An Investigation on Population Structure and Inbreeding of Sangsari Sheep

Research Article

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ABSTRACT

The aim of this study was to describe inbreeding and population structure in Sangsari sheep breeding station. For this reason, data from 7028 Sangsari sheep which were collected during 1987-2014 in Sangsari sheep breeding station located near to Damghan city, Semnan province were used. Lambs born during 2010-2014 were considered as reference population. The genetic structure analysis of the population was realized by the ENDOG (v.4.8) software. Mean inbreeding of total population and reference population was 0.28% and 0.70%, respectively. Average relatedness, realized effective population size based on individual increase in inbreeding, effective numbers of founders (f_e), and founder genome equivalents (f_g) were estimated 0.59%, 148.75, 140 and 49.97, respectively. Mean generation interval in present population was 4.24 years and average number of equivalent to discrete generations was estimated as 1.64. Average coancestry, effective number of ancestors (f_a) and average equivalent complete generation were calculated 1.0005%, 76 and 3.02, respectively. Ratio of f_e/f_a which expresses the effect of population bottlenecks was 1.84. 50% of total genetic variation was explained by the 32 most influential ancestors. By monitoring parameters associated with genetic diversity and breeding management, the reduction of genetic diversity and probable harmful effects resulting from excessive increase of inbreeding can be prevented.

KEY WORDS genetic diversity, inbreeding, population structure, Sangsari sheep.

INTRODUCTION

Sangsari is one of the Iranian fat-tailed sheep breeds and are reared in the north of Semnan province, in an area called Sangsar. This breed is used for meat and wool and is one of the hardiest Iranian sheep breeds, well adapted to the high ranges and long-distance travelling. Sangsari breed is also adapted to long drought periods (Kasiriyan *et al.* 2011). In small and closed herds such as closed nucleus breeding herds in which intensive selection methods is undergoing within small populations, reduction of genetic diversity and increase of inbreeding may occur (Mokhtari *et al.* 2014). Definition of inbreeding is given by mating of individuals whose relatedness between them is greater than the average degree of relationship existing in the population (Lush, 1945), and capable of changing the genotypic frequencies of a population without modifying the gene frequencies (Pedrosa *et al.* 2010; Eteqadi *et al.* 2014). Inbreeding has a direct relation with effective population size and genetic diversity, so that increased inbreeding in a population could indicate a decrease in effective population size and as a result, loss of genetic diversity (Falconer and Mackay, 1996). Therefore, loss of founder alleles through selection and genetic drift is an undesirable consequence of genetic improvement programs (Vozzi *et al.* 2007; Mokhtari *et al.* 2013; Mokhtari *et al.* 2014).

On the other hand, long-term increase of inbreeding, in addition to influence on the response to selection of economic traits, decrease the heterozygosity and consequently increase in homozygosity and loss of genetic diversity (Kristensen and Sørensen, 2005; Hinrichs and Thaller, 2011), may lead to decrease of growth, production, health, fertility and survival (Selvaggia *et al.* 2010; Mokhtari *et al.* 2014). The effect of inbreeding on different traits in sheep has been reported in some studies; most of these studies have been shown reduced animal performance by inbreeding (Lamberson and Thomas, 1984; Ercanbrack and Knight, 1991; Analla *et al.* 1998; Dario and Bufano, 2003; Khan *et al.* 2007; Van Wyk *et al.* 2009).

Rzewuska *et al.* (2005), Van Wyk *et al.* (2009), Gowane *et al.* (2013), Pedrosa *et al.* (2010), Ceyhan *et al.* (2011) and Eteqadi *et al.* (2014) have estimated inbreeding coefficients and its effects on some growth traits in Booroola, Elsenburg, Bharat Merino, Santa Inês and Guilan sheep breeds, and found average inbreeding coefficients of 9.81, 22, 2.32, 2.33, 2.25 and 0.15 percent for the whole population, respectively.

Study of genetic diversity in a population using pedigree analysis is an efficient method to identify factors affecting the genetic history of a population (Valera *et al.* 2005). In animal breeding, implementation of the effective selection program is dependent on the population structure and evaluation of genetic variability in the population (Gowane *et al.* 2013). A complete pedigree is necessary for accurate evaluation of inbreeding, effective population size, generation interval, genetic diversity, and other important population parameters (Martínez *et al.* 2008). Lack of identification information, incomplete pedigree, and introduction of new animals to the population can lead to incorrect estimation of inbreeding coefficient and other parameters (Goyache *et al.* 2003) and therefore, lead to spurious interpretations.

There are several factors that affect increase in inbreeding. One of these is the size of the base population or the number of founders that has a considerable role in increasing the inbreeding (Sørensen *et al.* 2005). All the animals with both parents unknown are regarded as founders. In addition, if an animal has one known and one unknown parent, the unknown parent is regarded as a founder (Sørensen *et al.* 2005).

On the other hand, given that some of these animals have a greater contribution in the genetic structure of present population than other animals, two parameters of effective number (equivalent) of founders and founder genome equivalents to correct for this effect were suggested (Sørensen *et al.* 2004).

The founder equivalents (f_e) of a population are the number of equally contributing founders that would be expected to produce the same genetic diversity as in the population under study (Lacy, 1989); therefore, the genetic diversity created by the founders are the same in future generations. Founder genome equivalents (f_g) can be defined as the number of founders that would be expected to produce the same genetic diversity as in the population under study if the founders were equally represented and no lost of alleles occurred (Ballou and Lacy, 1995).

Maintaining genetic diversity at the high level and inbreeding at the low level is a primary goal in the management of animal populations (Fernandez *et al.* 2005). Genetic variation is prerequisite for populations to be able to face future environmental changes and to ensure long-term response to selection for traits of economic interest (Frankham *et al.* 2003).

The aim of the present investigation was to study of inbreeding and genetic diversity in a population of Damghan's Sangsari sheep using pedigree analysis in order to manage breeding programs and preventing possible negative and harmful effects of excessive increase of inbreeding.

MATERIALS AND METHODS

In the present study, data from 7028 Sangsari sheep (3180 males and 3848 females) which were collected during 27 years (1987-2014) in the breeding station of Sangsari sheep located near to Damghan city, Semnan province, Iran, were used. Pedigree information including animal, sire, and dam and also sex and birth date of lambs were used to determine genetic diversity, inbreeding and coancestry coefficients, effective population size and parameters estimates based on the analysis of probabilities of gene origin by ENDOG v4.8 software (Gutierrez and Goyache, 2005).

Before estimation of inbreeding and relatedness coefficients between the animals, it is very important to be sure about completeness and depth of the pedigree. For this purpose, the following parameters were calculated. Pedigree completeness level, which was computed as the proportion of ancestors known per parental generation (MacCluer *et al.* 1983); and also the equivalent complete generation numbers (EqG) for each animal in the pedigree was calculated according to:

$$EqG_i = \Sigma \left(\frac{1}{2}\right)^n$$

Where:

n: number of generations separating the individual from each known ancestor (Maignel *et al.* 1996); then average of equivalent complete generation numbers of lambs born each year were estimated.

Pedigree completeness level has a direct effect on the calculation of population inbreeding coefficients. Because, by increase in the pedigree completeness level, probability of finding common ancestor for the individuals of present generation has increased.

Number of equivalent to discrete generations (g_e) for each individual in a pedigree (Boichard *et al.* 1997) which is an index to measure the depth of pedigree and represents the number of complete discrete generations in the reference population, was obtained as:

$$g_e = \sum_{i=1}^{n_j} \frac{1}{g_{ij}}$$

Where:
n_j: number of ancestors of animal j.
g_{ij}: number of generations between animal j and its ancestor I (Woolliams and Mantysaari, 1995).

Individual inbreeding coefficient (F) that is the probability of having two alleles at the same locus, which are identical by descent, was computed according to Meuwissen and Luo (1992).

Average relatedness coefficient (AR) (Goyache *et al.* 2003; Gutiérrez *et al.* 2003) was used to predict inbreeding coefficient in the next generation. Coancestry coefficient (C) between two individuals is defined as the probability that two alleles taken at random at any locus, one from each individual, are identical in state (Malecot,1948) and it was used to calculate relatedness between individuals (Bink *et al.* 2008; Karhunen and Ovaskainen, 2012).

Average coancestry of animals ($\overline{C}$) in a population predicts the average inbreeding of the next generation. Therefore, this parameter would provide information on the effective size of a population under random mating (Cervantes *et al.* 2008). Within-population coancestry (f_i) was computed by averaging all pairwise coancestry coefficients of the individuals belonging to a given population *i*.

Generation interval was estimated as the average age of parents at the birth of their progeny kept for reproduction (James, 1977). This parameter was computed for the four pathways: sire–son (L_{ss}), sire–daughter (L_{sd}), dam–son (L_{ds}) and dam–daughter (L_{dd}) and the average generation interval was defined as the average of the four pathways.

The parameters related to analysis of the probabilities of gene origin including effective number of founders (f_e) (James, 1972), was computed as:

$$f_e = 1 \Big/ \sum_{k=1}^{f} q_k^2$$

Where:
q_k: genetic contribution of the k^{th} founder that obtained through relationship between the founder and any of animals in the population and f represents the number of founders (Lacy, 1989).

Effective number of ancestors (f_a) which is defined as the minimum number of ancestors, not necessarily founders and explaining the complete genetic diversity of a population (Boichard *et al.* 1997) was computed in a similar way to the effective number of founders:

$$f_a = 1 \Big/ \sum_{j=1}^{a} q_j^2$$

Where:
q_j: marginal contribution of an ancestor j, which is the genetic contribution made by an ancestor that is not explained by other ancestors chosen before.

Founder genome equivalents (f_g) which is the most important index to measure genetic diversity and was obtained following Caballero and Toro (2000) as the inverse of twice the average coancestry of the individuals included in a reference population (Ballou and Lacy, 1995).

The effective population size (Ne) is the number of breeding animals that would lead to the actual increase in inbreeding if they contributed equally to the next generation (Gutiérrez *et al.* 2003) and is a key parameter in conservation and population genetics because of its direct relationship with the level of inbreeding, fitness and the amount of genetic variation loss due to random genetic drift (Caballero and Toro, 2000; Falconer and Mackay, 1996). This parameter was computed by several methods; by calculation of the regression coefficient (*b*) of the individual inbreeding coefficient over the number of full generations traced; the maximum number of generations traced and the equivalent complete generations; and also by individual increase in inbreeding (ΔFi), as proposed by Gutiérrez *et al.* (2008).

Wright´s fixation statistics (f_{IS}) describe the measure of inbreeding-like effects within subpopulations and were estimated assuming that the population has a structure of two levels [from the individual (I) to the subpopulation (S) and the subpopulation to the total (T)]. *F*-statistic (Wright, 1978) was computed by using pedigree information for any subpopulation according to Caballero and Toro (2000) and Caballero and Toro (2002).

These calculations were carried out on all records available and the reference population defined as all animals with both parents known and on a subgroup of animals born since January 2010 to March 2014 (most recent).

RESULTS AND DISCUSSION

The results of pedigree analysis obtained from this study are presented in Table 1. Of all the registered animals, 4772 animals had both parent known. About 7.21% of the lambs were inbred and produced from half-sibs and parents-offspring matings (0.55% and 0.48% of matings, respectively). Figure 1 shows the level of completeness for each generation of parents in the pedigree. Completeness of the first and second ancestor generations of all animals were 78.52% and 44.33%, respectively, and the completeness decreased progressively for the next generations. Maximum number of known generations was 10. The average number of equivalent to discrete generations was estimated 1.64 with a maximum of 5.26 and a minimum of 0.

Average equivalent complete generation, mean inbreeding and mean individual increase in inbreeding of animals across the years of birth are given in Figure 2. Low values of F observed from 1987 to 1994 were mainly because of the lack of or incomplete pedigree information. After 1994, average coefficient of inbreeding of animals had an irregularly trend and fluctuations in mean inbreeding coincide with the trend of EqG of animals. That can be due to the ratio of breeding rams to breeding ewes or the parent's pedigree completeness level.

In the present study, average equivalent complete generation, as a measure of pedigree completeness level, estimated as 3.02 for the reference population. Lower average equivalent complete generation has been reported by Mokhtari *et al.* (2013) in Kermani sheep (2.22) and higher values reported by Tahmoorespour and Sheikhloo (2011) in Baluchi sheep (5.47).

Mean inbreeding of total population and reference population estimated as 0.28% and 0.70%, respectively and average relatedness estimated as 0.59%. Maximum and minimum inbreeding coefficients for the inbred animals were 31.25% and 0.024%, respectively. Low average coefficients of inbreeding can be mostly due to controlled mating in the flock and also due to having many animals with inbreeding coefficients of zero. Zero inbreeding coefficients were mainly due to lack of pedigree information in the early years. Inbreeding as well as average relatedness was increased over generations (Table 2), and it was especially evident in generation 10 (there was almost a 0.67% increase in inbreeding).

Average relatedness provides complementary information to the values of inbreeding to explain mating relatives (Gutiérrez *et al.* 2003). Mokhtari *et al.* (2013) reported a value of 0.51% for mean inbreeding in reference population of Kermani sheep. The difference in mean inbreeding could be attributed to the population size structure and different number of equivalent generations.

As shown in Table 2, with increasing average inbreeding coefficients of the population, average inbreeding coefficients of the inbred animals was reduced. Because, in earlier generations, pedigree completeness was low and common ancestors were highly inbred animals. Increasing in pedigree completeness resulted in more relations between the common ancestors of inbred animals and previous generations.

Mean generation interval was 4.24 years which were estimated in four pathways as L_{ss}= 4.32, L_{sd}= 4.34, L_{ds}= 4.19, and L_{dd}= 4.20 years that was similar to the mean obtained by Mokhtari *et al.* (2013). Relatively high generation interval obtained may be partly attributed to intensive use of a few breeding animals within the flock. Since breeding rams had usually been employed longer than the ewes to produce offspring, the generation interval in the sire-progeny pathways was a bit longer than dam-progeny pathways.

Average coancestry in the reference population was estimated as 1.00%. Average coancestry of the animals in a population forecasts the average of inbreeding coefficient in the subsequent generations.

As indicated in Figure 2, after 1994, inbreeding trend has been irregular over the years and under such conditions, the estimate of realized effective population size using the method proposed by Gutierrez *et al.* (2008) and Gutierrez *et al.* (2009) seems suitable. Realized effective population size estimates based on individual increase in inbreeding were 148.75, and was slightly higher than the critical level of N_e defined by the FAO (1998), however, determination of an exact critical level is not right and depends on such factors as the method used, species and population structure (Leroy *et al.* 2013).

N_e was also estimated by the regression coefficient of the inbreeding coefficient over the number of full generations, 399.87, the maximum number of generations, 120.20, and the equivalent complete generations, 164.48. The difference between these values is a reflection of the different methods used and the number of animals used in each case. *Ne* quantifies genetic drift and the rate of inbreeding in a population (Teegen *et al.* 2009).

Genetic diversity in the present population was indicated by estimation of number of ancestors, *fe*, *fa* and number of ancestors explaining 50% of genetic variation. These parameters, unlike the inbreeding and effective population size, which explains genetic diversity within flocks or breeds after a long time, are powerful tools to explain the genetic diversity within a few short generations (Boichard *et al.* 1997).

Effective numbers of founders (f_e) was estimated 140, while the number of founders in the reference population was 664 which represent the overuse of some animals as parents.

Table 1 Summary statistics of the pedigree analysis in Sangsari sheep

Item	Value
No. of animals in whole population	7028
No. of animals with both known parents	4772
No. of inbred animals	507
Mean inbreeding (%)	0.28
Mean average relatedness (%)	0.59
Base population (one or more unknown parents)	2256
Actual base population (one unknown parent=half founder)	1509.50
Effective population size of founders	242.54
Expected inbreeding by unbalancing of founders (%)	0.21
No. of animals in reference population	1251
No. of ancestors contributing to the Reference Population	506
No. of founders in reference population	664
Effective number of founders in reference population	140
Effective number of ancestors in reference population	76
No. of ancestors explaining 50%	32
Mean maximum generations	2.89
Increase in inbreeding by maximum generation (%)	0.13
Effective population size	399.87
Mean complete generations	0.86
Increase in inbreeding by complete generation (%)	0.42
Effective population size	120.20
Mean equivalent generations	1.64
Increase in inbreeding by equivalent generation (%)	0.30
Effective population size	164.48
Ne regression on birth date	1544.79
Ne log regression on birth date	1453.69

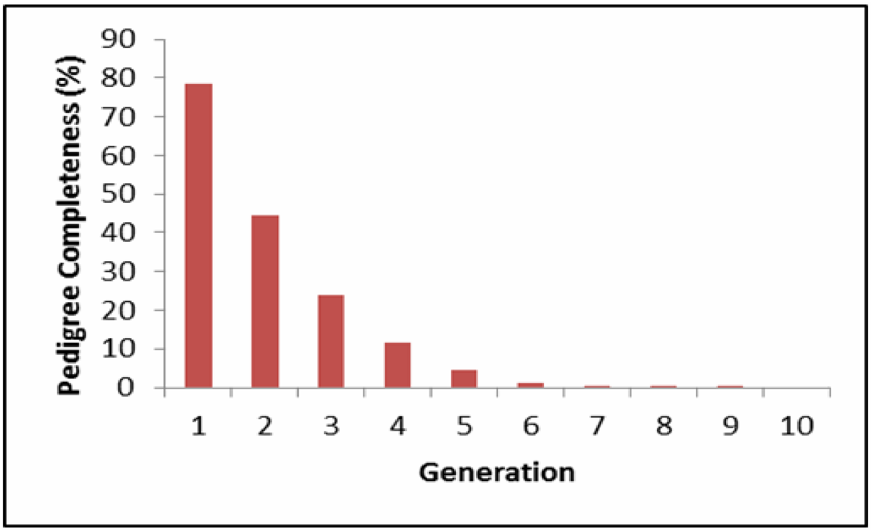

Figure 1 Pedigree completeness per generation
(generation 1=parents, generation 2=grandparents, etc)

tive of an imbalance in contribution of founders to the reference population (Lacy, 1989).

Mokhtari *et al.* (2013) reported a value of 149 for f_e in Kermani sheep with a total of 292 individuals in the reference population.

In the present study, ratio of the effective numbers of founders to the total numbers of founders was estimated 0.21 and the difference between these two values is indicative of an imbalance in contribution of founders to the reference population (Lacy, 1989).

Higher proportion (0.35) was reported by Mokhtari *et al.* (2013). Based on the other studies, if all founders had contributed equally to the genetic structure of reference population, then the actual number of founders and the effective number of founders should be equal (Cole *et al.* 2004).

Effective number of ancestors (f_a) and the total numbers of ancestors contributed in the reference population were obtained as 76 and 506, respectively.

Table 2 Inbreeding (F), average relatedness (AR) and effective population size (Ne) per generation

Generation	Number of animals	Mean F (%)	% Inbred individuals	Mean F for inbred (%)	% Mean AR	Ne
Inbreeding per complete generation[1]						
0	2256	0	-	-	0.22	-
1	3664	0.26	5.27	4.99	0.69	189.90
2	978	0.81	24.13	3.37	1.02	90.70
3	130	1.62	60	2.69	1.21	61.07
Inbreeding per generation[2]						
0	763	0	-	-	0.09	-
1	1374	0	-	-	0.04	-
2	1371	0.16	0.66	23.61	0.55	322.50
3	963	0.32	2.08	15.47	0.65	300.20
4	888	0.32	4.73	6.71	0.81	-
5	710	0.66	11.55	5.68	0.84	148.80
6	599	0.75	28.55	2.61	0.89	549.70
7	271	0.60	47.60	1.25	0.88	-
8	75	0.92	61.33	1.49	0.92	290.70
9	13	1.16	53.85	2.16	1.05	202.30
10	1	7.86	100	7.86	1.19	7.30

[1] Number of full generations traced.

[2] Maximum numbers of generations traced as defined by Gutiérrez *et al.* (2009).

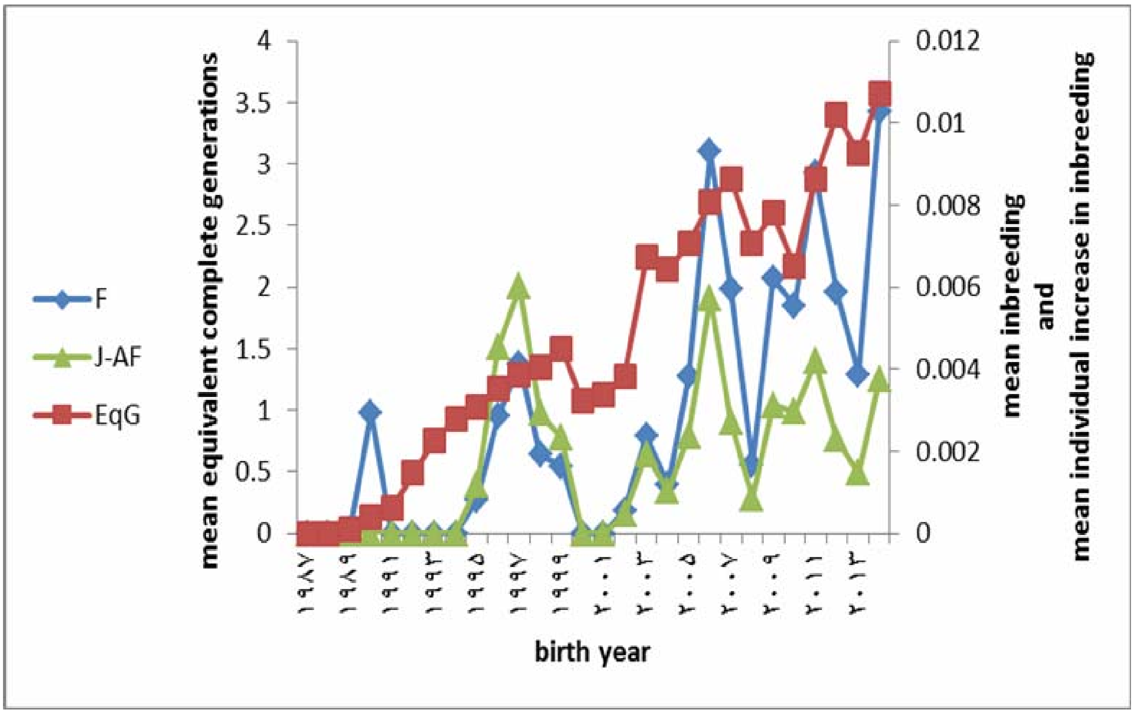

Figure 2 Evolution of the mean inbreeding (F, right axis), mean individual increase in inbreeding (J-AF, right axis) and mean equivalent complete generations (EqG, left axis) of animals by birth year over the period 1987-2014

The f_a value in the present study was in accordance with the value estimated by Ghafouri-Kesbi (2010) in Zandi sheep (74).

The founder genome equivalents (f_g) were computed as 49.97. The lower the f_g in a reference population, the lower the proportions of the genes of founder individuals. Actually, the founder genome equivalents represent that loss of genetic diversity in the population is not only because of different contributions of founders, but also because of random genetic drift.

Therefore, more accurate estimates for existence or absence of diversity will be expected (Melka and Schenkel, 2010; Sørensen *et al.* 2005; Hammami *et al.* 2007).

As reported by Gutiérrez *et al.* (2003), differences between f_e, f_a and f_g indicating the existence of the bottlenecks in the pedigree. Boichard *et al.* (1997) stated that loss of genetic diversity of the founders due to the bottlenecks between the base and the reference populations which their importance can be indicated using a ratio of the effective numbers of founders to the effective numbers of ancestors f_e/f_a. The optimum ratio would be one and the value obtained in this population was 1.84 that shows genetic diversity has decreased because of imbalance between the ancestors and founders. This estimate explained that excessive use of some individuals as breeding animals lead to a significant reduction in the genetic stock. Expected inbreeding by unbalancing of founders was 0.21%. Increasing genetic contribution of a part of the population lead to strengthening the kinship and resulted in increased inbreeding and reduced effective population size. The value of f_e/f_a was found 1.18 by Mokhtari *et al.* (2014) for Iran-black sheep, and also estimate of 1.61 reported for Malpura sheep by Gowane *et al.* (2014).

Wright´s fixation statistic (F_{IS}) was -0.0011 in this population. Positive values of this parameter indicating more inbreeding compared to random mating and negative values means that inbreeding arisen is lower than expected inbreeding in random mating (Lukas and Donald, 2002). F_{IS} may vary from -0.1 (all individuals heterozygous or totally outbred) to +0.1 (no observed heterozygotes or totally inbred) (Wright, 1965; Wright, 1978).

F_{IS} index in each population, indicating decrease or increase in the frequency of observed heterozygosity than expected heterozygosity and reflecting the mating system (random and non-random mating) in the population (Nei and Chesser, 1983) and the negative F_{IS} estimates in the population, indicating that the frequency of observed heterozygosity is higher than expected heterozygosity within the population.

Negative values of the index in this population, indicating lack of inbreeding and existence of enough diversity. Self-coancestry and inbreeding were estimated 0.5 and 0.0028, respectively, showing that no immediate problems in maintenance of genetic diversity within the herd was seen.

CONCLUSION

The results showed that the average coefficient of inbreeding in the studied Sangsari sheep population was lower than the values reported in other breeds which could be because of lack of clear information of some parents and common ancestors and also because of the purposive and largely controlled mating. Considering the estimated genetic diversity indexes, the present population had relatively high genetic diversity. In the early years the number of inbred animals was low, but over time, the average coefficient of inbreeding was increased due to the selection of breeding male and female animals within the flock and mating of the related animals. The increase in inbreeding was insignificant. But, by increase in inbreeding, it will be problematic in the future, because of the harmful effects of inbreeding on different traits. Therefore, with monitoring parameters associated with genetic diversity and breeding management, we can prevent the reduction of genetic diversity and probable harmful effects resulting from excessive increase of inbreeding.

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