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Inbreeding and Inbreeding Depression on Body Weight in Iranian Shal Sheep

Research Article

Z. Patiabadi[1], S. Varkoohi[1*] and S. Savar-Sofla[2]

[1] Department of Animal Science, Faculty of Agriculture, Razi University, Kermanshah, Iran
[2] Animal Science Research Institute of Iran, Agricultural Research, Education and ExtensionOrganization (AREEO), Karaj, Iran

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*Correspondence E-mail: s.varkoohi@gmail.com

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ABSTRACT

The aim of this study was to estimate amount of inbreeding coefficient in Shal sheep and its impact on growth performance. Pedigree information and body weight at different ages (birth weight, 3 month weight, 6 month weight, 9 month weight and 12 month weight) were used from 6692 lambs from 90 rams and 1007 ewes. Data were collected on Ghazvin sheep breeding station during 1997-2013. Estimation of inbreeding coefficient was done by CFC program and quantifying the individual inbreeding regression of traits was run by wombat software. Number of inbred animals at pedigree was 1616 lambs, equal to 24.15% of total population. The average of inbreeding coefficient on whole population and inbred population were 1.51% and 6.28%, respectively. Regression coefficients per 1% inbreeding for birth weight, 3 month weight, 6 month weight, 9 month weight and 12 months weight were estimated as -0.001, -0.017, -0.005, -0.019 and -0.019 kg, respectively. The highest inbreeding coefficient was 31.25% and most of inbred animals had inbreeding coefficients lower than 5%. These results confirmed the low level of inbreeding in the population. Annual trend of inbreeding coefficient on population average was 0.07 and non significant statistically. Applying a designed mating system like crossbreeding could be a suitable method to avoid inbreeding depression.

KEY WORDS growth traits, inbred population, inbreeding depression, regression coefficients.

INTRODUCTION

Any genetic improvement programs applied for livestock are based on two main approaches: selection and crossbreeding. By contrast to crossbreeding, intensive selection within a single population reduces genetic diversity and increases the inbreeding rate (Barczak *et al.* 2009). A definition for inbreeding is given by mating of individuals whose relatedness between them is greater than the average degree of relationship existing in population and capable changing genotypic frequencies on a population without modifying the gene frequencies (Lush, 1945). The rate of inbreeding needs to be limited to maintain diversity at an acceptable level, so that genetic variation will ensure that future animals can respond to changes in the environment and to selection. Without genetic variation, animals cannot adapt to these changes (Van Wyk *et al.* 2009). Heterozygosity and allelic diversities can be lost from small, closed, selected populations at a rapid rate. The loss of diversity and resulting increase in homozygosity might result in decreased productions and / or fitness of inbred animals (Lamberson and Thomas, 1994; Ercanbrack and Knight, 1991; Analla *et al.* 1998; Dario and Bufano, 2003). Furthermore, inbreeding depression in domestic animals can lead to a decrease in selection response and in potential genetic gains in economic traits. Measuring the effect of inbreeding on productive traits is important in order to estimate the magnitude of change associated with increases in inbreeding (Negussie *et al.* 2002; Barczak *et al.* 2009).

The initial consequence of inbreeding is inbreeding depression, which reduces the performance of growth, production, health, fertility and survival traits (Fernandez and Toro, 1999). Furthermore, inbreeding depression in domestic animals can lead to a decrease in selection response and genetic gains potential on economic traits. The emergence of disorders due to recessive gene action might occur, as well. It is apparent that different breeds and populations, as well as different traits vary in their response to inbreeding. Some populations might show a very pronounced effect of increased inbreeding for a trait, whereas others might not demonstrate much of an effect (Negussie *et al.* 2002; Barczak *et al.* 2009).

Many studies have reported the rate of inbreeding and inbreeding depression in sheep. Pedrosa *et al.* (2010) reported that average of inbreeding was 2.33% in Santa Inês sheep in Brazil. Van Wyk *et al.* (2009) and Selvaggi *et al.* (2010) reported that inbreeding rates was 16% in Elsenburg Dormer sheep and 8.1% in Leccese sheep, respectively. Akhtar *et al.* (2000) showed that inbreeding depression in Hissardale sheep in Pakistan was -0.093, -0.130 and -0.190 kg for BW_6, BW_9 and BW_{12}, respectively. Dorostkar *et al.* (2012) found that inbreeding depression for body weight traits in Iranian Moghani sheep at birth, 3, 6, 9 and 12 months of age was 0.7, -0.291, -0.260, -0.180 and -0.410 kg, respectively, (per 1% increase in individual coefficient).

Therefore, inbreeding is an important parameter to monitor and control in breeding programs. The aim of this study was to evaluate the effects of inbreeding on body weight at the ages of birth (BW_0), 3 (BW_3), 6 (BW_6), 9 (BW_9) and 12 months (BW_{12}) in Iranian Shal sheep.

MATERIALS AND METHODS

Data description

Pedigree of 6692 animals from 90 sires and 1007 dams that were collected on Shal Breed Station in Ghazvin, during 1997 to 2013 years, were used to estimate inbreeding coefficients. In the pedigree, 16.40% of animals had unknown sire, 12.19% of animals had unknown dam and 12.13% both parents were unknown. Inbreeding coefficients for animals with unknown parents considered as zero. The modified algorithm of Colleau was used to estimate individuals inbreeding coefficient CFC software, (Sargolzaei *et al.* 2006). Description of pedigree is presented in Table 1.

Details of used data for estimation of inbreeding depression are given in Table 2, where the number of records is shown after editing i.e. animals with weight > weight at the same month ± 2 SD are deleted.

There were fewer records at 9 months than 6 months of age, possibly because the heavier animals at 8 or 9 months of age were sent to the market.

Table 1 Data description of the studied Shal sheep flock

Items	n	% of total	The mean of inbreeding (%)
Total number of animals	6692	100	1.51
Non inbreed	5076	75.85	0
Inbreed	1616	24.15	6.28
Number of animals with unknown sires	1098	16.40	-
Number of animals with unknown dam	816	12.19	-
Number of animals with both parents unknown (foundation animals)	812	12.13	-

Table 2 Number of observations, mean and standard deviation of traits

Items	BW_0	BW_3	BW_6	BW_9	BW_{12}
No. of records	6690	6654	6662	6599	6528
Mean body weight (kg)	4.31	20.90	34.13	47.42	60.46
Standard deviation (SD), (kg)	0.92	3.46	3.92	4.21	4.28
Coefficient of variation (CV) (%)	21.34	16.55	11.48	8.87	7.07
Minimum (kg)	1.50	9.36	18.60	30.06	42
Maximum (kg)	7.30	33.21	50.80	64.71	78.80

BW_0: birth weight; BW_3: body weight in 3 month of age; BW_6: body weight in 6 month of age; BW_9: body weight in 9 month of age and BW_{12}: body weight in 12 month of age.

Data analysis

Data were analyzed by least squares analysis of variance using the general linear model (GLM) procedure of the SAS software package (SAS, 2004). The fixed effects were including: sex of lambs in two classes (male-female), type of birth in four classes (single, twins, triplets, quadruplet), age of the dam at lambing in seven classes (2 to 8 years old) and year of birth in 17 classes (1997 to 2013), respectively.

Therefore, these effects were excluded from the final model. Moreover, the age of lambs was placed in the model as a covariate factor. By excluding or including various random effects, six univariate linear animal models were fitted for each trait. Direct additive genetic effect was presented in all models and only random effect in Model 1. Models 2 and 3 included maternal permanent environmental effect and maternal additive genetic effect, respectively.

There was an additional effect [direct-maternal genetic covariance ($\sigma_{a,m}$)] in model 4 compared to model 3. Models 5 and 6 included both maternal effects and also with and without covariance between animal effects. Six univariate models were described as below:

$y = Xb + Z_1a + e$ Model 1

$y = Xb + Z_1a + Z_3c + e$ Model 2

$y = Xb + Z_1a + Z_2m + e$ Model 3
Cov (a,m)= 0

$y = Xb + Z_1a + Z_2m + e$ Model 4
Cov (a,m)≠ 0

$y = Xb + Z_1a + Z_2m + Z_3c + e$ Model 5
Cov (a,m)= 0

$y = Xb + Z_1a + Z_2m + Z_3c + e$ Model 6
Cov (a,m)≠ 0

Where:
y: n×1 vector of observations in each considered trait.
b: vector of fixed effects with a significant effect on related traits. Overall, fixed effects were included: lamb's sex (male and female, 2 classes), year of birth (1997 to 2013, 17 classes), birth type (single, twins, triplets, quadruplet, 4 classes) and dam age (2-8 years and older ewes, 7 classes), maternal permanent environmental effects, and residual effects, respectively.
a, m, c, and e: vectors of direct genetic effects, maternal genetic effects, maternal permanent environmental effects, and residual effects, respectively. It is assumed that these random effects are normally distributed with a mean of zero and variances $A\sigma^2_a$, $A\sigma^2_m$, $I_d\sigma_c^2$ and $I_d\sigma_e^2$, respectively. Also, σ_a^2, σ_m^2, σ_c^2 and σ_e^2 are direct additive genetic variance, maternal additive genetic variance, maternal permanent environmental variance, and residual variance, respectively. A is the additive numerator relationship matrix that is created using pedigree information. I_d and I_n are identity matrices with dimensions equal to the number of dams and observations, respectively.
X, Z_1, Z_2 and Z_3: design matrices (0 and 1) that are related to fixed effects, direct additive genetic effects, maternal additive genetic effects, and maternal permanent environmental effects to observations.

Log-likelihood ratio (Log L) tests were performed to determine significant random effects and consequently the most appropriate model for each considered traits. By inclusion of a random effect in the model, a significant increase was seen in the Log L compared to the reduced model (model without this effect). However, when the difference between the values of Log L was not greater than a critical value of χ^2, the simplest model was considered to be the best model. Statistical significance for models set at 5% probability level. The best model for BW was the full model (Model 6) and for BW_3, BW_6, BW_9 and BW_{12} was model 4.

RESULTS AND DISCUSSION

With the use of dense genomic marker data it is now possible to estimate inbreeding levels using the data alone, thus avoiding the problems of incomplete pedigree and also accounting for Mendelian segregation, but we do not have data to do this. Distribution of animals in different classes of inbreeding was shown in Table 3.

Table 3 Distribution of animals in different classes of inbreeding

Classes of F	Number of animals	% of total
F=0	5076	75.84
$0 < F \leq 5$	879	13.13
$5 < F \leq 10$	318	4.75
$10 < F \leq 15$	285	4.27
$15 < F \leq 20$	70	1.04
$20 < F \leq 25$	49	0.73
$F > 25$	16	0.20

F: inbreeding coefficients.

Based on the distribution of inbreeding coefficients, the animals were divided into 7 classes of inbreeding (F=0, 0<F≤5, 5<F≤10, 10<F≤15, 15<F≤20, 20<F≤25 and F>25). Inbreeding coefficients for the animals in the founder population (year 0) and the animals brought into the flock during the period under study were considered zero because their parents were unknown and there was no pedigree information. The results showed that inbreeding among the groups, most inbred animals (13.13%) of the animals with inbreeding coefficients zero to 5 percent that these results are confirmed low levels of inbreeding in the herd. In the herd, the only 0.20 percent of all animals, inbreeding coefficient greater than 25 percent and 75.84 percent of the population has an inbreeding coefficient is zero. Accordingly the maximum number of animals were considered as the first class of inbreeding (F=0) and minimum number of animals as seventh class for all studied weights.

Descriptive statistics of inbreeding coefficients for whole population and inbred population are shown at Table 4. The mean of inbreeding coefficient in females and males were 1.40 and 1.58 %, respectively. Totally, 24.15% of animals were inbred with mean inbreeding coefficient of 6.28%.

This illustrated that low mating of close relatives was occurred in this population. Inbreeding coefficient in this study was lower than other published results (Rzewuska *et al.* 2005; Norberg and Sorenson, 2007). This estimates were higher than studies on Baluchi sheep (Mehmannavaz *et al.* 2002), Moghani sheep (Dorostkar *et al.* 2012) and other Iranian sheep breeds. These low estimates were due to low accuracy of data recording on the station made low pedigree completeness. The highest inbreeding coefficient was 31.25% and most of inbred animals had inbreeding coefficients lower than 5%. Some animals of the studied population had presented high levels of inbreeding, reflecting the intensive use of few sires. Increasing trend for mean of inbreeding in whole animals, females and males by 17 years were shown at Figure 1.

Table 4 Descriptive statistics for inbreeding coefficients for the studied population of Shal sheep

Items	All population			Inbred population		
	Female + male	Female	Male	Female + male	Female	Male
Number of animals	6692	2628	4064	1616	630	986
Mean inbreeding coefficients (%)	1.51	1.40	1.58	6.28	5.86	6.55
Standard deviation (SD) (%)	4.01	3.77	4.15	6.06	5.77	6.23
Minimum (%)	0	0	0	0.01	0.01	0.01
Maximum (%)	31.25	30.27	31.25	31.25	30.27	31.25

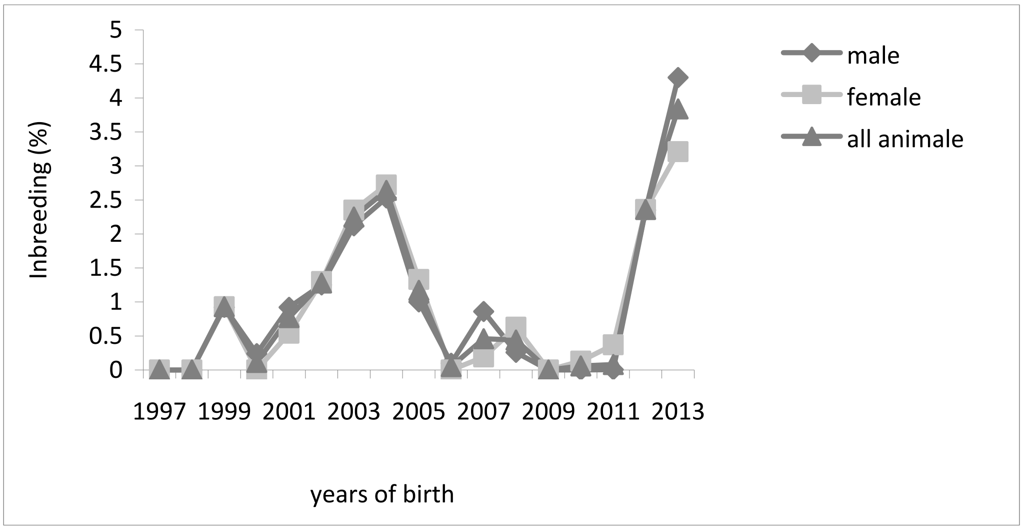

Figure 1 Annual mean of inbreeding for all, female and male animals

The proportion of inbred animals increased from zero in 1997 to 3.84 in 2013. The proportion of inbred animals in 2013 may be a cause for concern, although the average level of inbreeding was still very low. The mean of inbreeding was zero in early years of studied period. The maximum inbreeding was observed in 2013 for male animals. The increased values of inbreeding in some years may be due to poor controlling on close relative mating and excessive using of some individuals as breeding rams. Mean of inbreeding in females was zero in 2006. The mean level of inbreeding was decreased in whole animals at 2006 and 2009. The reason of this decrease was probably because of ram admittance in herd and the prevention of closed mating in sheep by the breeder by not using very few sires, and using them fairly equally. In those years, the station began to perform synchronization of ovulation and some female and male animals were imported to the station. This decrease was observed in all females and males and it could say that breeders selected non-related animals for mating. In 2010, the mean of inbreeding level for all animals was 0.06%.

This percentage was very low, but it illustrated that the mean of inbreeding had been increased compared to the base year (1997). Annual inbreeding rate for whole animals was 0.07% per year during 17 years of study.

It was observed that the average inbreeding coefficient increased due to the reason that inbred males and female individuals belonging to the same population or flock are mated together. This estimate of inbreeding rate was less than 0.40, 1.00 and 1.53% reported by Huby *et al.* (2003), Norberg and Sorenson, (2007) and Van Wyk *et al.* (2009), respectively.

Totally the inbreeding coefficient of 17 years was a non-significant and positive trend, so that in some years of decline but increase again, these fluctuations could be due to various factors such as the ram productive ewe percentage, rams herd displacement levels pedigree, the evolution of the parent changes in the number of sheep center and management methods different over the years. In this study, the average of inbreeding total sheep population Shal was born consistent throughout the year 1997 to 2013 was equal to 1.51 percent. Possibly resulting amount at causes due to lack of specific information regarding the number of parents and grandparents animals common, under-estimated. But inbreeding coefficients of inbred animals according to the number of these animals show in the population, the Sexual Intercourse of targeted largely and been controlled. Furthermore, the number of animals with high inbreeding coefficients in population indicates a lack of understanding in control mating close relatives in the population.

The result of variance analysis showed that the year of birth had significant effects on all studied traits ($P<0.01$). Sex of lamb had significant effect on all traits ($p<0.01$). The significant effect of fixed factors in these characters could be assigned partly to the differences in the endocrine system of female and male lambs. Also, age of dam had significant effect on birth weight, BW_3, BW_6, BW_9 and BW_{12} ($P<0.05$). Type of birth had a significant effect on weight changes in all traits ($P<0.01$). Single born lambs had higher body weights and pre-weaning growth rate than twins and triplets.

Due to climate conditions, feedstuff availability and ewe nutrition, especially during late pregnancy in sheep, it is expected that the birth year affects growth traits. The effect of sex and type of birth can also be caused by differences in the endocrine system, possible loci related to growth on sex chromosome and competition between twins for uterine space, milk consumption and other maternal ability compared to single-born lambs.

Single-born lambs were weighty than twins, which may be due to intense competition between twins; low milk production by ewe will not provide feed requirement of lambs and consequently they cannot express their potential capacity. It seems that increase in dam age had no effect on milk production and nursing of ewe of this breed. Nevertheless, there is a relationship between age of dam and BW because uterine environment will be better with increasing age.

Regression coefficients per 1 % increase of inbreeding for birth weight, BW_3, BW_6, BW_9 and BW_{12} were -0.001, -0.017, -0.005, -0.019 and -0.019 kg, respectively (Table 5).

Table 5 Inbreeding depression for studied traits per 1 percent increase in inbreeding coefficient

Trait	Regression coefficient of all animals (kg)
BW_0	-0.00±0.0009
BW_3	-0.017±0.0048
BW_6	-0.005±0.001
BW_9	-0.019±0.0051
BW_{12}	-0.019±0.0051

BW_0: birth weight; BW_3: body weight in 3 month of age; BW_6: body weight in 6 month of age; BW_9: body weight in 9 month of age and BW_{12}: body weight in 12 month of age.

These regression coefficients show no significant inbreeding depression. These estimates for BW were higher than -0.0005 kg estimated for Baluchi sheep (Mehmannavaz *et al.* 2002), but, lower than those was reported by some other researchers like as Van Wyk *et al.* (2009) for Dormer sheep (-0.006 kg/1% inbreeding); Dorostkar *et al.* (2012) for Moghani sheep (-0.007 kg/1% inbreeding); Mandal *et al.* (2005) for Muzaffarnagari sheep (-0.01 kg/1% inbreeding).

Also, individual regression coefficients for BW were estimated -0.0001, -0.00008 and -0.00009 kg per 1% inbreeding for Texel, Shropshire and Oxford Down, respectively (Norberg and Sorensen, 2007). Reason of variation in inbreeding coefficients could be due to differences among breeds in alleles segregating, amount of genetic variation in the base population, location, management, and diversity of the founders in the tested flock (MacKinnon, 2003).

Dorostkar *et al.* (2012) reported that inbreeding coefficient was -0.007 kg/1% inbreeding; Mandal *et al.* (2005), Mehmannavaz *et al.* (2002) and Yavarifard *et al.* (2014) reported that inbreeding effect for Muzaffarnagari, Baluchi, and Mehraban breeds are -0.048, -0.026 and -0.014 kg per 1% inbreeding, respectively; current result of this paper for BW_3 was lower than the mentioned reports.

Inbreeding depression for BW_6 and BW_9 per 1% increase in inbreeding coefficient were -0.005, -0.019 kg, respectively. Estimation of inbreeding depression for BW_6 per 1% inbreeding was -0.260 kg that reported by Dorostkar *et al.* (2012) in Moghani sheep and Akhtar *et al.* (2000) reported that -0.093 kg in Hissardale sheep; likewise, estimation of inbreeding depression for BW_9 was -0.129 kg that reported by Mandal *et al.* (2005) in Mozafarnagari sheep, -0.180 kg by Dorostkar *et al.* (2012) in Moghani sheep and -0.130 kg by Akhtar *et al.* (2000) in Hissardale sheep that was lower than result of current study.

The average of regression coefficient for body weight in 10 to 12 months age per 1% inbreeding was -0.112 kg (Mandal *et al.* 2005), -0.410 kg (Dorostkar *et al.* 2012) and -0.190 kg (Akhtar *et al.* 2000) in Mozafarnagari sheep, Moghani sheep and Hissardale sheep, respectively, which are in disagreement with the regression coefficients that found in this study (-0.019 kg % for 12 month weight).

Inbreeding is generally associated with deterioration in growth in reproductive traits in small ruminants (Lamberson and Thomas, 1994; Wocac, 2003) and level of inbreeding may be an important factor for such effects to appear. Level of inbreeding was generally low (1.51%), mainly due to periodic introduction of unrelated ewes and rams which helped in controlling the rate of increase in the level of inbreeding. Although, some of the animals introduced may be relatives, but were assumed unrelated because of lack of pedigree recording at filed level from where such animals were purchased. This may be one of the factors that resulted in estimation of low level of inbreeding in the present flock. With the exception of few years, most of the animals were always inbred across different years but level of inbreeding was low. The inbreeding may accumulate quickly for a flock of this size due mainly to small effective population size as indicted by Ilkin (1979), where inbreeding increased to 28 percent over a period of about 15 years in a flock of British Alpine goats. Increasing number of breeding males for each breeding season would help to improve the effective population size. The level of inbreeding was comparatively low in the flock under study, due mainly to twice introduction of unrelated ewes and rams during the study period. The continuous rise in the level of inbreeding over the years however, warns that matings in the future should be more planned to avoid matings of close relatives. Increase in number of breeding males and their more frequent replacement would help the level of inbreeding to be reduced.

There are several methodological and biological factors which determine the estimated inbreeding impact on performance traits. It is well known that both negative effects and positive ones exist. Hence, in a given population, »bad« and »good« inbreeding effects are mixed (Barczak *et al.* 2009). Reasons of variation in inbreeding effects could be due to differences between the breeds in allele separation, amount of genetic variation in the base population, management, and diversity of the founders of the flocks examined (MacKinnon, 2003). The inbreeding level estimates are strongly determined by the two main factors: depth and completeness of pedigree and selection intensity. Selection intensity is often increased by the reproductive technologies being focused on a few superior animals (especially sires) and the application of advanced methods of genetic evaluation. Embryo transfer and artificial insemination technology currently allow the intensive use of the same sires, leading to increase in the relationship coefficient between animals and therefore inbreeding in the population. A high inbreeding level is observed for populations rebuilt from small number of founders, but on the other hand the accuracy is strongly improved despite the incompleteness of pedigrees (Barczak *et al*. 2009).

Animal breeding emphasis on the genetic breeding values of traits as criteria for sires and dams selection can also raise the inbreeding coefficient, since relationship between animals tend to present similar genetic values, having as a consequence the selection of the most frequent relatives (Pedrosa *et al*. 2010). Breeders should be aware that inbreeding levels can increase rapidly and become a problem in their flocks, therefore, monitoring the inbreeding situation may be of benefit. The following can be used to reduce the increase in inbreeding:

1) purchasing the sires (or ewes) that are not related or only remotely related to the flock.

2) not mating close relatives such as half sibs or sire and the daughter.

3) reduction in generation interval by replacing all sires after two or three years' use and replacing older ewes with new ones.

4) reduce variation in family size by mating each ram to a similar number of ewes and selecting one ram progeny from each sire used. Artificial insemination and other developments in reproductive technology need to be used cautiously in meat sheep flocks.

This technology can lead to rapid increases in inbreeding through a dramatic reduction in effective population size within individual flocks and also within a breed as whole.

CONCLUSION

The average of inbreeding coefficient on whole population and inbred population in Iranian Shal sheep were 1.51% and 6.28%, respectively, which was comparatively low. An increasing trend for inbreeding was observed over the years. A negative effect of inbreeding was seen on all body weight ranges. Regression coefficients per 1% inbreeding for birth weight, 3 month weight, 6 month weight, 9 month weight and 12 months weight were estimated as -0.001, -0.017, -0.005, -0.019 and -0.019 kg, respectively. Although inbreeding depression was not generally a possible cause of reduction in growth performance of Iranian Shal sheep in the current situation, but caution needs to be taken in the utilization of designed mating system to maintain the level of inbreeding under control.

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