Studying Genetic Diversity in Moghani Sheep Using Pedigree Analysis

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ABSTRACT

Studbook information collected from 1988 to 2011 in Jafarabad breeding station of Moghani sheep, north-west of Iran, related to 9,457 lambs were used to study the genetic diversity and to evaluate the effectiveness of an implemented rotational mating scheme using pedigree analysis. Lambs born during 2009-2011 were considered as reference population. Means inbreeding and average coancestry for the reference population were computed as 0.40 and 0.74%, respectively. The mean generation interval was 4.48 years with a longer generation interval on dam-progeny pathways. Average equivalent complete generation, as a measure of pedigree completeness, was 3.37. Effective population sizes were estimated to be 226 and 276 from the individual rate in coancestry and from the individual increase in inbreeding, respectively. Genealogical parameters estimated based on probabilities of gene origin including the effective numbers of founders, the effective numbers of ancestors, the effective numbers of founder genomes (founder genome equivalents) and the effective numbers of non-founder genomes considering the reference population were estimated as 143, 117, 67, and 126, respectively. Approximately, 50% of the total genetic variation was explained by the 43 most influential ancestors, with a maximum individual contribution of 3.27%. The results indicated that although some evidences on bottlenecks and genetic drift during recent years were identified in the studied population, a considerable genetic variability existed in this population due to implementation of an efficient rotational mating scheme for controlling inbreeding.

Keywords: Closed flock, Inbreeding trend, Rotational mating scheme, Genealogical parameters.

INTRODUCTION

Indigenous breed types of small ruminants, especially in the tropical regions, play an important role in the livelihood of a sizeable portion of human population. They are mainly kept under low-input production systems by local pastoralists and well adapted to the dry and harsh climatic conditions that are prevalent in the tropics (Kosgey and Okeyo, 2007). An undesirable consequence of genetic improvement programs is the loss of genetic diversity mainly due to the increased inbreeding and loss of founder alleles through genetic selection and drift (Vozzi *et al.*, 2007). The erosion of animal genetic resources and, at the same time, the need to provide sustainable livelihoods to small holders, as the main part of animal husbandry systems in the tropics, are challenging issues and necessitate setting up appropriate breeding strategies for enhancement of production efficiency with considering genetic conservation constrains (Cardellino, 2009). Coordinated attempts in terms of managerial practices and genetic

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improvement programs to promote production efficiency are of great importance. Characterization of the genetic structure within breeds is prerequisite for estimating future breeding potential of a livestock breed. In the developing countries, under-recorded sheep populations are mainly kept as captive ones, with limited exchange of animals from outside the population. Such populations are kept often in the small-sized flocks and, consequently, the rate of inbreeding can be high with associated depression in the functional traits (Boakes *et al*., 2007) and higher loss of genetic diversity (Windig and Kaal, 2008). Rotational mating schemes, as a managerial tool, organize the exchange of individuals in a structured way so that genetic diversity at the population level is maintained and inbreeding at the subpopulation level is reduced (Windig and Kaal, 2008). A great advantage involved in implementation of the rotational mating schemes is that detailed pedigree records are not required to restrict inbreeding. Despite their usefulness, literature on the effectiveness of rotational mating schemes in control of inbreeding in the sheep breeds is scarce.

Studying the structure of population using pedigree analysis is an efficient approach to identify influencing factors that affect the genetic history of a population (Valera *et al*., 2005). Genealogical parameters of several European sheep breeds have been reported (Norberg and Sørensen, 2007; Danchin-Burge *et al*., 2010; Pedrosa *et al*., 2010). Given that pedigree recording is exception in Iran, there are few reports concerning the pedigree analysis of Iranian native sheep breeds and mainly limited to recently published papers (Ghafouri-Kesbi, 2010, 2012; Tahmoorespur and Sheikhloo, 2011; Mokhtari *et al*., 2013, 2014).

Moghani sheep breed is one of the most important meat types among Iranian native sheep breeds and comprises a population of 5.5 million heads (Tavakolian, 1999), which may be lowered through the recent years mainly due to successive droughts, well known for their large body size, tolerance, and capability to produce heavy lambs. The

breeding station of Moghani sheep may act as a main part of nucleus-based breeding schemes for genetic improvement of this breed, dissemination of superior animals into local flocks, and thereby enhancement of production efficiency. Since 1994, a rotational mating scheme has been adopted in order to avoid unfavorable consequences of inbreeding. Inbreeding depression effects on growth traits of Moghani sheep breed under an animal model were studied by Dorostkar *et al*. (2012). In another study, Ghavi Hossein-Zadeh (2012) studied the effects of inbreeding on body weights of Moghani sheep. But, there is no information regarding demographic parameters of Moghani sheep breed. In Iran, official recording of pedigree information and performance records of native sheep breeds, which is true in the case of Moghani sheep, are limited to experimental flocks kept in breeding stations. Therefore, the aim of the present investigation was to study genetic diversity of an experimental Moghani sheep, as a typical representative of the breed, using pedigree analysis. Furthermore, the effectiveness of the implemented rotational mating scheme was assessed.

MATERIALS AND METHODS

Pedigree Records and Designed Rotational Mating Scheme

Pedigree information used in the present study were collected during 1988 to 2011 at Jafarabad breeding station of Moghani sheep, located in north-west of Iran. To overcome the undesirable effect of inbreeding, which are common in small and closed populations, a supervised mating strategy was planned. The rams and ewes were first mated at approximately 18 months of age. The breeding season lasts from mid-August to mid-September. Ewes were organized into groups of 10-15 heads and in a breeding period each group was allocated to a fertile ram, approximately 30-35 fertile rams were used annually for mating. In the next breeding period, each group of ewes was mated to a

different ram. In other words, rams were used rotationally among ewe groups. Rams were used in the flock, depending on their health and fertility status, for approximately three mating period (generally, one ram per one mating group of ewes per one year) and ewes were kept up to 8 years depending on ewe health and reproductive performance. Lambs were weighed and ear-tagged at birth time and their sex, birth type, and identifications of their sire and dam were recorded.

Pedigree Analysis

Pedigree records of 9,457 Moghani lambs collected during a 23-year period (1988-2011) were analyzed, the lambs born from 2009 to 2011 were considered as reference population. The coefficient of inbreeding (F) for each individual was computed using an algorithm from Meuwissen and Luo (1992). The coancestry coefficients (f) of animals were also calculated (Malécot, 1948). The generation interval (GI) was defined as the average age of the parents at the birth time of their progeny kept for reproduction and was computed by averaging the four genetic pathways, sire to son (L_{ss}), sire to daughter (L_{sd}), dam to son (L_{ds}), and dam to daughter (L_{dd}) as follows:

$$G.I. = \frac{L_{ss} + L_{sd} + L_{ds} + L_{dd}}{4} \quad (1)$$

Pedigree completeness was assessed by computing individual equivalent complete generation (EqG_i) following Maignel *et al.* (1996):

$$E_q G_i = \Sigma (\frac{1}{2})^n \quad (2)$$

Where, *n* denotes the number of generations separating the individual from each known ancestor. Average equivalent complete generations for the whole and reference populations were computed simply by averaging the corresponding individual equivalent complete generations.

The effective population size (N_e) was calculated under two approaches for

concluding about the effectiveness of rotational mating scheme. The first approach was based on the individual increase in inbreeding. The coefficients of individual increase in inbreeding (ΔFi) in the reference population were computed according to the method described by Falconer and Mackay (1996) and modified by Gonzalez-Recio *et al.* (2007) and Gutierrez *et al.* (2009) using the following formula:

$$\Delta F_i = 1 - {}^{EqG_i - 1}\sqrt{1 - F_i} \quad (3)$$

Where, F_i and $EqGi$ are the coefficient of inbreeding and the equivalent complete generation for individual *i*, respectively. The coefficients of ΔFi were averaged and the realized effective population size was estimated as follow:

$$NeF = \frac{1}{(2\overline{\Delta F})} \quad (4)$$

The second approach was based on the approach proposed by Cervantes *et al.* (2011) using the rate of coancestry for all pairs of individual *j* and *k* (ΔC_{jk}) in reference population and computed as:

$$\Delta C_{jk} = 1 - {}^{\left(\frac{g_j + g_k}{2}\right)}\sqrt{1 - C_{jk}} \quad (5)$$

Where, C_{jk} is the inbreeding coefficient of a progeny from individuals *j* and *k*, and g_j and g_k are the discrete equivalent generations of individuals *j* and *k*, respectively. Consequently, the realized effective population size in a reference population was estimated by averaging in coancestry for all pairs of the individuals as:

$$NeC = \frac{1}{(2\overline{\Delta C})} \quad (6)$$

If *NeC* is lower than *NeF*, it can be concluded that the implemented rotational mating is efficient for controlling of inbreeding in the considered population. Considering the reference population, four measures on probability of gene origin including the effective number of founders, the effective number of ancestors, the effective number of founder genomes, and

the effective number of non-founder genomes were estimated. The effective number of founders (f_e) denote the numbers of equally contributing founders that would result in the same level of genetic diversity in the current population and was obtained according to Lacy (1989):

$$f_e = \frac{1}{\sum_{k=1}^{m} q_k^2} \qquad (7)$$

Where, q_k is the expected proportional genetic contribution of founder k, computed by the average relationship of the respective founder to each animal in the population and m is the total number of founders. The effective number of ancestors (f_a) is the minimum numbers of ancestors, not necessarily founders, explaining the complete genetic diversity of the current population and was computed according to Boichard *et al.* (1997):

$$f_a = \frac{1}{\sum_{k=1}^{n} p_k^2} \qquad (8)$$

Where, p_k is the marginal contribution of each ancestor; the contribution made by an ancestor not explained by a previously chosen ancestor, and n is the total number of ancestors. The effective numbers of founder genomes or founder genome equivalents (f_g) indicate how many founders would be required to produce the same genetic diversity as found in the population if all founders contributed equally and no founder alleles were lost by drift under random mating (Caballero and Toro, 2000). This parameter was computed as the inverse of twice average coancestry of the individuals defined in a reference population as follow:

$$f_g = \frac{1}{2\overline{f}} \qquad (9)$$

Due to the fact that f_g accounts for all of the factors affecting gene loss during segregation, it is always lower than both f_a and f_e. The effective numbers of non-founder genomes f_{ne} consider only the effect of genetic drift in non-founder generations and was computed as follows (Caballero and Toro, 2000):

$$\frac{1}{f_{ne}} = \frac{1}{f_g} + \frac{1}{f_e} \qquad (10)$$

The program of ENDOG v4.8 was used for pedigree analysis (Gutierrez and Goyache, 2005).

RESULTS AND DISCUSSION

Genealogical Parameters

The results of pedigree analysis are presented in Table 1. Among the registered lambs, 87.7% of the lambs had both parents known, and for 12.3%, both parents were unknown; implying a deep pedigree in terms of completeness. In the present study, average equivalent complete generation was 2.40 and 3.37 for the whole and reference populations, respectively. The completeness of pedigree has important influence on quality of inbreeding estimation (Kadlecik *et al.*, 2011) and is essential to obtain accurate estimates of genealogical parameters. The mean generation interval was 4.48 years. The generation intervals across four pathways were as L_{ss}= 4.51 years, L_{sd}= 4.05 years, L_{ds}= 4.94 years and L_{dd}= 4.43 years, indicating that the breeding ewes had usually been employed longer to produce offspring than the rams as generation interval for ewe-progeny pathways was longer than ram-progeny ones.

A value of 143 was estimated for f_e, while the number of founders contributed in the reference population were 504. The ratio of the effective numbers of founders to the total numbers of founders in the reference population was 0.28, implying unbalancing contribution of founders to the reference population. The corresponding ratio of 0.24 was obtained by Goyache *et al.* (2003) in Xalda sheep. Effective number of founders account for unequal contribution of founders in populations (Lacy, 1989). The obtained values for f_e in some of Iranian native sheep

Table 1. Summary statistics of the pedigree analysis in Moghani sheep.

Item	Value
No. of animals in whole population	9457
No. of animals with progeny	3296
No. of animals without progeny	6161
No. of animals with both known parents	8296
No. of animals with both unknown parents	1161
No. of animals with one unknown parent	-
No. of animals in reference population	1130
Average inbreeding in reference population (%)	0.40
Average coancestry in reference population (%)	0.74
Average no. of equivalent complete generations	3.37
No. of founders	504
No. of ancestors	459
Effective population size based on individual increase in coancestry (NeC)	226
Effective population size based on individual increase in inbreeding (NeF)	276
Effective no. of founders (f_e)	143
Effective no. of ancestors (f_a)	117
Founder genome equivalent (f_g)	67
Effective no. of non-founder genomes (f_{ne})	126
No. of ancestors explaining 50% of genetic variation	43

breeds were 13 in Iran-Black sheep (Mokhtari *et al*., 2014), 40 in Afshari sheep (Ghafouri-Kesbi, 2012) and 86 in Zandi sheep (Ghafouri-Kesbi, 2010). When a population experienced the bottleneck, the f_e is overestimated due to ignoring the possible bottleneck effects. This is more pronounced in animal breeding where selection for prominent animals imposes bottleneck. Therefore, estimation of f_a is of paramount importance. This parameter complements the information presented by the effective numbers of founders considering the loss of genetic variation caused by the unbalanced use of reproductive individuals (Boichard *et al*., 1997). The f_a and the total number of ancestors that contributed in the reference population were 117 and 459, respectively. Lower values of 11, 34, and 47 were obtained for f_a in Iran-Black (Mokhtari *et al*., 2014), Afshari (Ghafouri-Kesbi, 2012) and Baluchi (Tahmoorespur and Sheikhloo, 2011) sheep breeds, respectively.

If the effective number of founders is larger than the effective number of ancestors, bottlenecks have played an important role in population formation (Sørensen *et al*., 2005). Boichard *et al*.

(1997) pointed out that the loss in genetic diversity that exists in the founders due to the bottleneck between the base and the reference populations can be evaluated using the ratio of the effective numbers of founders to the effective numbers of ancestors (f_e/f_a). The importance of bottleneck in the population under consideration can be assessed applying the above mentioned ratio; the greater the f_e/f_a ratio, the more stringent the bottleneck (Boichard *et al*., 1997). The ideal value for this ratio would be one. In the present study, a value of 1.22 was obtained for the f_e/f_a ratio in the reference population, implying that unbalancing between ancestors and founders may result in reduction of genetic variability. Pedrosa *et al*. (2010) reported a value of 1.35 for f_e/f_a in Santa Ines sheep breed. A similar corresponding lower value of 1.18 was obtained by Mokhtari *et al*. (2014) in Iran-Black sheep. In a previous study, Mokhtari *et al*. (2013) reported a higher value of 2.07 for f_e/f_a in Kermani sheep. Different obtained values for f_e and f_a in mentioned various sheep breeds with the value obtained in the present study may be explained to a great extent by different

genealogical structure of the studied flocks mainly in terms of pedigree completeness, different mating policies, and excessive use of some breeding animals.

The founder genome equivalents (f_g) was estimated as 67. The lower f_g in a reference population suggests the presence of lower proportions of the genes of founders. The f_g parameter accounts for the total loss in genetic diversity, but it does not consider mutation (Caballero and Toro, 2000). Tahmoorespur and Sheikhloo (2011) reported a value of 19.5 for f_g in Iranian Baluchi sheep. The obtained value for f_g in Zandi sheep was 74 (Ghafouri-Kesbi, 2010) which is close to our estimate in the present study. The effective numbers of non-founder genome (f_{ne}) was 126**.** Mokhtari *et al*. (2014) reported a value of 12 for f_{ne} in Iran-Black sheep. It considers the effect of genetic drift in non-founder generations and provides indication on the relative importance of random genetic drift accumulated in non-founder generations and unequal contribution of founders regarding the loss of genetic diversity. If f_e is higher than f_{ne}, as observed in the present study, the reduction in genetic diversity is more attributable to genetic drift accumulated in non-founder generation; and where f_e is lower than f_{ne}, the unequal contribution of founders is considered as the main influencing factor affecting the loss of genetic diversity (Caballero and Toro, 2000).

Realized Effective Population Size and Effectiveness of Implemented Rotational Mating Scheme

The increase in inbreeding greatly affected by population structure (Gutierrez *et al*., 2008) and the effective population size can be estimated via the increase in coancestry instead of increase in inbreeding, as a more effective approach, when dealing with structured population. In the present study, *NeF* and *NeC* were 276 and 226, respectively. It is an important parameter in population genetics studies and indicates the

degree of genetic drift and viability of population (Frankham *et al*., 2002). Previously, an effective population size of 50 was determined by FAO (1998) as a critical level for an animal population, but, in animal populations, it ranges between 50 and 100 (Bijma, 2000). Evolutionary biologists have recommended that an effective population size of 500–5,000 is required to ensure evolutionary ability of natural populations (Frankham *et al*., 2002). The results of a recently published paper on estimation of effective population size using pedigree data under different methods across several domestic species have shown that the determination of a strict critical level for effective population size is not straightforward and estimates of effective population size should be interpreted in the light of factors such as method used, species, and population structure (Leroy *et al*., 2013). The estimated value of N_e in the present study suggests an acceptable level of effective population size. Nevertheless, it should be noted that estimates of N_e may vary following changes in inbreeding level of the population across generations. The estimated effective population size based on the individual increase in coancestry (NeC) was lower than that obtained based on the individual increase in inbreeding (NeF), implying the effectiveness of implemented rotational mating system for controlling the inbreeding. Comparing the three parameters of f_e , f_a and f_g with *Ne* estimated based on individual increase in inbreeding allows concluding if the population can be considered as increasing or decreasing in the genetic variability. Here, in the foundation f_e was 143, but then decreased due to bottleneck (f_a= 117) and other causes (f_g= 67), while being actually reproducing animals as more (NeF= 276), probably because an increase in the census and an effectively designed rotational mating scheme. The comparison of results obtained from pedigree analysis of other species may be interesting. Pavlik *et al*. (2012) studied the genetic diversity in Holstein bulls of Slovakia. They obtained effective population

size via individual increase in inbreeding as 94.50.

Approximately, 50% of the total genetic variation was explained by the 43 most influential ancestors, with a maximum individual contribution of 3.27%, implying the excessive use of some ancestors in mating. Mokhtari *et al*. (2013) reported that about 50% of total genetic variation in Kermani sheep was explained by the 33 most influential ancestors, and maximum individual contribution was 4.8%.

Among all the registered lambs, 18.4% were inbred; about 88% of them had individual inbreeding coefficient of higher than zero and equal to 0.05 (0< Fi≤ 0.05), 6% had individual inbreeding coefficient of higher than 0.05 and equal to 0.10 (0.05< Fi≤ 0.10), and 6% had inbreeding coefficient of higher than 0.10 (Fi> 0.10). Evolution of annual average inbreeding (only inbred lambs were considered) and equivalent complete generation through the study period is presented in Figure 1. Fluctuations were observed in average inbreeding of inbred lambs from 1988 to 1993. Afterwards, the average inbreeding decreased annually as 0.53 % (P< 0.01).

Inbreeding statistics over nine maximum traced generations are presented in Table 2. An increasing trend was observed in the average inbreeding of the total lambs, ranging from 0.11% in the second generation to 0.61% in the ninth generation.
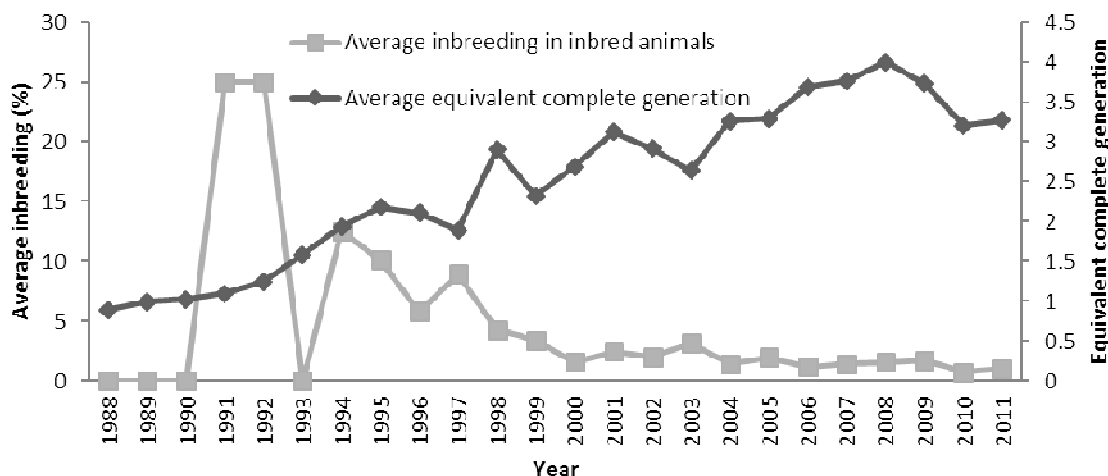
Figure 1. Evolution of average inbreeding (in inbred animals) and pedigree completeness through the studied period.

Table 2. Inbreeding coefficient (F) statistics over nine maximum generation.

Generation	No of animals	Average F (%)	Inbred (%)	Average F for inbred (%)
0	1161	-	-	-
1	802	0.00	0.00	0.00
2	1065	0.11	0.75	14.06
3	1289	0.38	4.27	8.86
4	1003	0.59	13.36	4.40
5	1207	0.55	19.72	2.80
6	1221	0.70	34.32	2.04
7	1017	0.61	47.69	1.27
8	504	0.65	55.75	1.16
9	188	0.61	65.22	0.94

Considering the average inbreeding in inbred animals revealed that the proportion of inbred lambs followed by a decreasing pattern from the second generation (14.06%) to the ninth generation (0.94%). Norberg and Sørensen (2007) analyzed the trend in inbreeding of three Danish populations of sheep and observed the increase in inbreeding was about 1% per generation for all breeds. Huby *et al*. (2003) studied the inbreeding trends in six French sheep breeds and no higher than inbreeding rate of 0.40% per generation were found in the considered breeds. Pavlik *et al*. (2012) found an average inbreeding of 2.48% in Holstein bull of Slovakia. Such differences may be partly ascribed to different mating strategies and depth of the pedigree used. Average values of inbreeding and coancestry in the reference population were 0.40 and 0.74%, respectively.

Among all mating that occurred in the population, 91 mating were between half-sibs (0.96% of total mating) and 14 mating were between parent and offspring (0.15% of total mating). It seems that execution of a rotational mating scheme in the flock helped to keep the inbreeding level under control. Effectiveness of the rotational mating scheme for controlling the inbreeding in Kermani sheep was also shown by Mokhtari *et al*. (2013). Rotational mating schemes appeared to be an efficient approach to restrict inbreeding rates. The advantage of these schemes is that inbreeding reduction can be achieved simply (Windig and Kaal, 2008).

Pedigree analysis of Moghani sheep showed evidence for controlling the inbreeding by implementation of rotational mating scheme. Although the obtained effective population sizes were not in the range of the critical levels, it should be noted that these values should be interpreted in the light of factors such as pedigree structure. It can be concluded that the genetic variability of Moghani sheep was poorly affected by both gene losses during segregation and bottlenecks, but it still seems being far from danger.

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بررسی تنوع ژنتیکی در گوسفند مغانی با استفاده از تجزیه شجره

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چکیده

اطلاعات ۹۴۵۷ بره که از سال ۱۳۶۸ تا ۱۳۹۰ در ایستگاه اصلاح نژاد گوسفند مغانی در جعفر آباد، شمال غربی ایران، جمع آوری شده بودند برای بررسی تنوع ژنتیکی و کارآمدی طرح تلاقی چرخشی با استفاده از تجزیه شجره بکار رفتند. بره های متولد شده طی سال های ۱۳۸۸ تا ۱۳۹۰ به عنوان جمعیت مرجع در نظر گرفته شدند. میانگین هم خونی و هم تباری جمعیت مرجع به ترتیب ۰/۴۰ درصد و ۰/۷۴ درصد محاسبه شدند. میانگین فاصله نسلی ۴/۴۸ سال و فاصله نسلی در مسیر میش–فرزندان بیشتر از مسیر قوچ–فرزندان بود. میانگین معادل نسل، به عنوان معیاری از تکامل شجره، ۳/۳۷ بود. اندازه موثر جمعیت با استفاده از افزایش در همتباری ۲۲۶ و با استفاده از افزایش انفرادی در هم خونی ۲۷۶ برآورد گردید. پارامترهای جمعیتی بر اساس احتمالات منشاء ژن شامل تعداد موثر پایه گذاران، تعداد موثر اجداد، تعداد موثر ژنوم های پایه گذار (معادل های ژنوم پایه گذار) و تعداد موثر ژنوم های غیر پایه گذار با در نظر گرفتن جمعیت مرجع به ترتیب ۱۴۳، ۱۱۷، ۶۷ و ۱۲۶ برآورد گردیدند. تقریباً ۵۰ درصد کل تنوع ژنتیکی توسط ۴۳ جد که بیشترین تاثیر را داشتند توضیح داده شد و حد اکثر مشارکت ۳/۲۷ درصد بود. نتایج نشان دادند که اگرچه شواهدی دال بر بروز باتلنک و رانش ژنتیکی در جمعیت مطاله شده طی سال های اخیر بدست آمد ولی به دلیل اجرای یک طرح تلاقی چرخشی کارآمد برای کنترل هم خونی، هنوز تنوع ژنتیکی قابل توجهی در جمعیت وجود دارد.