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Pedigree analysis of Iran-Black sheep and inbreeding effects on growth and reproduction traits

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ABSTRACT

Pedigree information and data on growth and reproduction traits in Iran-Black sheep breed, collected during a period of 28 years (1980–2008) in Abbasabad breeding station, north-east of Iran, were used to genealogical characterization of the breed using pedigree analysis and investigation the effect of inbreeding on growth related traits including birth weight (BW) and weaning weight (WW) and reproduction traits including litter size at birth per ewe lambing (LSB), litter size at weaning per ewe lambing (LSW), total litter weight at birth per ewe lambing (TLWB) and total litter weight at weaning per ewe lambing (TLWW). The Iran-Black is a composite breed; the first cross of Chios rams with Iranian Baluchi ewes. Inbreeding depression was investigated for all the studied traits by fitting individual increase in inbreeding coefficient (ΔF_i) of the lambs and the ewes as linear covariates under univariate animal models. The average inbreeding coefficient during the study period for all and inbred animals were 8.08% and 9.90%, respectively. The animals born in the last 3 years (2006–2008) were considered as reference population and genealogical analysis was performed. The values of effective population size estimated from the individual increase rate in coancestry and the individual increase in inbreeding were 28 and 27, respectively. Genealogical parameters estimated based on the 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 were estimated as 13, 11, 6 and 12, respectively. Generation interval (in years) and the average equivalent complete generation were 3.39 and 7.10, respectively. Significant individual inbreeding depression was only found for BW ($P < 0.05$) as −7 g per 1% ΔF_i. Maternal inbreeding depressions were estimated as −17 g, −37 g, −346 g and −62 g per 1% ΔFi for BW, TLWB and TLWW ($P < 0.01$) and WW ($P < 0.05$), respectively.

1. Introduction

Indigenous breeds of the small ruminants in the developing countries are mainly kept by local pastoralists under low-input production systems and the livelihood of the flock holders depends on the promotion of production efficiency under such systems. Therefore, coordinated

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attempts in terms of managerial practices and genetic improvement programs are of crucial importance (Kosgey and Okeyo, 2007). Intensive selective practices within small populations can result in reduction of genetic diversity and increase of the inbreeding rate. Selective practices using the breeding values estimated based on animal model result in more emphasis on the records of the related animals. Consequently, although more genetic gain would be attained through selection of the best animals to be the parents of the next generation, an unfavorable phenomenon called inbreeding depression may occur. Inbreeding has long been a serious concern in animal breeding due to its detrimental effect on genetic variance as well as on phenotypic values (Falconer and Mackay, 1996). Inbreeding impairs growth, production, health, and reproduction of inbred animals. Thus, loss of genetic diversity mainly due to the increased inbreeding and loss of founder alleles through genetic selection and drift is an undesirable consequence of genetic improvement programs (Vozzi et al., 2007). The knowledge of genetic diversity of a population is the main prerequisite for designing efficient genetic improvement and/or conservation programs (Gutierrez et al., 2003). Maintaining genetic diversity at a high level and inbreeding at a low level is a primary goal in the management of animal populations (Fernandez et al., 2005). Studying the genetic diversity in population using pedigree analysis is an efficient approach to identify influencing factors that affect the genetic history of a population (Valera et al., 2005).

Iran-Black is the first synthetic sheep breed in Iran, developed for improving the litter size, weaning performance and tolerance to harsh environmental conditions (prevalent in the region) of Baluchi sheep (Rashidi, 2012) and kept closed since inception in the breeding station of Abbasabad, north-east of Iran.This breeding station may act as a main part of nucleus-based breeding schemes for genetically improvement of this breed, dissemination of superior animals into local flocks and thereby enhancement of production efficiency. Assessment of genetic diversity, inbreeding level and its possible effect on productive and reproductive traits in this breed are of crucial importance to establish a nucleus-based breeding scheme for dissemination of this breed into commercial flocks. There are several reports regarding the inbreeding depression associated with implementation of genetic improvement programs on growth and reproductive performance of sheep breeds (Norberg and Sørensen, 2007; van Wyk et al., 2009; Dorostkar et al., 2012) but there are no corresponding published reports on Iran-Black sheep as the first crossbred Iranian sheep. Given that pedigree recording of sheep breeds is exception in Iran, there are rare reports concerning pedigree analysis of Iranian sheep breeds and mainly limited to recently published papers (Ghafouri-Kesbi, 2010, 2012; Tahmoorespour and Sheikhloo, 2011). Therefore, the objectives of the present study were assessment of genetic diversity in Iran-Black sheep using pedigree analysis and investigation of the possible effects of inbreeding on growth and reproductive traits.

2. Materials and methods

2.1. Flock history and management

Iran-Black sheep is a composite breed, resulting from a cross of Chios rams with Iranian Baluchi ewes. The breeding project commenced in the sheep breeding station of Abbasabad, located in Khorasan Razavi province, north-east of Iran. The project was started in 1975 and performance data recording was begun in 1984 (Rashidi, 2012). During the breeding season which lasting from late in August to late in October the ewes in heat were detected by teaser rams. Annually, 10–12 rams were randomly allocated to mate with about 20–25 ewes per ram, with sire identification recorded. The maiden ewes were exposed to fertile rams at approximately 18 months of age. Ewes were kept in the flock for a maximum of 7 parities (until 8 years of age) while the rams were used for 2–3 mating seasons. Lambing occurred late in January to late in March. A detailed description on flock management was presented by Rashidi (2012).

2.2. Pedigree analysis

2.2.1. Inbreeding and coancestry coefficients

Pedigree records collected during a 28-year period (1980–2008) were analyzed and the lambs born from 2006 to 2008 were considered as reference population. Inbreeding coefficient (F) denotes the probability that two alleles at any locus are identical by descent. The coefficient of inbreeding for each individual was computed using an algorithm from Meuwissen and Luo (1992). Coancestry coefficient (f) is defined as the probability that any two alleles, sampled at random one from each individual, were identical copies of an ancestral allele and calculated following the method of Malécot (1948).

The average inbreeding and/or coancestry coefficients per year were computed and annual increases in inbreeding and coancestry were estimated by linear regression of average inbreeding and coancestry coefficients on year, respectively.

2.2.2. Generation interval

The generation interval was defined as the average age of the parents at the birth time of their progenies 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}). The average generation interval (G. I.) was computed as follow:

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

2.2.3. Equivalent complete generations

Completeness of pedigree was assessed by the proportion of animals in the pedigree with both known parents and by addressing the equivalent complete generations. Individual equivalent complete generations (EqG_i) were computed following Maignel et al. (1996):

$$\mathrm{EqG}_i = \sum \left(\frac{1}{2}\right)^n$$

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

2.2.4. Realized effective population size

The effective population size is the size of an ideal population, characterized by equal sex ratio, absence of mutation, migration and selection and random mating,which has the same inbreeding rate as the real population under study. The effective population size (N_e) was obtained using two approaches to see if the rotational mating applied in this population to avoid inbreeding has been effective. The first approach was that proposed by Cervantes et al. (2011) using the rate of coancestry for all pairs of individual j and k ($\Delta \mathrm{C}_{jk}$) in a reference population and computed as:

$$\Delta C_{jk} = 1 - \sqrt[(g_j+g_k/z)]{1 - C_{jk}}$$

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

$$Ne = \frac{1}{2\overline{\Delta c}}$$

The second approach was based on individual increase in inbreeding. The coefficients of individual increases in inbreeding (ΔF_i) 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:

$$\Delta F_i = 1 - \sqrt[\mathrm{EqG}_i - 1]{1 - F_i}$$

in which F_i and EqG_i are the coefficient of inbreeding and the equivalent complete generation for individual i, respectively. The coefficients of individual increase in inbreeding (ΔF_i) were averaged and the realized effective population size was estimated as follow:

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

2.2.5. Measures on probabilities of gene origin

Considering the reference population, four measures based on the probability of gene origin including the effective numbers of founders, the effective numbers of ancestors, the effective numbers of founder genomes and the effective numbers of non-founder genomes were estimated.

There is a probability of 0.5 that a gene randomly sampled form an autosomal locus originating from its sire with a sililar value about its dam origin. Corresponding value about originating from each of grandparents is 0.25 and so on. If this simple rule applied to complete pedigree of an individual provides the probability that the gene originate from any of its founders. A founder can be considered as an ancestor with unknown parent. Applying this simple rule to a population consisting of k founder, each founder k is characterized by it expected contribiution to the gene pool of population. In other words, the q_k is the probability that a gene randomly sampled from population originates from the founder k (Boichard et al., 1997). The preservation of the genetic diversity from the founder to the present population may be measured by the balance of the founder contribution and this balance may be measured by the effective numbers of founders (f_e) which denotes the numbers of equally contributing founders that would result to the same level of genetic diversity in the current population and was obtained according to Lacy (1989):

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

in which, 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.

In intensive breeding programs when the genes of a limited number of breeding animals is widely distributed, as observed in the case of Iran-Black sheep in the present study, the f_e is overestimated due to ignoring the potential bottleneck in the pedigree. To overcome this problem the concept of the effective numbers of ancestors (f_a) has been proposed by Boichard et al. (1997) to explain total genetic variability of the population studied. It denotes 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):

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

in which, 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 that how many founders would be required to produce the same genetic diversity found in the population if all founders contribute equally and no founder alleles were lost by drift under random mating (Caballero and Toro, 2000). This parameter was computed as the inverse of the twice average coancestry ($\bar{f}$) of the individuals defined in a reference population:

$$f_g = \frac{1}{2\bar{f}}$$

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 degree of genetic diversity (G.D.) in the reference population in comparison with that of exists in the base population is approximated as follow, where genetic diversity is expressed as the expected heterozygisity (Lacy, 1989):

$$\text{G.D.} = 1 - \frac{1}{2f_g}$$

The effective numbers of non-founder genomes (f_{ne}) consider only the effect of genetic drift in non-founder generations and was computed as presented by Caballero and Toro (2000):

$$\frac{1}{f_{ne}} = \frac{1}{f_g} - \frac{1}{f_e}$$

Genealogical analyses were performed using the ENDOG v4.8 program (Gutierrez and Goyache, 2005).

2.3. Inbreeding depression

The effect of inbreeding on growth traits including birth weight (BW) and weaning weight (WW) that recorded at 3 months of age and on reproduction traits including litter size at birth per ewe lambing (LSB), litter size at weaning per ewe lambing (LSW), total litter weight at birth per ewe lambing (TLWB) and total litter weight at weaning per ewe lambing (TLWW) were investigated. TLWB refers to the sum of the birth weights of all lambs born per ewe lambed and TLWW is the sum of the weights of all lambs weaned per ewe lambed.

Under animal models individual and maternal inbreeding depressions were estimated as the linear regression of the trait, corrected for fixed effects, on the coefficients of individual increase in inbreeding of lambs and ewes, respectively. Fitting animal models was carried out by ASReml program (Gilmour et al., 2002). The fixed effects included in the model for BW and WW were sex of lamb in two classes, birth year in 24 classes (1984–2008), dam age at lambing in six classes (2–7 years old) and birth type in four classes (single, twin, triplet and quadruplet). The effect of sex on birth and weaning weight of the lambs was corrected and TLWB and TLWW were computed using adjusted birth and weaning weights, respectively. Age of the lambs at weaning (in days) was considered as a linear covariate for WW and TLWW. The animal models used for BW and WW were those of Rashidi (2012). Therefore, the following model was used for BW:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_1a} + \mathbf{Z_2m} + \mathbf{Z_3c} + \mathbf{Z_4l} + \mathbf{e} \quad \mathbf{Cov}(\mathbf{a},\mathbf{m}) = \mathbf{0}$$

The following model was fitted for WW:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_1a} + \mathbf{Z_4l} + \mathbf{e}$$

The repeatability model was fitted for LSB, LSW, TLWB and TLWW as below:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_1a} + \mathbf{Wpe} + \mathbf{e}$$

In which, $\mathbf{y}$ is a vector of the records for the studied traits; $\mathbf{b}$, $\mathbf{a}$, $\mathbf{m}$, $\mathbf{c}$, $\mathbf{l}$, $\mathbf{pe}$ and $\mathbf{e}$ are vectors of the fixed, direct genetic, maternal genetic, maternal permanent environmental, maternal temporary environmental (common litter), permanent environmental effects related to repeated records of ewes and the residual effects, respectively. $\mathbf{X}$, $\mathbf{Z}_1$, $\mathbf{Z_2}$, $\mathbf{Z_3}$, $\mathbf{Z}_4$ and $\mathbf{W}$ are design matrices associating the corresponding effects to $\mathbf{y}$. The sire service initially was fitted as a random effect for reproductive effects but found to be non significant ($P > 0.05$), thus was excluded from final model.

3. Results and discussion

Descriptive statistics of inbreeding coefficients in the whole population and inbred animals are presented in Table 1. The male and female lambs constituted 49.47% and 50.53% of the total lambs, respectively. Among all the registered lambs 81.58% were inbred. It was observed that the mating among the related animals in the population studied herein inculded 0.30% mating between full-sibs, 8.20% mating between half-sibs and 1.40% mating between

Table 1
Inbreeding statistics in the whole population and inbred animals.

Item	Whole population			Inbred animals		
	Total	Male	Female	Total	Male	Female
No. of records	6082	3009	3073	4962	2491	2471
Average F (%)	8.08	8.19	7.98	9.90	9.89	9.92
Min. F (%)	0.00	0.00	0.00	0.04	0.04	0.04
Max. F (%)	38.48	38.48	37.68	38.48	38.48	37.67

Table 2
Summary statistics of the pedigree analysis in Iran-Black sheep.

Item	Value
No. of animals in whole population	6082
No. of animals with progeny	1550
No. of animals without progeny	4532
No. of animals with both known parents	5696
No. of animals with both unknown parents	126
No. of animals with one unknown parent	260
No. of animals in reference population	924
Mean inbreeding in reference population (%)	11.11
Average coancestry in reference population (%)	8.71
No. of equivalent complete generations in reference population	7.10
No. of founders	150
No. of ancestors	146
Effective population size[a]	28
Effective population size[b]	27
Effective No. of founders (f_e)	13
Effective No. of ancestors (f_a)	11
Founder genome equivalent (f_g)	6
Effective No. of non-founder genomes (f_{ne})	12
No. of ancestors explaining 50% of genetic variation	4

[a] Estimated based on individual increase in coancestry.
[b] Estimated based on individual increase in inbreeding.

parent and offspring. van Wyk et al. (2009) reported an average inbreeding of 16% in the Elsenburg Dormer sheep stud which was kept closed from 1941 to 2002.

3.1. *Trends in inbreeding, coancestry and individual increase in inbreeding*

The results of the pedigree analysis are shown in Table 2. Animals with both known parents, both unknown parents and one unknown parent constituted 93.65, 2.07 and 4.28% of the population, respectively. Animals with progeny constituted 25.49% and those of without progeny 74.51% of the total registered animals. The annual average inbreeding and coancestry through the study period are presented in Fig. 1. A steady increase in the mean inbreeding level was observed and annual rate of increase in inbreeding from 1984 to 2008 was estimated approximately 0.41% and about 1.39% per generation ($P < 0.01$). Mean inbreeding in the reference population was 11.11%. The increase in inbreeding in three Danish populations of sheep reported as 1% per generation for all breeds by Norberg and Sørensen (2007). Huby et al. (2003) studied the inbreeding trends in six French sheep breeds and no higher than inbreeding rate of 0.40% per generation was found in the studied breeds. Such differences may be partly ascribed to the different mating strategies and depth of the analyzed pedigree. It is recommended that the rate of inbreeding to be maintained at most 0.5–1.0% per generation in animal breeding programs (FAO, 1998). Sørensen et al. (2005) pointed out that the rate of increase in coancestry is a more important measure of diversity than inbreeding. Both are a function of past effective population size but increase in inbreeding is influenced by non-random mating while increase in coancestry is not (Norberg and Sørensen, 2007). Rates of increase in coancestry during the studied period were 0.26% and 0.88% per annum and per generation, respectively (Fig. 1). In the present study the increase rate in inbreeding was higher than the increase rate in coancestry, implying that inbreeding has occurred to a higher amount than that expected under random mating. Average coancestry in the reference population was 8.71%. The average coancestry of the animals in a population forecasts the average of inbreeding coefficient in the subsequent generations. Therefore, it is considered as an informative measure of genetic diversity (Gutierrez et al., 2008). The rate of ΔF_i during the study period is presented in Fig. 2. A significant annual decrease in ΔF_i (0.07) was observed from 1985 to 2008 ($P < 0.01$).

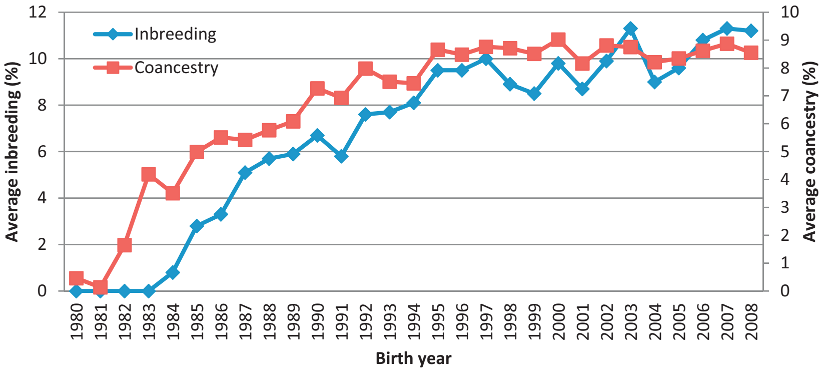

Fig. 1. Evolution of average inbreeding and coancestry through the studied period.

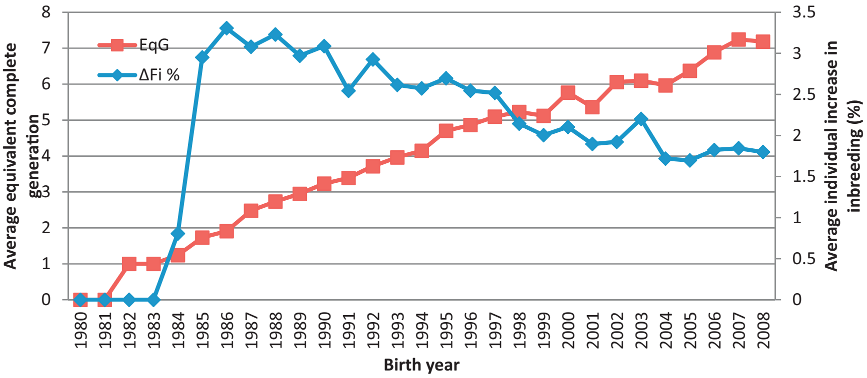

Fig. 2. Average individual increase in inbreeding and average equivalent complete generation through the studied period.

3.2. Genealogical parameters

3.2.1. Generation interval and pedigree completeness

The mean generation interval was 3.39 years. The generation intervals across four pathways were as $L_{ss} = 3.12$ years, $L_{sd} = 3.03$ years, $L_{ds} = 3.73$ years and $L_{dd} = 3.66$ years. The generation interval in sire-progeny pathways was shorter than the dam-progeny pathways and is attributable to the fact that breeding ewes had usually been employed longer to produce offspring than the rams. In other words, replacement policy of the breeding animals was so designed that the rams were replaced after 2 or 3 years of their first time use, but ewes were kept in the flock until 5 successful lambing. The obtained average generation interval in the present study was higher than the value reported by Li et al. (2009) in Finnsheep breed (2.85 years) and was similar to that reported by Tahmoorespur and Sheikhloo (2011) in Baluchi sheep (3.33 years). Evolution of average equivalent complete generation through the years is presented in Fig. 2. The average equivalent complete generation, as a measure of pedigree completeness, in the reference population was 7.10 (Table 2).

3.2.2. Effective population size and measures based on the probability of gene origin

Effective population size is an important parameter in population genetics studies and indicates the degree of genetic drift and viability of population (Frankham et al., 2002). As shown in Table 2, the estimates for realized effective population size based on individual increase in coancestry and on individual increase in inbreeding were 28 and 27, respectively. An effective population size of 50 was determined by FAO (1998) as a critical level for an animal population. However, the determination of a strict critical level for effective population size is not straightforward and estimated effective population size should be interpreted in the light of factors such as the method used, species and population structure (Leroy et al., 2013).

As shown in Table 2, a value of 13 was estimated for the effective numbers of founders (f_e) while the numbers of founders contributed in the reference population was 150, indicating the excessive use of some animals as parents. In our study, the ratio of the effective numbers of founders to the total numbers of founders was computed about 0.09, indicating unbalanced contribution of founders to the reference population. Effective numbers of founders accounts for unequal contribution of founders in populations (Lacy, 1989). When a population that has experienced demographic bottlenecks, the f_e is overestimated due to ignoring the possible bottleneck effects. Therefore, estimation of the effective numbers of ancestors (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 breeding individuals (Boichard et al., 1997). The f_a and the total numbers of ancestors contributed in the reference population were obtained as 11 and 146, respectively (Table 2).

The founder genome equivalents (f_g) was estimated as 6 (Table 2). 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 diversity and is directly associated with genetic diversity but it does not consider mutation.The approximated value for G.D. was approximately 92%, indicating that about 8% of genetic diversity existed in the base population was lost during the studied period. As pointed out by Gutierrez et al. (2003) the differences between f_e, f_a and f_g imply the existence of bottlenecks in the pedigree. Boichard et al. (1997) stated that evaluation of the loss in genetic diversity that exists in the founders due to the bottleneck between the base and the reference populations can be accomplished using a ratio of the effective number of founders to the effective number of ancestors (f_e/f_a). The importance of bottleneck in the population can be assessed applying the above mentioned ratio; the greater the f_e/f_a ratio, the more stringent the bottlenecks. The ideal value for this ratio would be one. In the present study, a value of 1.18 was obtained for the f_e/f_a ratio in the reference population implying that unbalancing between ancestors and founders resulted in reduction of genetic variability.The estimated value for the effective numbers of non-founder genome (f_{ne}) was 13, this measures 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 (Caballero and Toro, 2000). The number of ancestors contributing

Table 3
Descriptive statistics of the studied traits.

Item		Traits[a]					
		BW (kg)	WW (kg)	LSB	LSW	TLWB (kg)	TLWW (kg)
No. of records		4927	4191	3986	3986	3974	3371
Mean		3.64	20.80	1.56	1.32	5.81	29.90
S.D.		0.84	5.15	0.63	0.80	1.99	10.77
C.V. (%)		23.08	24.76	40.38	60.60	34.25	36.02
Min.		1.20	5.50	1	0	1.70	10
Max.		6.40	40.00	5	5	16.10	83.00
No. of sires		100	99	100	100	100	94
No. of dams		1186	1134	789	789	789	675
$F_i = 0$[b]	Lamb	533	407	792	792	790	537
	Ewe	1194	993	808	808	803	737
$0 < F_i \leq 6.25$	Lamb	1486	1259	836	836	829	787
	Ewe	1531	1354	800	800	798	740
$6.25 < F_i \leq 12.5$	Lamb	1846	1611	1478	1478	1476	1294
	Ewe	1461	1220	1642	1642	1637	1331
$12.5 < F_i \leq 25$	Lamb	968	834	818	818	817	701
	Ewe	696	586	694	694	694	533
$Fi > 25$	Lamb	94	80	62	62	62	52
	Ewe	45	38	42	42	42	30

[a] BW: birth weight; ADG: average daily gain from birth to weaning; WW: weaning weight; LSB: litter size at birth; LSW: litter size at weaning; TLWB: total litter weight at birth; TLWW: total litter weight at weaning.

[b] Range of inbreeding coefficients for lambs and ewes in a percentage basis.

to the reference population was 2.04% of the registered animals (Table 2). The half of the total genetic variation was explained only by 4 ancestors with a maximum individual contribution of 23.21%, implying the excessive use of these breeding animals.

3.3. *Effects of inbreeding on the studied traits*

A detailed statistics on the studied traits is presented in Table 3. The lowest and highest C.V. were related to BW and LSW, respectively. Estimates of the individual and maternal inbreeding depressions for all the studied traits are presented in Table 4. One percent increase in ΔF_i of the lambs significantly reduced BW by 7 g ($P < 0.05$). No significant inbreeding depressions due to ΔF_i of the lambs on the other traits were evident ($P > 0.05$). Individual increases in inbreeding of the ewes by 1%, significantly reduced WW ($P < 0.05$), BW, TLWB and TLWW ($P < 0.01$) as 62 g, 17 g, 37 g and 346 g, respectively. The interpretation of inbreeding depression when ΔF_i is considered as a linear covariate in the model can be facilitated by transforming it into the inbreeding coefficient of an individual with an average pedigree completeness applying the formula that describes the relation between ΔF_i, F_i and EqG_i (that explained in the Section 2). Average number of equivalent complete generations of the animals with records was 3.69. Considering this average equivalent complete generations, one percent of ΔF_i corresponds to F_i of 2.66%. Therefore, the estimated values for maternal inbreeding depressions of BW, WW, TLWB and TLWW would be −6.39 g, −23.31 g, −13.91 g and −130.07 g per 1% increase in inbreeding, respectively. The respective value for individual inbreeding depression of BW would be −2.63 g.

Table 4
Estimates of the regressions on direct and maternal inbreeding ± S.E.for the studied traits.

Trait[a]	Regression coefficient on individual increase in inbreeding of	
	Lamb	Ewe
BW (kg)	−0.007 ± 0.003[*]	−0.017 ± 0.003[**]
WW (kg)	−0.037 ± 0.031[ns]	−0.062 ± 0.0370[*]
LSB	−0.421 ± 0.201[ns]	0.821 ± 0.388[ns]
LSW	0.003 ± 0.003[ns]	−0.008 ± 0.004[ns]
TLWB (kg)	0.002 ± 0.010[ns]	−0.037 ± 0.012[**]
TLWW (kg)	−0.013 ± 0.056[ns]	−0.346 ± 0.066[**]

[a] For traits abbreviations see footnote of Table 3.

[*] $P < 0.05$.

[**] $P < 0.01$.

ns: $P > 0.05$;

Dorostkar et al. (2012) studied the effect of inbreeding on body weights of Iranian Moghani sheep and significant inbreeding depression was found only for body weight in 3 months of age as −291 g per 1% increase in inbreeding. Norberg and Sørensen (2007) reported significant reductions of 112, 82 and 88 g per 10% increase in lamb inbreeding for birth weight of Texel, Shropshire and Oxford Down sheep breeds, respectively. Corresponding significant reductions per 10% in ewe inbreeding were 140, 65 and 53 g in Texel, Shropshire and Oxford Down sheep breeds, respectively. The direct inbreeding depression in litter size at birth per 10% inbreeding was identified to be significant in Texel (0.032 lambs per lambing), Shropshire (0.019 lambs per lambing) and Oxford Down (0.030 lambs per lambing) sheep breeds by Norberg and Sørensen (2007). Maternal inbreeding depressions in litter size were only significant in Texel (0.023 lambs per lambing) and Oxford Down (0.035 lambs per lambing) breeds. Prod'Homme and Lauvergne (1993) reported an increased prolificacy with increasing inbreeding in a highly inbred population of Merino Rambouillet sheep during a 60-year period. They concluded that positive effects of selection and improved management on prolificacy traits were larger than the negative effect of inbreeding.

4. Conclusions

Analysis of pedigree information in Iran-Black sheep showed evidence for changes in population structure. Based on our results, the genetic variability of Iran-Black sheep was affected by both gene losses during segregation and bottlenecks. A significant increase in inbreeding rate was observed. Therefore, it seems that the mating strategies to minimize inbreeding in Iran-Black sheep were not effective. The present study confirmed the adverse effects of inbreeding on TLWW as a composite reproductive trait in ewes, which contains important traits such as pre-weaning growth and survival of lambs and also mothering ability of the ewes.

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