease in generation interval, relatively small reference population sizes are needed to obtain a response equal to that with selection on traditional BLUP-EBV based on own performance or progeny information. Thus, when the trait of interest cannot be recorded on the selection candidate, GS schemes are very attractive, even when the number of phenotypic records is limited, because traditional breeding schemes would have to rely on information from relatives with many phenotypic records and long generation intervals in the case of progeny testing.

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