

Genetic variability and population structure of Raeini Cashmere goats determined by pedigree analysis

M. S. Mokhtari^{1*}, M. Moghbeli Damaneh¹ and J. P. Gutierrez²

¹Department of Animal Science, Faculty of Agriculture, University of Jiroft, Jiroft, P.O. Box 364, Iran.

²Departamento de Producción Animal, Facultad de Veterinaria, Universidad Complutense de Madrid, Avda. Puerta de Hierro s/n, E-28040 Madrid, Spain.

* Corresponding author, E-mail address: msmokhtari@ujiroft.ac.ir

Abstract Pedigree information collected from 1979 to 2012 were used to study the genetic variability and population structure of Raeini Cashmere goats, taking kids born from 2009 to 2012 into account as the reference population. The mean inbreeding coefficients in the whole and inbred populations were computed to be 0.04% and 4.41%, respectively. Considering the reference population, the average inbreeding coefficient and average relatedness were 0.14 % and 0.11%, respectively. The mean of generation interval, computed from four gametic pathways (sire-son, sire-daughter, dam-son and dam-daughter), was 3.72 years, with a longer interval from dam-progeny pathways relative to sire-progeny ones. In the reference population, the average equivalent complete generation, as a measure of pedigree completeness, was 1.25. The effective population sizes estimated from the individual rate in coancestry and from the individual increase in inbreeding were 332 and 229, respectively. The effective numbers of founders (f_e) and the effective numbers of ancestors (f_a) were estimated at 240 and 137, respectively. Approximately, 50% of the total genetic variations were explained by the first 57 influential ancestors, with a maximum individual contribution of 3.94%. The ratio of f_e to f_a , as measure of bottleneck, was 1.75. The results revealed the evidences for occurrence of bottlenecks in the population, mainly because of unbalanced contribution of breeding animals to the gene pool of the studied population of Raeini Cashmere goat.

Keywords: genealogical parameters, inbreeding, effective population size, goat

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Introduction

An animal population face environmental change over time and for adapting to these changes genetic diversity is needed. Therefore, for estimating the future breeding potential of a given breed it is necessary to characterize its genetic structure and to study the within population genetic variability of the breed (Baldursdottir et al., 2012). Small ruminants, especially in the tropics, 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 tropical areas (Kosgey and Okeyo, 2007). Falconer and Mackay (1996) pointed out that selection under animal models brings genetic gain accompanied with the loss of genetic variation. Maintenance of genetic variation at an acceptable level by controlled inbreeding is of great importance and will ensure that animals in the future can respond to changes caused by selection (van Wyk et al., 2009). Setting up an efficient

genetic improvement program requires the knowledge of genetic variation and genealogical structure of the population (Gutierrez et al., 2003). Genetic variation is defined as the variety of alleles and genotypes that exist in a population; such diversity may be expressed through morphological, physiological and behavioral differences at the level of individuals and populations (Frankham et al., 2002). The accuracy of demographic parameters estimated using pedigree analysis may be influenced by several factors; with the level of pedigree completeness as a main factor (Boichard et al., 1997). Application of pedigree information for studying the genetic variation is an efficient approach and provides useful information regarding managerial decisions practiced in historical background of a population through the past years.

Raeini Cashmere breed, the most important Iranian Cashmere goat and numbering approximately 2 million heads, is predominantly distributed in the south and sou-

th-eastern part of the country (Maghsoudi et al., 2009). Raeini Cashmere goat is a dual-purpose breed mainly kept for Cashmere production by small holder farmers under traditional management systems and harsh climatic conditions. The breeding station of Raeini Cashmere goat was established in 1965 with 180 goats including 120 does, 8 bucks and 52 kids for improving the economic traits of Raeini goats such as body weight at different ages and Cashmere weight via trait recording and genetic evaluation (Shamsaddiny Nejad and Bahreini Behzadi, 2015). The breeding station was to function as a nucleus-based breeding activity for selection of the superior animals, dissemination into local flocks, and thereby enhancement of production efficiency.

There are limited reports regarding the study of genetic variation using pedigree analysis of goat breeds (Rashidi et al., 2015; Menezes et al., 2015; Oliveira et al., 2016). Therefore, the aims of the present study were to assess the genetic variability and population structure of an experimental population of Raeini Cashmere goats by through pedigree analysis.

Material and methods

Data collection and management

The pedigree information used in the present study were collected from 1979 to 2012 at Raeini Cashmere goat breeding station located in Baft city, Kerman province, south-eastern part of Iran. Animals were raised under semi-intensive managerial conditions which were similar to the prevalent conditions for the nomadic flocks in the region. Mating period was from August to October with the corresponding kidding period from December to February. Does were first exposed to the bucks at about 18 months of age. Total numbers of sires and dams with progeny were 397 and 4160, respectively. Considering animals with progeny, the average numbers of offspring per sire and dam were 15.07 ± 17.00 and 2.13 ± 1.71 , respectively. Approximately, 73% of the bucks produced less than 20 offspring, and 15 bucks sired more than 50 offspring, producing about 18% of the kids.

Genealogical parameters

Kids born from 2009 to 2012 were considered as the reference population. The individual inbreeding coefficient (F) was computed using the algorithm of Meuwissen and Luo (1992). The average relatedness coefficient (AR) of each individual to its population was estimated as the probability that an allele randomly chosen from the entire population included in the pedigree belonged

to a given animal (Gutierrez et al., 2003). The generation interval was defined as the average age of the parents at the birth time of their progeny kept for reproduction. It was computed across four pathways, sire to son (L_{ss}), sire to daughter (L_{sd}), dam to son (L_{ds}), and dam to daughter (L_{dd}). The average generation interval (G. I.) was computed as:

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

Completeness of pedigree was evaluated by equivalent complete generations. Individual equivalent complete generation for individual i ($EqGi$) was computed according to Maignel et al. (1996) as:

$$EqGi = \sum \left(\frac{1}{2}\right)^n$$

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

The effective population size is the size of an ideal population, characterized by equal sex ratio, absence of mutation, migration and selection, which has the same inbreeding rate as the real population under consideration. The effective population size (N_e) was estimated by two methods. The first was based on the rate of coancestry for all pairs of individual j and k (ΔC_{jk}) in a reference population (Cervantes et al., 2011) as:

$$\Delta C_{jk} = 1 - \sqrt{\frac{g_j + g_k}{2}} \sqrt{1 - C_{jk}}$$

where, C_{jk} is the inbreeding coefficient of a progeny from individuals j and k , and g_j and g_k are the equivalent complete generation of individuals j and k , respectively. In this method, effective population size was estimated by averaging the rate of coancestry for all pairs of the individuals as:

$$N_e = \frac{1}{2\Delta c}$$

The second approach was based on the individual increases in inbreeding. The coefficients of individual increases in inbreeding (ΔF_i) were computed according to the method described by Gutierrez et al. (2008) and modified by Gutierrez et al. (2009) using the following formula:

$$\Delta F_i = 1 - \frac{EqGi-1}{\sqrt{1-F_i}}$$

where, the components of F_i and $EqGi$ are the coefficient

of inbreeding and the equivalent complete generation for individual i , respectively. The coefficients of individual increase in inbreeding are averaged and effective population size was estimated as:

$$Ne = \frac{1}{2\Delta F}$$

Considering the reference population two measures on probability of gene origin including the effective number of founders and the effective number of ancestors were computed.

Effective number of founders (f_e) denotes the numbers of equally contributing founders that would result in the same level of genetic diversity in the current population and was computed according to Lacy (1989):

$$f_e = \frac{1}{\sum_{k=1}^m q_k^2}$$

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.

Effective number of ancestors (f_a) is the minimum number of ancestors, not necessarily founders, explaining the complete genetic diversity of the current population and was computed according to Boichard et al. (1997):

$$f_a = \frac{1}{\sum_{k=1}^n p_k^2}$$

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 program of ENDOG 4.8 was used for pedigree analysis (Gutierrez and Goyache, 2005).

Results and discussion

Pedigree completeness, equivalent complete generation and generation interval

Pedigree completeness level has considerable effect on the computation of inbreeding coefficient due to the fact that the chance of finding common ancestors increases along with the level of pedigree completeness (Gutierrez et al., 2003). The averages percentages of an

cestors known per generation were 58.08%, 23.47%, 8.65%, 3.04% and 0.95% for the first, second, third, fourth and fifth generations, respectively. After the fifth generation, pedigree completeness was approximately zero. This situation is reflected by the low average equivalent generation of 0.98 in the whole population, showing a shallow structure for the studied pedigree of Raeini Cashmere goats. The corresponding value for equivalent complete generation in the considered reference population of Raeini Cashmere goats was 1.25. For evaluating the accuracy of the computed population parameters and the genetic variability of population pedigree integrity, which can be evaluated by applying the equivalent number of generations, is of crucial importance (Boichard et al., 1997). Oliveira et al. (2016) obtained a value of 0.64 for equivalent complete generation in Spanish Murciano-Granadina which was lower than the obtained value in the present study. The higher corresponding value of 5.84 was also has been reported by Rashidi et al. (2015) in Markhoz goat. The evolution of equivalent complete generation throughout the years is presented in Figure 1.

In the present study, the calculated mean generation interval of 3.72 years was higher than 2.5 years reported by Portolano et al. (2004) in Girgentana goats. Generation intervals of 3.55 years and 2.77 years were reported by Rashidi et al. (2015) and Oliveira et al. (2016) in Markhoz and Spanish Murciano-Granadina goats, respectively. The higher mean generation interval of the dam-progeny pathways (3.77 years), relative to the corresponding value for sire-progeny pathways (3.68 years), is probably attributable to the fact that breeding dams are usually kept for more years to produce offspring than the sires. The same trend was observed in Markhoz goats (Rashidi et al., 2015).

Inbreeding and average relatedness

A summary of the descriptive statistics on inbreeding coefficient in kids is shown in Table 1. Overall, 50.15% of the kids were males and 49.85% were females. A small proportion of kids (0.90%) were inbred. Of all registered animals, 52.58% had unknown sires which

Table 1. Inbreeding statistics for whole population and inbred animals in Raeini Cashmere goats

| Item | Whole animals | | | Inbred animals | | |
|----------------|---------------|-------|--------|----------------|-------|--------|
| | Total | Male | Female | Total | Male | Female |
| No. of records | 12622 | 6330 | 6292 | 110 | 55 | 55 |
| Average F (%) | 0.04 | 0.04 | 0.03 | 4.41 | 4.90 | 3.93 |
| Minimum F (%) | 0.00 | 0.00 | 0.00 | 0.05 | 0.05 | 0.10 |
| Maximum F (%) | 25.00 | 25.00 | 12.50 | 25.00 | 25.00 | 12.50 |

F: Inbreeding coefficient.

Table 2. Summary statistics of the pedigree analysis in Raeini Cashmere goats

| Item | Value |
|--|-------|
| Whole population | |
| No. of animals with progeny | 4557 |
| No. of animals without progeny | 8065 |
| No. of animals with both known parents | 5985 |
| No. of animals with both unknown parents | 3622 |
| No. of animals with one unknown parent | 3015 |
| Reference population | |
| No. of animals | 1473 |
| Mean of inbreeding coefficient (%) | 0.14 |
| Average relatedness (%) | 0.11 |
| Average No. of equivalent complete generations | 1.25 |
| Effective population size ^a | 332 |
| Effective population size ^b | 229 |
| No. of founders | 1419 |
| No. of ancestors | 1163 |
| Effective No. of founders (f_e) | 240 |
| Effective No. of ancestors (f_a) | 137 |
| No. of ancestors explaining 50% of genetic variation | 57 |

^aEstimated based on individual increase in coancestry^bEstimated based on individual increase in inbreeding

may be a reason for low inbreeding observed in the studied population. Joezy-Shekalgorabi et al. (2016) studied pedigree structure in the Iranian Cashmere goat breed of south Khorasan and found low average inbreeding coefficient of 0.07%. They ascribed this level of inbreeding to the factors such as lack of sire registration in the pedigree and extensive production system. In the present study, the numbers of matings between parent-offspring and between half-sibs in the whole of population were 0.02% and 0.14%, respectively. As shown in Table 2, animals with progeny constituted 36.11% of the total

registered animals.

The averages inbreeding coefficients in the whole population and inbred kids were 0.04% and 4.41%, respectively. Oliveira et al. (2016) reported a value of 0.18% for average inbreeding in Spanish Murciano-Granadina goats. According to Joezy-Shekalgorabi et al. (2016), the average inbreeding in Iranian Cashmere goats of south Khorasan was 0.85%. The evolution of average inbreeding coefficients and average relatedness of kids across the study period are shown in Figure 1. As shown in Figure 1, inbreeding has been kept at levels

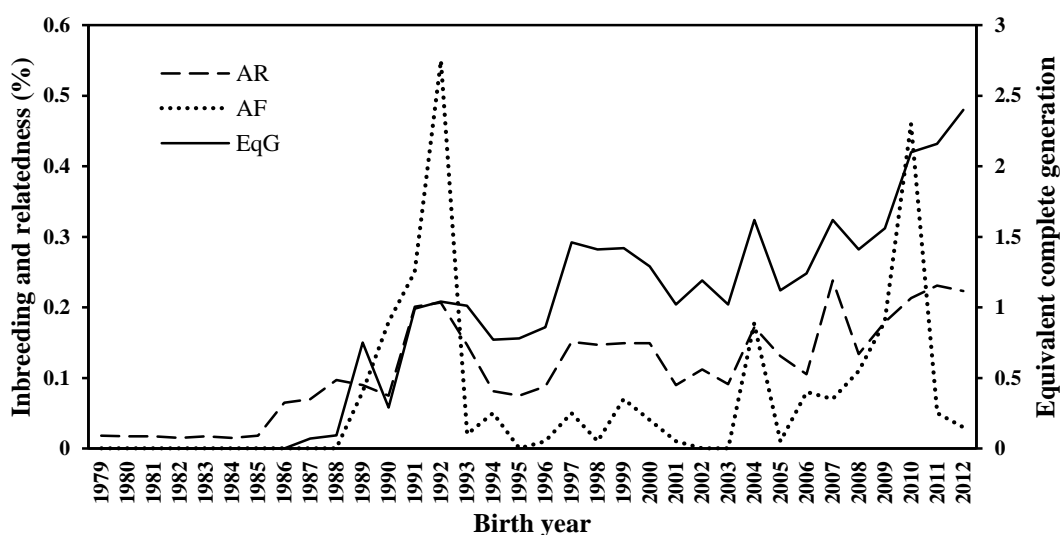


Figure 1. Evolution of average inbreeding (AF), average relatedness (AR) and average equivalent complete generation (EqG) for Raeini Cashmere goats across the years

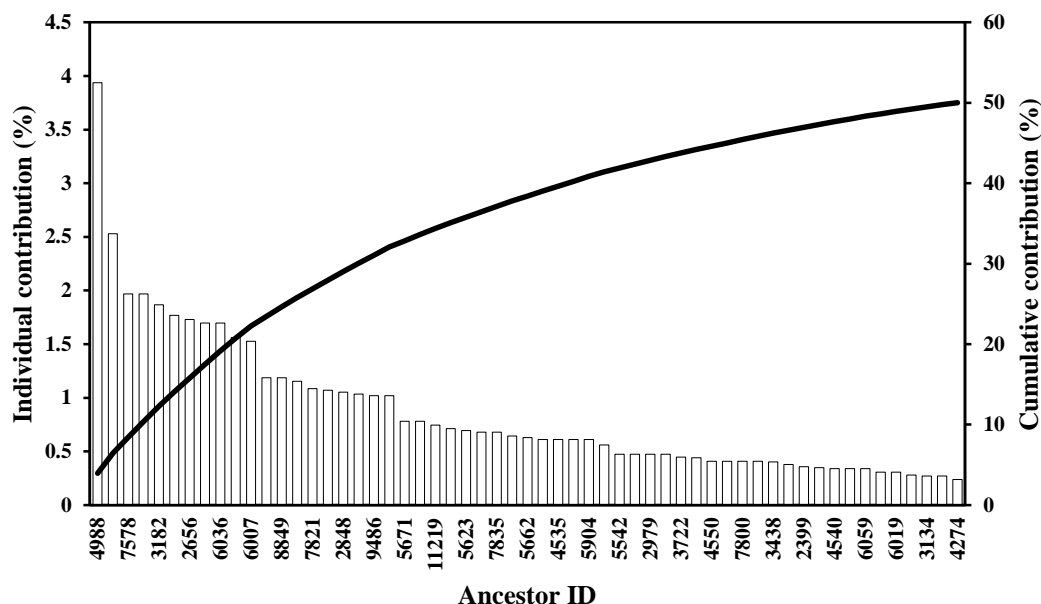


Figure 2. Individual and cumulative contributions of the first 57 ancestors explained 50% of the genetic diversity

not exceeding 0.55%, with fluctuations throughout the years. The means of inbreeding coefficients were increased from 1987 to 1992 and abruptly decreased in 1993 but several fluctuations were observed, afterwards. Such fluctuations may be ascribed to the introduction of unrelated sires from other herds, as well the low quality of pedigree and/or mating policy planned for avoiding mating between related individuals. In the present study, a positive but statistically non-significant annual inbreeding rate of 0.33 ± 0.22 was observed ($P > 0.05$). Baldursdottir et al. (2012) reported an annual inbreeding rate of 3% in Icelandic goats.

The average relatedness considering all individuals and those in the reference population was 0.11% and 0.20%, respectively. The average relatedness throughout the years showed a behavior similar to that of the average inbreeding coefficient (Figure 1). Similar trends were observed in Brazilian Boer (Menezes et al., 2015) and Spanish Murciano-Granadina (Oliveira et al., 2016) goats. Oliveria et al. (2016) pointed out that such trend is probably because of the introduction of a foreign sire in the population. Joezy-Shekalgorabi et al. (2016) obtained a value of 2.36% for the average relatedness in Iranian Cashmere goat of south Khorasan which is higher than the value obtained in the present study. Due to this fact that the average relatedness is inversely associated with the genetic diversity in a population it is a useful measure to manage the genetic diversity (Oliveira et al., 2016).

Effective population size, effective numbers of founders and effective numbers of ancestors

The effective population size is an important parameter in population genetics and indicates the genetic viability of populations (Frankham et al., 2002). The realized effective population sizes estimated based on individual increases in coancestry and inbreeding were 332 and 229, respectively (Table 2). The effective population size based on the individual increases in coancestry was higher than that obtained based on the individual increase in inbreeding. Menezes et al. (2015) obtained the values of 173.5 and 340 for effective population sizes via individual rate of inbreeding and annual rate of inbreeding in Boer goats of Brazil, respectively. In Markhoz goats, Rashidi et al. (2015) reported effective population sizes from the individual rates in coancestry and from the individual increases in inbreeding methods of 84 and 69, respectively which are lower than those obtained in the present study. In another study, Baldursdottir et al. (2012) reported an effective population size of 5.1 in Icelandic goats using the population data. Danchin-Burge et al. (2012) studied genetic variability in three breeds of goats, including the Alpine, Saanen and Angora with estimated values of 149, 129 and 76 for effective population sizes in these breeds, respectively. Oravcova (2013) obtained values of 182 and 142 animals for the effective population size in White Short-haired goats estimated via the individual increase in inbreeding and the individual increase in coancestry, respec-

ectively.

The effective population size denotes the number of breeding animals that would contribute to the observed rate of inbreeding in the recent generation under ideal conditions (Falconer and Mackay, 1996). Generally, determination of a strict critical level for the effective population size is not straightforward and should be interpreted considering factors such as the method applied, animal species and the structure of the population studied (Leroy et al., 2013).

In the present study, the numbers of founders contributed to the reference population and the effective numbers of founders were 1419 and 240, respectively; indicating the excessive use of some animals as parents. Portolano et al. (2004) reported the total number of founders and effective numbers of founders in Girgentana goat breed as 93 and 22.94, respectively, which were lower than the obtained values in the present study. A high corresponding value of 967 was obtained by Oliveira et al. (2016) in Spanish Murciano-Granadina goats. The ratio between effective number of founders to the total number of founders was approximately 0.17; indicating disequilibrium among founder contributions in the studied population of Raeini Cashmere goat. The corresponding ratios of 0.25 and 0.14 were obtained in Italian Girgentana (Portolano et al., 2004) and Markhoz (Rashidi et al., 2015) goats, respectively. Unequal contribution of founders in a population was taken into account by using the effective number of founders (Lacy, 1989). Whenever a bottleneck is imposed on a population, f_e will be overestimated due to ignoring the possible effects of bottleneck (Boichard et al., 1997). Therefore, estimation of the effective number of ancestors (f_a) as an more important measure of genetic diversity is of crucial importance (Boichard et al., 1997).

Boichard et al. (1997) pointed out that f_a complements the information provided by the f_e taking the losses of genetic variation into account; caused by the unbalanced use of breeding animals producing bottleneck. The effective number of ancestors (f_a) and the total number of ancestors contributed in the reference population were 136 and 1163, respectively. Menezes et al. (2015) estimated the effective number of ancestors in a population of Brazilian Boer goats as 56 which is lower than the corresponding value in the present study. A larger estimate of 965 for f_a was also reported in Spanish Murciano-Granadina (Oliveira et al., 2016). Oravcova (2013) analyzed the pedigree information in White Shorthaired goats of Slovakia and found values of 73 and 45 for f_e and f_a , respectively.

Boichard et al. (1997) stated that evaluation of the loss in genetic diversity that exist in the founders beca-

use of the bottleneck between the base and the reference population can be studied by applying the ratio of f_e/f_a ; the ratio of effective number of founders to effective number of ancestors. The importance of bottleneck in the population under consideration can be evaluated by applying this ratio; the greater the f_e/f_a ratio, the more stringent the bottlenecks. If all founders contribute to pass their genes to the next generations, the maintenance of the original genetic diversity is ensured and, in such situation f_e will be equal to f_a (Oliveira et al., 2016). Anyhow, it should be noted that the parameters related to probability of gene origin measures highly influenced by pedigree completeness.

In the present study, the ratio of f_e/f_a was 1.76, implying bottleneck in the studied Raeini Cashmere goat population. A corresponding ratio of 1.37 was obtained by Rashidi et al. (2015) in Markhoz goat. Oliveira et al. (2016) obtained an ideal value of 1 for ratio of f_e/f_a in Spanish Murciano-Granadina goat breed. They also pointed out that despite the existence of ideal corresponding ratio in the population of Spanish Murciano-Granadina goat, 50% of the genetic diversity of the population was explained by only 366 ancestors out of 5828 ancestors, which may contribute to future genetic bottlenecks if the current mating policy is implemented.

Individual and cumulative contributions of the first 57 ancestors explained 50% of the genetic diversity is shown in Figure 2. Amongst them, 50 animals were sires; implying excessive use of some sires for breeding. The prolonged use of certain sires can increase the probability of mating between close relatives if no restriction is applied (Oliveira et al., 2016). The most influential ancestor explained 3.94% of the genetic diversity in the reference population. It was a buck with 144 progenies.

Conclusions

Pedigree analysis of Raeini Cashmere goat revealed some appropriate indications regarding changes in the population structure across the years. The level of inbreeding was low with high values for the effective population size. Because the animals with unknown parents (one or both ones) constituted about 53% of total animals, the inbreeding coefficient of animals might have been underestimated. Therefore, for setting up any breeding and / or conservation program in Raeini Cashmere goats accurate registration of pedigree information is required. Evidence for the presence of bottleneck was found mainly due to intensive use of some sires. Because of low quality pedigree available, the obtained genealogical parameters should be interpreted with cautious in the light of the factors such as pedigree completeness.

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ارزیابی تنوع ژنتیکی و ساختار جمعیتی بز کرکی رائینی با استفاده از تجزیه شجره

م. س. مختاری^{۱*}، م. مقبلی دامنه^۱، خ. پ. گوتیئرز^۲

^۱ گروه علوم دامی، دانشکده کشاورزی، دانشگاه جیرفت، جیرفت، ایران.

^۲ گروه تولیدات دامی، دانشکده دامپزشکی، دانشگاه کامپلوتنس مادرید، مادرید، اسپانیا.

*نویسنده مسئول، پست الکترونیک: msmokhtari@ujiroft.ac.ir

چکیده در این پژوهش، از اطلاعات شجره‌ای جمع‌آوری شده در ایستگاه اصلاح نژاد بز کرکی رائینی طی سال‌های ۱۳۵۸ تا ۱۳۹۱ برای مطالعه تنوع ژنتیکی و ساختار جمعیتی بز کرکی رائینی با در نظر گرفتن بزغاله‌های متولد شده طی سال‌های ۱۳۸۸ تا ۱۳۹۱ به عنوان جمعیت مرجع استفاده شد. میانگین ضریب همخوانی در کل جمعیت و در جمعیت همخون به ترتیب ۰/۰۴ درصد و ۴/۴۱ درصد محاسبه شد. میانگین ضریب همخوانی و میانگین خویشاوندی در جمعیت مرجع به ترتیب ۰/۱۴ درصد و ۰/۱۱ درصد به دست آمدند. میانگین فاصله نسلی حاصل از چهار مسیر گامتی (پدر-پسر، پدر-دختر، مادر-پسر و مادر-دختر) ۳/۷۲ سال به دست آمد که در مسیر مادر-فرزندان بیشتر از پدر-فرزندان بود. میانگین معادل نسل کامل، به عنوان معیاری از کامل بودن شجره، ۱/۲۵ به دست آمد. اندازه‌های موثر جمعیت بر اساس افزایش انفرادی در همبستگی و افزایش انفرادی در همخوانی به ترتیب ۳۳۲ و ۲۲۹ برآورد شدند. تعداد موثر پایه گذاران و تعداد موثر اجداد به ترتیب ۲۴۰ و ۱۳۷ تخمین زده شدند. تقریباً ۵۰ درصد کل تنوع ژنتیکی را ۵۷ جد با بیشترین تاثیرگذاری توضیح دادند که حداکثر مشارکت انفرادی در تنوع ژنتیکی ۳/۹۴ درصد بود. نسبت تعداد موثر پایه گذاران به تعداد موثر اجداد، به عنوان معیاری از باتلنک، ۱/۷۵ به دست آمد. نتایج به دست آمده در این پژوهش شواهدی از بروز باتلنک در این جمعیت را آشکار کرد که عمدتاً به دلیل مشارکت نابرابر حیوانات مولد در خزانه ژنی جمعیت مطالعه شده بز رائینی است.