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Optimization of the Structure of a Nucleus Breeding Program under Genotype-Environment Interaction Effects Using Simulation

Research Article

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ABSTRACT

A crucial challenge in nucleus breeding programs is the potential impact of genotype-environment interaction (GxE) on identifying the optimal configuration. This study aims to investigate the optimal structure of a nucleus breeding program in the presence or absence of GxE effects. Thirty-six distinct scenarios were created based on two levels of nucleus size (5% and 15% of population), three levels of female transfer rate from the base to the nucleus (0, 25 and 50%), three levels of male transfer rate from the nucleus to the base (25%, 50 and 100%). The mean genetic value in the last generation of the nucleus was higher than that of the base population, due to initial selection for nucleus formation and the selection method applied in subsequent generations. The mean genetic value in the nucleus ranged from 19.75 to 23.89, while in the base population, these values ranged from 17.16 to 23.76. Genetic gain in the nucleus over 20 generations ranged from 11.82 to 14.89, whereas in the base population, it fluctuated between 12.26 and 18.87. Genetic variance in the 20th generation ranged from 0.1 to 5.08 in the nucleus and from 0.18 to 9.02 in the base population. Overall, the presence of GxE interaction led to a reduction in both genetic mean and genetic gain in the nucleus and base populations. The findings indicate that GxE interaction can influence the optimal structure of base populations in a nucleus breeding program.

KEY WORDS breeding program, genetic gain, genetic variance, genotype-environment interaction, stochastic simulation.

INTRODUCTION

One of the breeding methods for animals raised in extensive and nomadic systems is the nucleus breeding program. The use of this program leads to the creation of a hierarchical system with at least two layers in the population: the upper layer consists of a nucleus, and the lower layer contains the base populations. In this method, pedigree and performance recording, measurement of various traits, and genetic evaluation are performed within the nucleus, and the resulting genetic improvement is transferred to the base populations (Van der Werf, 2010). Nucleus breeding programs are classified into two types—open and closed—based on the relation between the layers. The genetic exchange between the nucleus and the base population significantly influences genetic progress (Simm, 1998). In a closed nucleus, there is no genetic flow from the lower layers to the nucleus, and all record-keeping is limited to the nucleus population. In contrast, an open nucleus allows high-performing animals from the commercial herd to migrate to the nucleus for breeding (Kosgey *et al*. 2006; Santos *et al*. 2015). Maximizing the genetic efficiency of a nucleus breeding program depends on optimizing the combination of factors affecting genetic progress within the system. Several studies have investigated the effect of these factors on the annual genetic progress resulting from nucleus breeding programs. Askari-Hemat *et al*. (2014), in a study using deterministic simulation, demonstrated that if

the nucleus remains open to base ewes up to 25% of the required ewes in the nucleus, the maximum annual genetic progress can be achieved. They also showed that genetic progress increases as the nucleus size is increased to 11% of the total population (Askari-Hemmat *et al*. 2014). Safari *et al*. (2021a) examined genetic progress in a nucleus breeding program across various levels of nucleus size and male and female transfer rates and found that genetic gain decreased with increasing nucleus size. When accounting for inbreeding levels, the optimal combination included a nucleus size of 10% of the total population, 75% male transfer from the nucleus to the base, and an open nucleus with 25% female transfer from the base to the nucleus. However, in previous studies on optimizing the combination of factors (nucleus size and transfer rates of males and females between nucleus and base), the genotype-environment interaction (GxE) effect has not been considered. Thus, the aim of the current study is to examine the optimal structure of a nucleus breeding program in the presence or absence of GxE effects.

Due to the widespread use of artificial insemination in breeding programs, superior animals can be distributed in environments with completely different climatic conditions. However, the average genetic values of offspring may not remain constant across these varying environments. This is the result of GxE (Silva Neto *et al*. 2023). GxE occurs when genotypes exhibit different responses across different environments, meaning that some genes may express themselves differently depending on the environmental conditions (Dickerson, 1962). Dickerson (1962) defined GxE interaction as the additional variance resulting from the joint effects of genotype and environment, which cannot be predicted from their main effects.

None of the simulation studies performed to optimize the combination of factors affecting the efficiency of selection in nucleus breeding programs has taken the GxE phenomenon into account. Therefore, the first objective of this study is to compare the optimal structure of a nucleus breeding program under presence/absence of GxE. The second objective is to examine the optimal structure of a nucleus breeding program with regard to the maintenance of genetic variance in the studied trait over the course of multiple generations of selection.

MATERIALS AND METHODS

In this study, a stochastic simulation was conducted using the AlphaSimR package (Faux *et al*. 2016). Initially, a founder population was created. At the next step the genetic variance, the initial mean genetic value of the population, the contribution of GxE to the phenotypic variance, the relative contributions of males and females in the population, and the heritability of the studied trait were included to the model. Subsequently, the first generation of a historical population was created. This historical population was subjected to random mating for 100 of generations. The first generation of both the nucleus and base populations was then extracted from the last generation of the historical population. Selection was carried out based on user-defined parameters and strategies for males and females over the specified number of generations. Genetic statistics for both the nucleus and base populations were subsequently extracted based on the designed strategies.

In this simulation, a breeding program consisting of a central population (the nucleus) and a peripheral population (the base) was implemented. Generations were considered separately. In forming the initial nucleus population, the highest-ranking males and females based on the simulated phenotypic values were selected from the last generation of the historical population, with the number selected depending on the defined parameters (Table 1). The remaining individuals from the historical population were randomly selected to form the base population. Mating within each population and each generation was random. From the second generation onward, selection within the nucleus was based on the predicted genetic values of the trait in question. For scenarios involving an open nucleus, from the second generation onward, some of the females required for the nucleus were randomly selected from those produced in the base population. However, all required males for the nucleus were selected from the nucleus population. For the base population from the second generation onward, males were selected from the surplus males in the nucleus based on their predicted genetic values. Females for the base population were selected randomly from the remaining females produced within the base population. The simulation parameters are shown in Table 1.

Eighteen scenarios were simulated with different nucleus sizes, female transfer rates from the base to the nucleus, and male transfer rates from the nucleus to the base. Given that each scenario was modeled under both the presence and absence of GxE, a total of 36 scenarios were simulated. The GxE was included as an additional component in the phenotypic variance function within the AlphaSimR program (Silva Neto *et al*. 2023). For each scenario, 20 generations were simulated, and genetic statistics such as initial genetic mean, final genetic mean, genetic gain over 20 generations, and genetic variance in the 20^{th} generation for both the nucleus and base populations were extracted and saved in an Excel file. All calculations were repeated 30 times for each scenario. Finally, the averages and variances of the results were computed for each of the output statistics.

Table 1 Simulation parameters for population structure

Parameter	Value
Historical population size	10000
Base population size	5000
Number of selection generations	20
Male-to-female offspring ratio	0.5
Mating system	Random
Nucleus size as a percentage of the total population	15%, 5%
Male-to-female ratio in nucleus	0.1
Female transfer rate from base to nucleus	0.5, 0.25, 0
Male transfer rate from nucleus to base	1, 0.5, 0.25
Trait heritability	0.25

RESULTS AND DISCUSSION

The results for the average genetic value of the last generation in the nucleus population, at different levels of nucleus size, male transfer rate from the nucleus to the base, and female transfer rate from the base to the nucleus, are presented in Table 2. In the absence of GxE, the average genetic value of the small nucleus (5%) was sometimes higher than that of the large nucleus, with no consistent pattern observed. Increasing the female transfer rate from the base to the nucleus and the male transfer rate from the nucleus to the base led to decreases in the average genetic value of the population in some cases and increases in others. The highest average genetic value of the last generation in the nucleus was 23.89 ± 1.1, obtained in the large nucleus (15%) with a 100% male transfer rate from the nucleus to the base and a 25% female transfer rate from the base to the nucleus. When considering GxE, changing the nucleus size did not consistently affect the average genetic value of the nucleus. Additionally, increasing the female transfer rate from the base to the nucleus and the male transfer rate from the nucleus to the base did not show a consistent pattern. The highest genetic value in the nucleus (22.46±1.7) occurred in the closed and large nucleus with complete male transfer from the nucleus to the base. A general review of the effect of GxE on the average genetic value of the last generation in the nucleus population showed that the presence of GxE resulted in a lower average genetic value. In general, when GxE was present, the highest average genetic value of the nucleus population was achieved when the nucleus was closed to the base females. However, regarding nucleus size, the maximum average genetic value was observed in the larger nucleus. This finding contradicted what was observed in the absence of GxE.

The results of the GxE effects on the average genetic value of the last generation in the base population for different levels of nucleus size, male transfer rate from the nucleus to the base, and female transfer rate from the base to the nucleus are presented in Table 3.

The analysis of results in the absence of GxE indicated no consistent pattern in the change of the average genetic value of the last generation of the base population with increasing female transfer rate from the base to the nucleus. For instance, when the male transfer rate from the nucleus to the base was 0.25 and the nucleus size was 5% of the base population, increasing the female transfer rate led to a decrease in the average genetic value of the base. However, with a male transfer rate of 0.5 and the same nucleus size, increasing the female transfer rate resulted in an increase in the genetic value of the population. In contrast, the male transfer rate from the nucleus to the base consistently increased the average genetic value in all scenarios. The effect of nucleus size did not follow a fixed pattern either.

In some cases, when the nucleus size was small, the average genetic value of the base was higher than when the nucleus size was large, while in other cases, the opposite was true. Overall, the highest average genetic value of the last generation in the base population (23.76±1.1) was observed in the open nucleus with a female transfer rate of 0.25, complete male transfer from the nucleus to the base, and a large nucleus size.

The results of the GxE effects on the average genetic value of the last generation in the base population indicated that when the female transfer rate from the base to the nucleus increased, the average genetic value of the population decreased. The effect of increasing the male transfer rate from the nucleus to the base followed a consistent pattern and resulted in an increase in the base population's genetic value across all combinations. The effect of nucleus size did not follow a fixed pattern; in some cases, it led to an increase, while in others, it caused a decrease in the average genetic value of the base. With the presence of GxE, the highest average genetic value of the base population (21.87±1.4) was observed when the nucleus was closed, the male transfer from the nucleus to the base was maximized, and the nucleus size was large.

Comparison of the values from Tables 2 and 3 revealed that for each level of GxE, the optimal combination of nucleus size, male transfer rate from the nucleus to the base, and female transfer rate from the base to the nucleus was identical.

However, when comparing the optimal combinations under the absence and presence of GxE, it became evident that the optimal combinations regarding nucleus size and male transfer rate from the nucleus to the base were the same. This indicates that for both the nucleus and the base, regardless of the presence of GxE, the highest average genetic value in the last generation of selection was achieved when the nucleus was large, and all required males for the base were supplied from the nucleus.

Table 2 Genetic mean with standard error of the last generation of the nucleus population for different levels of nucleus size and male transfer rate from nucleus to base and female transfer rate from base to nucleus

		Transfer rate of males from nucleus to base								
		1			0.5			0.25		
Interactions between genotype and environment	**Nucleus size**	0.5	0.25	0	0.5	0.25	0	0.5	0.25	0
0	0.05	23.34±1.2	23.59±1.0	23.59±1.1	23.42±0.9	23.26±1.1	23.29±0.9	22.33±1.1	23.12±1.1	23.56±1.3
	0.15	23.40±0.9	23.89±1.1	23.85±1.4	23.19±0.1	23.26±1.0	23.72±0.9	23.37±1.0	23.53±1.1	23.73±0.9
1	0.05	19.82±1.7	21.50±1.7	22.31±1.5	19.52±1.9	20.81±1.4	21.88±1.5	18.92±1.9	20.65±2.2	21.93±2.0
	0.15	20.42±1.6	21.51±1.4	22.16±1.4	20.19±1.2	21.46±1.9	21.95±2.1	19.75±1.7	20.52±1.7	23.46±1.7

Table 3 Genetic mean with error criterion of the last generation of the base population for different levels of nucleus size and male transfer rate from nucleus to base and female transfer rate from base to nucleus

		Transfer rate of males from nucleus to base								
		1			0.5			0.25		
Interactions between genotype and environment	**Nucleus size**	0.5	0.25	0	0.5	0.25	0	0.5	0.25	0
0	0.05	22.96±1.2	23.33±1.0	23.33±1.1	22.78±0.9	22.71±1.1	22.68±0.9	20.13±1.0	20.66±0.9	20.78±1.0
	0.15	23.25±0.9	23.76±1.1	23.71±1.4	22.70±1.0	22.66±1.0	23.12±0.8	20.23±0.9	20.89±0.8	20.71±0.8
1	0.05	19.22±1.8	21.11±1.6	21.84±1.5	18.71±2.0	19.84±1.4	20.67±1.5	16.47±1.8	17.80±1.7	18.94±1.5
	0.15	20.15±2.6	21.21±1.4	21.84±1.4	19.42±2.0	20.54±1.8	20.85±2.1	17.16±1.6	17.50±1.4	18.82±1.4

In contrast, no consistent pattern was observed for the female transfer rate from the base to the nucleus. In the presence of GxE, the optimal level was a 25% female transfer from the base to the nucleus. A comparison of the repeatability error criterion between Tables 2 and 3 showed that the variance of estimates under the GxE condition was higher than in the absence of this effect. No differences were observed between the values for the nucleus and the base.

The results regarding the role of GxE effects on genetic value changes from generations 1 to 20 in the nucleus, under varying levels of nucleus size, male transfer rate from the nucleus to the base, and female transfer rate from the base to the nucleus, are presented in Table 4. When GxE effects were present, genetic progress in the nucleus over 20 generations was consistently higher in the large nucleus size compared to the small nucleus size. Increasing the female transfer rate from the base to the nucleus led to a decrease in genetic progress in the nucleus. The increase in male transfer rate from the nucleus to the base exhibited more complex behavior, with no consistent trend observed. The highest genetic progress in the nucleus (14.89±1.45) was achieved in the large nucleus size, with a male transfer rate from the nucleus to the base of 1 and no female transfer from the base to the nucleus.

Table 4 indicates that in the presence of GxE, genetic progress in the nucleus over 20 generations was greater for the large nucleus size compared to the small nucleus size, except when the male transfer rate was 1 and the female transfer rate was 0.25, where the genetic progress in the small nucleus was higher than in the large nucleus (13.16±1.94 *vs*. 12.90±1.49). Increasing the female transfer rate to the nucleus resulted in a reduction of genetic progress in the nucleus. The increase in male transfer rate from the nucleus to the base did not show a distinct trend. The greatest changes in average genetic value over 20 generations (14.40±1.55) occurred in the large nucleus size, with a male transfer rate from the nucleus to the base of 1 and no female transfer from the base to the nucleus.

A comparison of the maximum genetic progress values in the absence and presence of GxE reveals that the optimal combination for genetic progress in the nucleus for traits with moderate heritability (0.25), which encompasses most traits of importance in animal breeding, is independent of the presence or absence of GxE.

The results of the GxE effects on the changes in the average genetic value over generations 1 to 20 in the base population, under different levels of nucleus size, male transfer rate from the nucleus to the base, and female transfer rate from the base to the nucleus, are presented in Table 5.

Table 4 Mean genetic change with standard error over generations 1 to 20 in the nucleus population for different levels of nucleus size and male transfer rate from nucleus to base and female transfer rate from base to nucleus

		Transfer rate of males from nucleus to base								
		1			0.5			0.25		
Interactions between genotype and environment	**Nucleus size**	0.5	0.25	0	0.5	0.25	0	0.5	0.25	0
0	0.05	13.85±1.31	14.04±1.03	14.15±1.12	13.89±0.92	13.62±1.2	13.69±0.9	12.78±1.13	13.51±1.15	13.96±1.31
	0.15	14.34±0.95	14.88±1.02	14.89±1.45	14.22±1.04	14.22±1.01	14.71±0.87	13.33±0.96	14.53±10	14.68±0.91
1	0.05	11.12±1.89	13.16±1.94	13.5±1.62	11.27±1.96	11.27±1.96	13.64±1.53	10.96±2.25	12.08±2.4	13.38±2.09
	0.15	12.39±2.46	12.90±1.49	14.4±1.55	12.18±1.84	12.18±1.84	14.14±2.01	11.82±2.06	12.72±2	14.27±1.42

Table 5 Mean genetic change with standard error over generations 1 to 20 in the base population for different levels of nucleus size and male transfer rate from nucleus to base and female transfer rate from base to nucleus

		Transfer rate of males from nucleus to base								
		1			0.5			0.25		
Interactions between genotype and environment	**Nucleus size**	0.5	0.25	0	0.5	0.25	0	0.5	0.25	0
0	0.05	17.98±1.18	18.37±1.05	18.42±1.06	17.82±0.89	17.74±1.11	17.65±0.92	15.18±1	15.69±0.98	15.77±1.02
	0.15	18.28±0.93	18.87±1.05	18.81±1.41	17.81±0.99	17.7±1.03	18.18±0.85	15.33±0.88	16±0.85	15.81±0.81
1	0.05	14.29±1.79	16.17±1.6	16.86±1.57	13.72±2.08	14.83±1.45	15.82±1.54	11.55±1.74	12.79±1.72	13.99±1.56
	0.15	15.17±2.56	16.17±1.31	16.86±1.34	14.49±2.02	15.61±1.82	15.9±2.14	12.26±1.63	12.52±1.51	13.89±1.51

In the absence of GxE effects, an increase in the male transfer rate from the nucleus to the base led to greater changes in the genetic value in the base population over 20 generations. No clear trend was observed for the female transfer rate. Regarding nucleus size, there was no consistent or significant difference between the small and large nucleus scenarios. The highest genetic growth, 1.05 ± 18.87, was achieved with a large nucleus size, a male transfer rate from the nucleus to the base of 1, and a female transfer rate from the base to the nucleus of 0.25. In the presence of GxE effects, the genetic growth over 20 generations in the base population was not dependent on whether the nucleus size was large or small. In some cases, genetic growth in the large nucleus scenario was higher, while in others it was lower, and no consistent trend was observed. However, increasing the female transfer rate to the nucleus resulted in a reduction in genetic growth across all scenarios. Increasing the male transfer rate from the nucleus to the base exhibited a clear trend, whereby genetic growth in the base population increased. The highest genetic growth observed over 20 generations in the base population was 1.34 ± 16.86, which was the same for both the large and small nucleus scenarios. This genetic growth occurred with a male transfer rate from the nucleus to the base of 1 and a female transfer rate from the base to the nucleus of 0. Overall, although the optimal structure of the breeding scheme in the absence of GxE effects and its presence were not exactly identical, it can be concluded that the optimal breeding structure for the base population in both cases will be when the nucleus size is 15% of the base population, with a male transfer rate from the nucleus to the base of 1 and a female transfer rate from the base to the nucleus below 0.5. However, the genetic value changes over 20 generations in all strategies were lower compared to the scenario without interaction effects.

The results of the GxE effects on the genetic variance of the 20th generation in the nucleus population, under different levels of nucleus size, male transfer rate from the nucleus to the base, and female transfer rate from the base to the nucleus, are presented in Table 6. In the absence of GxE effects, the genetic variance of the 20th generation in the nucleus population with a nucleus size of 5% of the base population was sometimes smaller than that of a nucleus size of 15% and at other times larger, without showing a consistent trend. Analysis of the genetic variance trend revealed that as the female transfer rate from the base to the nucleus increased, the genetic variance in the nucleus followed an increasing trend. Conversely, an increase in the male transfer rate from the nucleus to the base had the opposite effect. The highest genetic variance (0.5±2.9) occurred at a male transfer rate of 0.25, a female transfer rate of 0.5, and a nucleus size of 0.05. When considering GxE effects, no clear pattern was observed between the nucleus sizes of 5% and 15% of the base population. In some combinations, the genetic variance in the smaller nucleus size was higher, while in others, the opposite was true.

Additionally, as the female transfer rate from the base to the nucleus increased, the genetic variance in the 20th generation followed an increasing trend. However, increasing the male transfer rate from the nucleus to the base resulted in a decrease in genetic variance, although one exception was observed, which could be disregarded. Overall, the highest genetic variance in the nucleus, 1.2 ± 5.08, occurred when the nucleus size was 15% of the base population, with a male transfer rate from the nucleus to the base of 0.25 and a female transfer rate from the base to the nucleus of 0.5. Regardless of the presence or absence of GxE effects, the highest genetic variance was achieved when the nucleus was open, with the highest female transfer rate from the base to the nucleus (0.5) and the lowest male transfer rate from the nucleus to the base (0.25).

The results of the GxE effects on the genetic variance of the 20th generation in the base population, under different levels of nucleus size, male transfer rate from the nucleus to the base, and female transfer rate from the base to the nucleus, are presented in Table 7. In the absence of GxE effects, the genetic variance of the 20th generation in the base population showed no consistent pattern concerning nucleus size. In some scenarios, where the nucleus size was 5% of the base population, higher genetic variance was observed, while in other combinations, the genetic variance was higher for a nucleus size of 15% of the base population. As the female transfer rate from the base to the nucleus increased, the genetic variance in the base population also increased. Conversely, an increase in the male transfer rate from the nucleus to the base led to a decrease in genetic variance. The highest genetic variance, 1.05 ± 6.97, was observed in the scenario with a nucleus size of 15% of the base population, the lowest male transfer rate from the nucleus to the base (0.25), and a female transfer rate from the base to the nucleus of 0.25. When considering GxE effects, the change in nucleus size did not have a consistent effect on genetic variance. In most cases, genetic variance in the larger nucleus size was higher than in the smaller nucleus size.

The female transfer rate from the base to the nucleus had an increasing effect on genetic variance in the base population. The increase in male transfer rate from the nucleus to the base followed a consistent pattern, with an increasing male transfer rate leading to a decrease in genetic variance. The highest genetic variance, 1.4 ± 9.02, occurred at the lowest male transfer rate from the nucleus to the base (0.25), along with conditions such as a large nucleus size and maximum female transfer rate from the base to the nucleus. By comparing the genetic variance values for the nucleus and base populations in Tables 6 and 7, it can be observed that the presence of GxE was associated with higher genetic variance.

The genetic variance of the nucleus was always lower than that of the base. The highest genetic variance in the nucleus, regardless of interaction effects, occurred when the male transfer rate was at its lowest and the female transfer rate at its highest. A similar situation was observed in the base population. However, in the base population, when there was no interaction effect, the medium female transfer rate (0.25) provided the best result. Regarding nucleus size, the highest genetic variance in both the nucleus and base populations was associated with a large nucleus. An exception to this was observed in the nucleus population, where, in the absence of interaction effects, the highest genetic variance occurred when the nucleus size was small (5% of the total population).

Defining the selection objective is the first step in implementing any breeding program. Without determining the characteristics of a “good” animal, selective breeding cannot be effectively carried out (Shadparvar, 2012). Maximizing genetic growth is achieved by appropriately combining various factors affecting selection (Bourdon, 2000).

The main limitations in breeding programs for indigenous animals, especially sheep and goats, are the small flock size and the impracticality or even impossibility of recording performance and pedigree data in an economically feasible manner (FAO, 2010). Therefore, under these conditions, nucleus-based breeding models are recommended. In nucleus-based breeding programs, where various factors such as the nucleus proportion of the total population and the transfer rates of male and female animals between the nucleus and the base are involved, optimizing the selection program means finding the best combination of different levels of these factors (Hopkins, 1978).

Many studies have been conducted on optimizing nucleus-based breeding programs in Iran, including those by Askari-Hemat *et al*. (2014), Shahverdi *et al*. (2018), and Safari *et al*. (2021b). However, none of these evaluations considered the effects of GxE. Studies show that GxE, if present, can lead to greater phenotypic variation in animal performance when animals are exposed to different environments (Silva Neto *et al*. 2023). Therefore, when the environmental conditions of selected animals differ from those of the commercial population, this effect can result in reduced animal performance. This situation may occur in animals produced in a nucleus breeding program.

In the present study, by comparing the maximum genetic means in both the nucleus and base populations under different scenarios, it was observed that the best scenario was the same for both populations. For example, the highest genetic mean in the nucleus, in the absence of interaction effects, occurred under conditions where the nucleus size was large, the female transfer rate was 0.25, and the male transfer rate was 1.

Table 6 Genetic variance with standard error of the 20th generation in the nucleus population for different levels of nucleus size and male transfer rate from nucleus to base and female transfer rate from base to nucleus

		Transfer rate of males from nucleus to base								
		1			0.5			0.25		
Interactions between genotype and environment	**Nucleus size**	0.5	0.25	0	0.5	0.25	0	0.5	0.25	0
0	0.05	0.54±0.2	0.26±0.1	0.13±0.1	0.88±0.3	0.42±0.2	0.1±0.1	2.9±0.5	1.46±0.3	0.1±0.05
	0.15	0.34±0.1	0.19±0.1	0.12±0.1	0.75±0.2	0.41±0.1	0.11±0.1	2.74±0.5	1.63±0.3	0.11±0.05
1	0.05	2.34±1.2	0.93±0.6	0.32±0.2	3.12±1.3	1.57±1	0.48±0.3	4.77±1.4	3.05±1.2	0.32±0.18
	0.15	1.51±0.9	0.84±0.4	0.48±0.3	2.49±1.8	1.56±1	0.54±0.4	5.08±1.2	2.92±0.82	0.45±0.3

Table 7 Genetic variance of the 20th generation in the base population for different levels of nucleus size and male transfer rate from nucleus to base and female transfer rate from base to nucleus

		Transfer rate of males from nucleus to base								
		1			0.5			0.25		
Interactions between genotype and environment	**Nucleus size**	0.5	0.25	0	0.5	0.25	0	0.5	0.25	0
0	0.05	0.79±0.3	0.39±0.1	0.21±0.1	0.81±0.2	1.04±0.3	1.57±0.5	5.91±1.1	6.18±1	6.84±1.2
	0.15	0.36±0.1	0.24±0.1	0.18±0.1	0.88±0.2	1.1±0.2	1.26±0.3	6.38±0.7	6.97±1.05	6.68±1.1
1	0.05	2.84±1.1	1.29±0.7	0.57±0.3	1.86±0.6	2.71±1.2	4.01±1.3	6.45±1.3	7.53±1.8	8.51±1.6
	0.15	1.7±1	0.96±0.4	0.66±0.4	2.01±0.8	2.72±1	3.33±1.8	7.62±1.2	8.17±1.5	9.02±1.4

The same scenario in the base population also resulted in the highest genetic mean. Therefore, any optimal combination determined for the nucleus can also be applied to the base population.

However, the optimal combination differed between the absence and presence of interaction effects. For instance, the maximum genetic mean in the population with interaction effects occurred when the nucleus was closed, with a male transfer rate of 1 from the nucleus to the base and a large nucleus size. Therefore, a breeding program cannot be optimized without considering interaction effects and then generalized to a scenario where interaction effects are present. The difference in the results of this study compared to previous studies lies in this point.

Nevertheless, by examining the optimal breeding program combinations for both the nucleus and base populations, it can be observed that in all optimal scenarios, three features were common: a large nucleus size, a maximum male transfer rate from the nucleus to the base, and a female transfer rate from the base to the nucleus of less than 0.5. In all scenarios, the genetic mean in both populations was lower when interaction effects were present compared to when they were absent.

James (1977) reported that in a nucleus system, approximately 10% of the population should be in the nucleus, with all replacement males for the base population sourced from the nucleus, half of the nucleus replacement females sourced from the base, and all surplus females from the nucleus transferred to the base after selecting the replacements.

Askari-Hemat *et al.* (2014) showed that a 25% transfer rate of ewes from the base to the nucleus could result in maximum genetic growth. Safari *et al.* (2021b) demonstrated that the overall genetic value would reach its maximum value when the nucleus size was 10% of the base population, with a 25% female transfer rate from the base to the nucleus and a 75% male transfer rate from the nucleus to the base. However, Roden's results (Roden, 1995) differ from these findings. He showed that the optimal structure in a nucleus-based breeding program involved transferring 25% of the males and 50% of the females from the base to the nucleus.

The results of the genetic gain over generations 1 to 20 showed that, regardless of the presence or absence of GxE effects, the optimal combination of factors included a large nucleus size and a maximum male transfer rate from the nucleus to the base. In all cases, the optimal combination involved a closed nucleus, except for one scenario for the base population. In this case, the optimal female transfer rate from the base to the nucleus was 25%. Overall, the genetic mean growth over 20 generations was lower when GxE effects were present compared to when these effects were absent.

One of the key components of a breeding program is the genetic variance of traits. Selection, due to the Bulmer effect (Bulmer, 1971), reduces genetic variance between families. Moreover, the risk of genetic variance reduction is significantly higher in closed populations than in open ones (Falconer and Mackay 1996). Therefore, in this study, the reduction in genetic variance due to selection was examined

under both absence and presence of GxE effects. The results indicated that if the optimization basis for the structure of a nucleus-based breeding program is to maximize genetic variance in the 20th generation, the nucleus should always be open to base females, with at least 0.25 of the females transferred from the base to the nucleus. Furthermore, the male transfer rate from the nucleus to the base should also be at the minimum level, i.e., 0.25. Therefore, it can be concluded that it is not possible to define an optimal program that simultaneously maximizes genetic growth and maximizes genetic variance. Examining the optimal structure in the presence of GxE effects revealed that the best combination for both the nucleus and the base involved a large nucleus size, an open nucleus with a transfer rate of 0.5, and a minimum male transfer rate. If maximizing genetic variance is considered solely for the base population, the optimal structure for both the presence and absence of interaction effects is nearly identical. This structure includes a large nucleus size, a minimum male transfer rate from the nucleus to the base, and a female transfer rate from the base to the nucleus of at least 0.25. If the goal is maximizing genetic growth over 20 generations of selection while also maximizing genetic variance in the 20th generation in the base population, it is necessary to determine the relative importance of these two objectives. Determining this balance was not within the scope of this study. However, if we assume that both objectives are of equal importance for the production system, the optimal combination could be defined as a large nucleus size (15% of the base population), a male transfer rate from the nucleus to the base of 0.6, and a female transfer rate from the base to the nucleus of 0.35. In this case, this combination is expected to be optimal for both the presence and absence of GxE.

CONCLUSION

The results of the current study demonstrated that the presence of GxE effects can, in some cases, affect the optimal structure of the base populations in a nucleus breeding program. In general, these interactions lead to a reduction in both genetic growth and genetic variance within the population. If the optimization of a breeding program is based on genetic growth, determining the optimal structure for the nucleus and base populations under the presence of GxE is much more complex than in the absence of such effects. Optimizing a breeding program with regard to genetic variance becomes even more complex, as in most cases, the optimal structure for maximizing genetic growth is not the same as the optimal structure for genetic variance. If the goal is to combine maximizing genetic growth over 20 generations of selection and simultaneously maximizing genetic variance in the 20th generation of the base population for traits with a heritability of 0.25, such as a important trait, the optimal combination can be defined as a large nucleus size (15% of the base population), a male transfer rate from the nucleus to the base of 0.6, and a female transfer rate from the base to the nucleus of 0.35, assuming both objectives are equally important in the breeding program. In this case, it is expected that this combination will be optimal both in the presence and absence of GxE effects.

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