Inbreeding and Its Effects on Body Weight, Kleiber Ratio, Body Measurements, Greasy Fleece Weight and Reproductive Traits of Makooei Sheep Breed

Research Article

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ABSTRACT

A pedigree file consisting of 5860 individuals, 167 sires and 1582 dams collected at Makooei sheep breeding station (MSBS) during a period of 24 years (1990 to 2013) was used to calculate the inbreeding coefficients to reveal any probable effects of inbreeding (F) on the studied traits. The studied traits were classified to the five main groups including body weight, Kleiber ratio, body measurements, greasy fleece weight and reproductive traits. The inbreeding coefficient among the individuals ranged from 0 to 25% with an average of 0.33%, and ranged from 0 to 25% among the ewes with an average of 0.21%. Fluctuations in individual and maternal inbreeding were observed in the period under study. The average generation interval was calculated as 3.6 years. The effective population size of the flock was 51.8 animals. The rate of inbreeding was 0.08% per year and 0.53% per generation. Six different models were applied and likelihood ratio test (LRT) was used to select the appropriate model. Based on the LRT, model II was selected as appropriate model for growth, greasy fleece weight at 6 months of age and kleiber ratio traits. The traits related to the live body weight were affected negatively (P<0.001) by the quadratic individual F. The linear individual regression coefficient of the Kleiber ratio was estimated significantly (P<0.01) as 0.001, as well the linear maternal inbreeding regression was estimated significantly (P<0.05) as 0.0002. In general, body measurements were affected negatively by the quadratic effects of inbreeding (both individual and maternal) and positively by the linear effects of inbreeding. The reproductive traits were studied based on ewe inbreeding coefficient. Among the reproductive traits, the quadratic regression coefficient of conception rate was estimated significantly (P<0.05) as -0.22. Quadratic regression coefficient of litter mean weight per lamb born were estimated significantly (P<0.01) as -0.63 per 0.01 change in the ewe inbreeding coefficient. Therefore, inbreeding should be avoided, except for purposes of genetic breeding whose main objective is the fixation of certain alleles in the population.

INTRODUCTION

More than 20 indigenous sheep breeds are reared in Iran. Makooei sheep is one of the famous breeds of the country which is reared in Azerbaijan province with an approximate population size of 2.7 million heads (Abbasi and Ghafouri, 2011). Makooei is a multipurpose sheep whose main products are meat, milk and wool.

In animal breeding, active inbreeding where animals are mated according to family relatedness (inbreeding coefficient >6.25%) can be distinguished from passive inbreeding, that is the result of small effective population size (in-

breeding coefficient <6.25%). In the first case inbreeding accumulates at a faster rate and severe inbreeding depression is possible.

In the second case, inbreeding accumulates at slower rate, and natural and / or artificial selection eliminates most deleterious genes (Miglior, 2000). In general, inbreeding impairs growth, production, health, fertility and survival (Falconer and Mackay, 1996).

In the closed flocks, intensive selection reduces the genetic variability and increases the rate of inbreeding as compared to crossbreeding. Some theories have been proposed to explain the undesirable effects of inbreeding on the mean phenotypic values of traits. According to Crow and Kimura (1970), the heterozygotes generally present higher phenotypic values than the homozygotes. In contrast, Lush (1945) proposed that the desirable genes tend to be dominant or partially dominant.

On the basis of these two theories, inbreeding depression can be defined as a linear function of the inbreeding coefficient.

However, according to Lynch and Walsh (1998), if epistatic interactions are considered as a mechanism to explain the genetic basis of inbreeding depression, the decline in the phenotypic mean can be defined as a nonlinear function of the inbreeding coefficient.

Kleiber ratio is an useful approach because it does not require individual intake to be measured and allows classification of animals with high efficiency of growth relative to body size (Kleiber, 1947). Body measurement characteristics with simple genetic controls could be used as an indirect criterion in many domestic animal species to help meat yield improvement.

Body measurements beside weight measurements describe more completely an individual or population than the conventional methods of weighing and grading (Salako, 2006). Based on a report by Jafari (2014) there is a moderate to high genetic correlation between growth and body measurement traits in Makooei sheep. Regarding this fact the same response of growth and body measurement traits to the inbreeding coefficient is predicable. The inbreeding coefficients were categorized into five classes according to Queiroz et al. (2000).

The rates of inbreeding must be limited to maintain diversity at an acceptable level so that genetic variation will ensure that future animals can respond to changes in environment (Van Wyk et al. 2009).

Concerning the importance of the knowledge about the level of inbreeding, probable effects of inbreeding on studied traits and its influences on breeding decisions, the present study was aimed to determine the effect of inbreeding on growth, body measurements, fleece and reproductive traits in Makooei sheep.

MATERIALS AND METHODS

The breeding flock

Makooei sheep have been adapted to cold and highland environments. It is a medium-sized (ewe=45-48 kg, ram=51-53 kg), and fat-tailed sheep breed. The common color of its body is white and black rings are around its eyes, nose and knees. Because of the Makooei sheep's importance in Azerbaijan region economy, in 1986, Makooei Sheep Breeding Station (MSBS) was established in the city of Makoo, Western Azerbaijan, in Iran. The main goals of MSBS were protection and improvement of this sheep breed. MSBS rearing system consists mostly of extensive-migration on natural pastures in spring and summer (April to September) and semi-intensive in station rearing with barn feeding during autumn and winter (October to March). Alfalfa, barley, corn silage, concentrates, and grass are used to feed the animal during the semi-intensive rearing period. The breeding season begins in late summer and lasts until early autumn. Estrus synchronization is carried out in the flock with a progesterone-releasing intra-vaginal device (CIDR). Ewes are bred either *via* artificial insemination in the first cycle of estrus or with controlled rams in the second or third cycle of estrus. Two programs are applied to increase litter size: flushing (feeding ewes with a high-energy diet 2-3 weeks before breeding season) and equine chorionic gonadotropin (ECG) injection upon CIDR removal. Ewes are kept in the flock for a maximum of 7 parities and rams remain in the flock for 5 breeding seasons. Lambing occurs once a year, and lambing season begins in January.

Data

The pedigree file consisting of 5860 individuals, 167 sires and 1582 dams collected at MSBS during 24 years (1990 to 2013) was used in the present study (Table 1). The studied traits were classified to the five main groups including body weight, Kleiber ratio, body measurements, greasy fleece weight and reproductive traits. The live body weight traits were: birth weight (BW), weaning weight (WW=3 months weight), 6-month weight (6MW), 9-month weight (9MW), yearling weight (YW), average daily gain from birth to weaning (ADG_{0-3}). The Kleber ratio trait was Kleiber ratio from birth to weaning (KR_{0-3}). The body measurements were: height at wither (HW), height at rump (HR), body length (BL) and heart girth (HG). The greasy fleece weight traits were: greasy fleece weight at 6 months of age (GFW1) and greasy fleece weight at 18 months of age (GFW2). The reproductive traits were: conception rate (CR: with code of 1 or 0, that is whether a ewe exposed to a ram did or did not lamb), gestation length (GL: has continuous expression with a low range), number of lambs born (NLB: the number

of fully formed lambs born per ewe lambing), number of lambs alive at weaning (NLAW: the number of lambs alive at weaning, reared both by the ewe and in the nursery), litter mean weight per lamb born (LMWLB: the average weight of lambs at birth from the same parity), litter mean weight per lamb weaned (LMWLW: the average weight of lambs at weaning from the same parity). KR_{0-3} which defined as ADG_{0-3} / $WW^{0.75}$ is an indication of efficiency of feed conversion.

Statistical analysis

All known relationships among the animals were used to compute inbreeding coefficients by using according to Wright's formula:

$$F_X = [(1/2)^{n1 + n2 + 1} \times (1+F_A)]$$

The rate of inbreeding (ΔF) was estimated as the difference between the inbreeding of the individual (F_t) and the average inbreeding of the parents (F_{t-1}) divided by ($1-F_{t-1}$) (Falconer and Mackay, 1996). The effective population size (N_e) for the flock was calculated based on sex ratio by using:

$$N_e = (4N_m N_f) / (N_m + N_f)$$

Where:
N_m: the number of males.
N_f: the number of females.

The average generation interval was calculated as the mean age of the parents at the time their offspring were born.

The linear and quadratic effects of individual and maternal inbreeding (F) on the studied traits were analyzed using the GLM procedure of the SAS (2005), as well as statistical analysis to determine the significance of fixed effects on the traits. Six different univariate models were fitted for each trait.

They were different in the concept of random effect and their correlations. Maternal genetic or permanent environmental effects were taken into account by including them in appropriate models, as described by Meyer (1992).

The linear forms of six models were:

Model I: $Y_{ijklmn} = \mu + YR_i + SX_j + BT_k + AD_l + AN_m + b_1 x_{ijklmn} + b_2 x^2_{ijklmn} + e_{ijklmn}$

Model II: $Y_{ijklmno} = \mu + YR_i + SX_j + BT_k + AD_l + AN_m + PE_n + b_1 x_{ijklmno} + b_2 x^2_{ijklmno} + e_{ijklmno}$

Model III: $Y_{ijklmno} = \mu + YR_i + SX_j + BT_k + AD_l + AN_m + M_n + b_1 x_{ijklmno} + b_2 x^2_{ijklmno} + e_{ijklmno}$
($r_{am}=0$)

Model IV: $Y_{ijklmno} = \mu + YR_i + SX_j + BT_k + AD_l + AN_m + M_n + b_1 x_{ijklmno} + b_2 x^2_{ijklmno} + e_{ijklmno}$
($r_{am}\neq0$)

Model V: $Y_{ijklmno} = \mu + YR_i + SX_j + BT_k + AD_l + AN_m + PE_n + M_o + b_1 x_{ijklmnop} + b_2 x^2_{ijklmnop} + e_{ijklmnop}$
($r_{am}=0$)

Model V: $Y_{ijklmno} = \mu + YR_i + SX_j + BT_k + AD_l + AN_m + PE_n + M_o + b_1 x_{ijklmnop} + b_2 x^2_{ijklmnop} + e_{ijklmnop}$
($r_{am}\neq0$)

Where:
$Y_{ijk}\ldots$: each observation on traits under study.
μ: overall mean of population.
YR_i: 24 levels, fixed effect of year of birth i (for reproductive traits fixed effect of year of breeding i).
SX_j: 2 levels, fixed effect of sex of animal j (for reproductive traits this effect was omitted from the models).
BT_k: 3 levels, fixed effect of birth type k.
AD_l: 6 levels, fixed effect of age of dam l (for reproductive traits fixed effect of the parity of the ewe l).
AN_m: individual additive genetic effect of animal m.
PE_n: random effect of permanent maternal environment in n levels (n= number of maternal levels for each trait).
M_n: maternal genetic effect.
$X_{ijk}\ldots$: individual or maternal inbreeding coefficient of *ijklmnop*-th individual included as covariable ; b_1 and b_2 are linear and quadratic individual or maternal F regression coefficients, respectively.
$e_{ijklmnop}$: random error associated with *ijklmnop*-th observation.

In model I, the direct additive genetic, linear regression coefficient and quadratic regression coefficients of individual and maternal F were considered as the random effects. In model II, the maternal permanent environment was added to the model I as a random effect. Model III included the maternal genetic and those mentioned for model I. In model IV, the correlation between direct and maternal genetic effect was studied. Model V, the direct additive genetic, maternal genetic and maternal permanent environments were considered as the random effects beside the linear and quadratic regression coefficients of individual and maternal F. In model VI, the random effects in model V plus correlation between maternal and additive genetic were studied. The model VI was the full model. The best model was selected based on the likelihood ratio test (LRT). In LRT, the log-likelihood value of alternative model was compared with log-likelihood values of null models. LRT supposed to be distributed as chi-square (χ^2) then its degrees of freedom is differentiation between number of parameters of alternative model and null models.Statistical significance for models set at 5% probability level.

Table 1 Pedigree structure of Makooei sheep breed

	No. of animals	% of total	Average F (%)	SD (%)	SE
Total number of animals	5860	100	0.332	1.83	0.02
Non inbred	5301	90.46	0.000	-	-
Inbred	559	9.54	4.61	4.87	0.21
Sires in total	167	2.87	-	-	-
Dams in total	1582	26.99	0.210	1.70	0.02
Animals with progeny	1749	29.85	-	-	-
Animals without progeny	4111	70.15	-	-	-
Base animals	545	9.30	-	-	-
Non base animals	5315	90.70	-	-	-
Number of years	24	-	0.033	-	-

SD: standard deviation and SE: standard error.

If the LRT value was greater than a critical value from a (χ^2) distribution with appropriate degree of freedom (*df*), it can be concluded that the additional random effect had a significant effect in the model and null model was not a better model. When the differences were not significant, the null model which had fewer parameters was chosen as the appropriate model. Some genetic parameters including direct heritability (h^2) and heritability due to maternal permanent environment (C^2) were done using DFREML program (Meyer, 1989).

RESULTS AND DISCUSSION

Inbreeding

A major part of inbreeding in MSBS's flock was due to the small effective population size that can be considered as passive inbreeding coefficient. The animals with inbreeding coefficient lower than 6.25 were the main part of the inbred population (Table 2).

Descriptive statistics for individual inbreeding coefficients for the whole population and the inbred population are shown in Table 3. The mean of individual inbreeding coefficient in females and males was 0.33 and 0.29 %, respectively.

The maximum value of inbreeding coefficient (25%) indicated that some matings of close relatives occurred but the number of these matings were low. The same results have been reported for Muzaffarnagari sheep (Mandal *et al*. 2005) and Moghani sheep (Dorostkar *et al*. 2012). The inbreeding coefficient calculated in the present study was lower than those reported by Swanepoel *et al*. (2007); Norberg and Sorensen, (2007).

According to Figure 1, an increasing trend of the mean inbreeding (both individual and maternal) is observable over the 24 years.

The maximum individual and maternal F were observed in 1999 and 2002, respectively. The individual F was peaked again in 2013. The mean individual F and maternal F were zero in the early years of the studied period. The increased values of inbreeding in some years may be due to

the poor controlling of close relative matings and excessive using of some individuals as breeding rams.

The zero values of individual F in the years of 2001, 2002, 2008 and 2009 indicated that the prevention of close matings has been occurred. Fluctuations in the individual and maternal F tendency indicated that the control of inbreeding in the flock has not been managed properly. Effective population size as a criterion of the size of ideal population was calculated in average as 51.8 animals in Makooei sheep (Table 4). The maximum value of Ne accompanied with the minimum value of F (Figure 1). This would indicate that as the effective population size decreased (decreasing the hetrozygosity of alleles) the cumulative homozygosity and inbreeding is increased. Therefore, the inbreeding can be avoided by using an appropriate number of males and females in the breeding programs.

This was in agreement with other studies (Falconer and Mackay 1996; Caballero and Toro, 2000), in which an inverse relationship was observed between the effective population size and the inbreeding coefficient.

Leroy *et al*. (2013) revealed that depending on breed, species and computation method, effective population sizes may vary quite widely.

The correlation between individual and maternal inbreeding coefficient was estimated as 0.15. This value establishes a separation between the individual and maternal effects of inbreeding (Norberg and Sorensen, 2007).

In general the differences in studied traits between the categorical inbreeding levels were almost significant (Table 2). However, the effects of inbreeding based merely on inbreeding levels cannot be estimated exactly. To properly recognize the amount of probable harmfulness and / or usefulness effects of inbreeding, calculating of the numerical values of regression coefficients is essential. Along with the linear regression coefficient it is essential to consider the quadratic regression coefficient; as well (Santana *et al*. 2010). The quadratic regression coefficient clarifies the tail end of the linear regression of inbreeding coefficient on the traits. Generally, in the present study, the studied traits were affected negatively by the active inbreeding coefficients.

Table 2 Distribution of animals in different classes of individual F for studied traits

| Traits | Groups of F | | | | | | | | | |
| | F= 0 (group 1) | | 0 < F < 6.25 (group 2) | | 6.25 ≤ F < 12.5 (group 3) | | 12.5 ≤ F < 18.75 (group 4) | | F ≥ 25 (group 5) | |
	% animal	Mean	% animal	Mean	%animal	Mean	% animal	Mean	% animal	Mean
BW	89.48	4.29[a]	8.50	4.50[a]	8.50	4.50[a]	0.79	4.41[a]	0.25	3.70[b]
WW	90.17	19.69[ab]	8.00	20.40[a]	0.96	19.45[ab]	0.59	18.48[b]	0.28	16.46[c]
6MW	89.84	27.22[ab]	8.50	29.40[a]	0.85	27.70[ab]	0.50	26.09[b]	0.31	23.18[c]
9MW	90.21	28.40[ab]	8.12	30.17[a]	0.82	28.12[ab]	0.55	27.00[b]	0.30	22.96[c]
YW	89.22	33.07[a]	9.10	34.37[a]	0.85	33.61[a]	0.63	30.70[a]	0.20	29.75[a]
ADG_{0-3}	90.17	0.171[ab]	8.00	0.176[a]	0.96	0.166[ab]	0.59	0.155[bc]	0.28	0.140[c]
KR_{0-3}	90.17	0.018[a]	8.00	0.018[a]	0.96	0.017[a]	0.59	0.017[a]	0.28	0.017[a]
HW (cm)	87.00	63.20[ab]	11.00	65.00[a]	1.00	64.60[a]	0.70	60.70[b]	0.30	60.00[b]
HR (cm)	87.00	64.60[ab]	11.00	66.00[a]	1.00	66.10[a]	0.70	61.50[b]	0.30	63.00[ab]
BL (cm)	87.00	50.70[ab]	11.00	53.00[a]	1.00	52.00[ab]	0.70	49.00[b]	0.30	52.50[ab]
HG (cm)	87.00	82.00[a]	11.00	83.00[a]	1.00	81.00[a]	0.70	78.00[a]	0.30	75.70[a]
GFW1 (kg)	87.83	0.44[a]	10.00	0.46[a]	1.19	0.44[a]	0.70	0.42[a]	0.28	0.30[b]
GFW2 (kg)	89.13	1.19[abc]	9.05	1.42[a]	0.90	1.14[bc]	0.55	1.25[ab]	0.37	0.95[c]
CR (%)	93.24	88.08[a]	5.23	92.31[a]	0.64	87.50[a]	0.64	62.50[b]	0.25	66.67[b]
GL (day)	91.09	149.23[a]	7.20	149.68[a]	0.85	150.29[a]	0.61	148.80[a]	0.25	149.00[a]
NLB	93.14	1.03[a]	5.56	1.08[a]	0.65	1.00[a]	0.45	1.40[b]	0.20	1.00[a]
NLAW	93.14	0.97[a]	5.56	1.05[a]	0.65	1.00[a]	0.45	1.20[a]	0.20	1.00[a]
LMLB (kg)	93.12	4.12[a]	5.57	4.35[a]	0.65	4.27[a]	0.46	3.67[a]	0.20	3.90[a]
LMLW (kg)	92.84	19.22[a]	5.85	19.23[a]	0.71	19.59[a]	0.40	18.60[a]	0.20	18.25[a]

The means within the same column with at least one common letter, do not have significant difference (P>0.05).
BW: birth weight; WW: weaning weight; 6MW: 6months weight; 9MW: 9 months weight; YW: yearling weight; ADG_{0-3}: average daily gain from birth to weaning; KR_{0-3}: kleiber ratio from birth to weaning; HW: height at wither; HR: height at rump; BL: body length; HG: heart girth; GFW1: greasy fleece weight at 6 months of age; GFW2: greasy fleece weight at 18 months of age; CR: conception rate; GL: gestation length; NLB: number of lambs born; NLAW: number of lambs alive at weaning; LMWLB: litter mean weight per lamb born and LMWLW: litter mean weight per lamb weaned.

Table 3 Descriptive statistics for inbreeding coefficients for the studied population of Makooei sheep

| | All population | | | Inbred population | | |
	Female + male	Female	Male	Female + male	Female	Male
Animal, no	5860	3122	2738	559	299	260
Mean (%)	0.332	0.33	0.29	4.61	2.98	3.02
SD (%)	1.83	1.89	1.76	4.87	4.94	4.81
SE	0.02	0.0003	0.0003	0.21	0.003	0.003
Minimum (%)	0.00	0.00	0.00	0.003	0.012	0.003
Maximum (%)	25.00	25.00	25.00	25.00	25.00	25.00

SD: standard deviation and SE: standard error.

Table 4 Number of lambs and distribution in inbreeding classes from 1990 to 2013

Year of birth	No.	F= 0	0 < F < 6.25	6.25 ≤ F < 12.5	12.5 ≤ F < 18.75	F ≥ 25	Ne	GI
1990-1992	696	100.0	0.00	0.00	0.00	0.00	52.29	3.44
1993-1995	825	99.50	0.00	0.25	0.25	0.00	49.55	2.91
1996-1998	781	98.00	0.37	0.63	0.75	0.25	48.14	3.96
1999-2001	611	91.64	4.60	0.98	1.63	1.15	37.93	3.75
2002-2004	608	87.33	9.38	1.98	1.15	0.16	54.10	3.66
2005-2007	601	69.88	27.12	2.50	0.50	0.00	48.43	4.30
2008-2010	629	99.20	0.32	0.00	0.00	0.48	55.34	3.41
2011-2013	576	60.94	34.55	2.08	2.43	0.00	68.43	3.58

Ne: effective population size and GI: generation interval.

The rate of inbreeding was 0.08% for all animals per year during the 24 years of the period of the study. With an average generation interval of 3.6 years, it was calculated that the period from 1990 to 2013 involved approximately 6.6 generations.

The rate of inbreeding; therefore, seemed to accrue at a rate of 0.53% per generation. The rapid increase in inbreeding levels could be attributed to the declining population size and the ratio of males to females over the study period, especially in the later years.

In animal breeding, it is recommended to maintain ΔF of at most 0.5 to 1.0% per generation (Norberg and Sorensen, 2007). The annual inbreeding rate of this study was higher than the estimate of Dorostkar *et al.* (2012) and lower than those of Swanepoel *et al.* (2007) and Norberg and Sorensen (2007).

Model selection
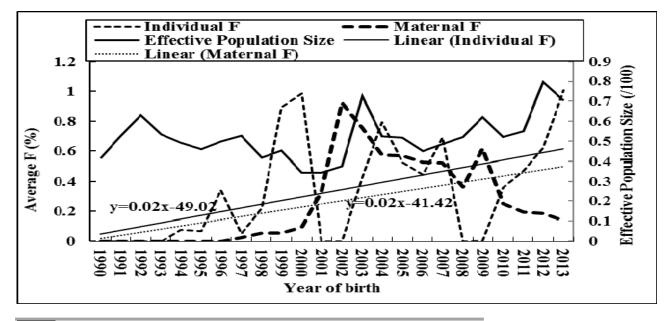Table 5 shows that the best model for growth traits, GFW1 and kleiber ratio was model II.

Figure 1 Average individual and maternal F (%) of population and effective population size by year of birth

Table 5 Linear and quadratic regression coefficients of individual and maternal F of studied traits for a 0.01 change in inbreeding

| Traits | MF | Fixed effects (mean square) | | | | Random effects | | | | h^2 | C^2 |
| | | | | | | Individual F | | Maternal F | | | |
		YR	SX	BT	AD	b_1 (S.E)	b_2 (SE)	b_1 (SE)	b_2 (SE)		
BW (kg)	II	27.44[***]	84.32[***]	429.76[***]	97.74[***]	0.166 (0.03)[***]	-0.064 (0.04)[***]	0.186 (0.366)[ns]	-0.060 (0.164)[ns]	0.27	0.10
WW (kg)	II	97.74[**]	2862.43[***]	1093.76[***]	1203.87[***]	3.978 (2.110)[ns]	-1.338 (0.950)[***]	1.192 (0.412)[*]	-0.419 (0.078)[*]	0.20	0.17
6MW	II	2149.55[***]	6552.31[***]	5332.15[***]	201.96[*]	11.513 (3.150)[**]	-3.963 (1.419)[***]	5.048 (3.725)[***]	-1.125 (1.672)[***]	0.42	0.08
9MW	II	122.65[*]	7013.60[***]	1957.49[***]	129.24[*]	8.985 (3.308)[ns]	-2.963 (1.492)[***]	-1.506 (3.684)[**]	1.263 (1.650)[ns]	0.37	0.05
YW (kg)	II	86.18[*]	2382.81[***]	660.04[***]	218.52[*]	7.986 (4.963)[ns]	-2.819 (2.273)[**]	-0.020 (5.730)[*]	1.105 (2.610)[**]	0.31	0.06
ADG_{0-3} (kg/d)	II	0.003[NS]	0.20[***]	0.90[***]	0.06[***]	0.039 (0.022)[ns]	-0.015 (0.009)[***]	0.010 (0.005)[*]	-0.004 (0.001)[*]	0.17	0.17
KR_{0-3}	II	0.0002[***]	0.0002[***]	0.0008[***]	0.0002[***]	0.001 (0.0009)[**]	-0.0004 (0.0004)[ns]	0.0002 (0.0001)[*]	0.00 (0.00)[ns]	0.15	0.09
HW (cm)	I	863.28[***]	7570.87[***]	308.07[***]	191.77[***]	9.46 (3.99)[*]	-3.21 (1.82)[***]	4.10 (2.60)[**]	-0.75 (0.09)[**]	0.20	-
HR (cm)	I	1370.65[***]	7751.62[***]	259.18[***]	186.47[**]	11.76 (3.98)[*]	-4.31 (1.82)[***]	4.98 (2.58)[***]	-1.05 (0.09)[**]	0.24	-
BL (cm)	I	1198.81[***]	1085.24[***]	135.92[*]	55.51[*]	18.10 (4.11)[***]	-6.90 (1.88)[***]	15 (4.72)[***]	-5.16 (2.15)[***]	0.10	-
HG (cm)	I	3339.55[***]	8979.89[***]	331.04[*]	49.68[ns]	10.23 (14.22)[ns]	-3.83 (6.51)[ns]	-4.73 (16.38)[ns]	2.45 (1.46)[ns]	0.14	-
GFW1 (kg)	II	29.77[***]	15.13[***]	0.15[ns]	0.61[*]	0.06 (0.07)[ns]	-0.007 (0.03)[***]	-0.12 (0.08)[ns]	0.05 (0.03)[ns]	0.20	0.06
GFW2 (kg)	I	0.80[NS]	10.86[***]	0.32[ns]	0.22[ns]	1.14 (0.31)[**]	-0.40 (0.14)[***]	0.82 (0.30)[*]	-0.32 (0.14)[*]	0.22	-
CR (%)	I	0.30[*]	-	0.12[ns]	0.14[ns]	-	-	0.55 (0.40)[ns]	-0.22 (0.18)[*]	0.07	-
GL (day)	I	20.37[*]	-	0.05[ns]	75.15[***]	-	-	1.46 (2.93)[ns]	-0.37 (1.32)[ns]	0.08	-
NLB	I	0.21[NS]	-	0.10[ns]	3.92[***]	-	-	-0.29 (0.27)[**]	0.16 (0.12)[ns]	0.03	-
NLAW	I	0.21[NS]	-	0.25[ns]	4.05[***]	-	-	0.09 (0.44)[*]	0.005 (0.20)[ns]	0.03	-
LMLB (kg)	I	8.44[***]	-	0.01[ns]	477.92[***]	-	-	1.68 (0.78)[ns]	-0.63 (0.35)[**]	0.20	-
LMLW (kg)	I	150.58[**]	-	0.17[ns]	450.12[***]	-	-	-0.43 (5.14)[ns]	0.27 (2.31)[ns]	0.12	-

BW: birth weight; WW: weaning weight; 6MW: 6months weight; 9MW: 9 months weight; YW: yearling weight; ADG_{0-3}: average daily gain from birth to weaning; KR_{0-3}: Kleiber ratio from birth to weaning; HW: height at wither; HR: height at rump; BL: body length; HG: heart girth; GFW1: greasy fleece weight at 6 months of age; GFW2: greasy fleece weight at 18 months of age; CR: conception rate; GL: gestation length; NLB: number of lambs born; NLAW: number of lambs alive at weaning; LMWLB: litter mean weight per lamb born; LMWLW: litter mean weight per lamb weaned; MF: model fitted; YR: year; SX: sex; BT: birth type; AD: age of dam; b_1: linear regression coefficient; b_2: quadratic regression coefficient; h^2: direct heritability and C^2: heritability due to maternal permanent environment.
* $P<0.05$; ** $P<0.01$ and *** $P<0.001$

Although the model I was selected for body measurement, GFW2 and reproductive traits. Then the direct additive genetic variance, maternal permanent environmental variance (so-called dam-lamb association such as uterus environment, amount of milk production, milk composition and udder conditions), linear regression coefficient, quadratic regression coefficient and residual variance were the main sources of variation for traits which are recorded in the early stages of life. In other words the younger individuals in addition to the direct additive genetic and inbreeding effects were the direct object of maternal perman-

nent environment (Safari *et al.* 2005).

Live body weight traits
Birth weight
Regarding the individual inbreeding regression, in present study, the WW and ADG_{0-3} were affected significantly ($P<0.001$) only by the quadratic regression coefficient. Concerning the birth weight Table 2 shows that among the categorical groups of individual F the group labeled as F ≥ 25 (group 5) was significantly ($P<0.05$) differ from other groups. The inbred animals with 25% or more inbreeding

coefficient were lighter by 0.59 kg than non-inbred ones. For inbreeding levels higher than 25, the losing of birth weight was 0.06 kg per 1% increasing in the inbreeding coefficient. BW was not affected significantly by both linear and quadratic regression coefficients of maternal F. For BW linear regression of individual inbreeding was estimated significantly (P<0.001) 0.17. In the Makooei sheep the birth weight losing occurred only in the range of 25% or more inbreeding coefficients. This indicates the homozygosity, in a low range, can be considered as an advantage of Makooei sheep. The individual regression coefficients of BW were estimated -0.11, -0.08 and -0.09 for Texel, Shropshire and Oxford Down, respectively (Norberg and Sorensen, 2007). Linear and quadratic regression coefficients of birth weight, weaning weight, average daily gain and kleiber ratio were studied by Van Wyk *et al*. (1993) in Elsenburg Dormer sheep. In the Van Wyk *et al*. (1993) investigation only the linear regression of individual and maternal F had a significant negative effect on the studied traits. Concerning the breed differences the appearance of inbreeding depression as linear or quadratic is predicable.

Hussain *et al*. (2006) revealed that the BW of Thalli sheep decrease 0.05 kg per 1% increasing in individual inbreeding coefficient. In the other species such as goat, Marete *et al*. (2011) revealed that the inbreeding coefficient had a positive significant effect on the birth and weaning weight. Santana *et al*. (2010) reported the linear and quadratic individual regression coefficient of 261.22 and-1122.90, respectively for Nellore cattle. Although the differences between species are notable, they follow generally almost the same manner in the field of inbreeding depression.

Weaning weight
Table 2 shows that the mean value of WW in non-inbred animals (19.69) is lower than that of calculated for inbreeding group 2, 0 < F < 6.25, (20.40). In other words the inbred individuals were by 0.71 kg superior to non-inbred ones. The inbreeding coefficients more than 6.25 (group 3, 4 and 5) affected the WW negatively (P<0.05). The linear declining of the mean values of weaning weight along with the inbreeding levels of 3, 4 and 5 are clearly visible in Table 2. The difference between group 2 (0<F<6.25) and group 5 (F>25) was 3.94 kg. In fact the losing of WW due to individual F higher than 6.25 was 0.21 kg per 1% increasing of inbreeding. Table 5 suggests no significant effects of linear regression of WW, whereas individual quadratic regression for WW was estimated -1.34. Linear and quadratic maternal regression coefficients of WW were estimated significantly (P<0.05) 1.19 and -0.42, respectively. The significant deleterious effect of inbreeding on WW was also reported for Iranian Moghani sheep (Dorostkar *et al*. 2012). Lucy *et al*.

(2007) documented that inbreeding depression may have two basic reasons: an expression of deleterious recessive alleles (partial dominance hypothesis) or the loss of favorable heterozygote combinations (over dominant hypothesis). The findings of present study were in accordance with those of Mandal *et al*. (2005); Santana *et al*. (2010).

6-month weight
Individual and maternal linear inbreeding regression of 6MW were estimated (P<0.01) 11.51 and 5.05, respectively. Table 2 shows that the inbred individuals were heavier by 2.18 kg than non-inbred ones. By introducing a quadratic regression to the model in Makooei sheep individual and maternal regressions were calculated (P<0.01) -3.96 and -1.13, respectively. This indicated that the judgement about the inbreeding depression merely based on linear regression in some breeds such as Makooei sheep is wrong. Linear and quadratic regression analysis may help us separating the useful and harmful levels of inbreeding coefficients. As a linear curve the 6-month weight was decreased along with the increasing of individual F. The mean values for group 2, 3, 4 and 5 were 29.4, 27.7, 26.1 and 23.18, respectively. Considering the group 2 and 5 the losing of body weight per 1% increase in individual F was 0.33 kg. Maternal F affected 6MW significantly (P<0.001). Linear and quadratic maternal F regressions were estimated 5.05 and -1.13, respectively. Individual and maternal linear regressions were estimated for Muzaffarnagari sheep (Mandal *et al*. 2005) -0.08 and -0.004, respectively.

9-month weight
Quadratic individual and linear maternal regressions for 9MW were estimated (P<0.01) -3.0 and -1.5, respectively. Table 2 shows the losing of 9-month weight per increasing of 1% inbreeding is 0.28 kg. Linear regression of Maternal F was calculated -1.5 for 9-month weight. Inbreeding depression of 9-month weight was estimated -0.13 by Mandal *et al*. (2005). In the mentioned research maternal inbreeding by using simple linear regression had no significant effect on 9MW. In a report by another author (Akhtar *et al*. 2000) linear regression of individual F was resulted non significantly 0.02 in Hissardale sheep. In Iranian Moghani sheep Dorostkar *et al*. (2012) revealed that the individual inbreeding coefficient had no significant effect on 9MW.

Yearling weight
Yearling weight was affected neither positively nor negatively by the low levels of individual inbreeding coefficient. Concerning maternal inbreeding YW was affected negatively (P<0.05) by the low levels of inbreeding and positively (P<0.01) by the high levels ones. Table 2 shows that the losing of YW per 1% increasing of individual F follow-

ing the 6.25% inbreeding level is 0.25 kg. Linear and quadratic regression coefficients of maternal F for YW were estimated -0.02 and 1.11, respectively. Quadratic regression coefficient of individual F for YW was estimated -2.82. The results of this study for YW were in contrast with the majority of previous studies (Akhtar *et al.* 2000; Sajjad-Khan *et al.* 2007; Maximini *et al.* 2011; Petrovic *et al.* 2012; Dorostkar *et al.* 2012).

Average daily gain from birth to weaning

ADG_{0-3} as a criterion of growth rate from birth to weaning followed the situation that has been mentioned for WW. The results of this study indicated that the active inbred animals, considering both individual and maternal F, had a declining manner in comparison with non-inbred ones. Quadratic regression coefficient of individual F for ADG_{0-3} was estimated -0.015. Mean ADG_{0-3} in non-inbred animals was 0.171 kg per day, whereas this mean was 0.140 kg for inbred animals with an individual F more than 25%. Regarding the quadratic regression of individual F, ADG_{0-3} was decreased by 0.015 kg per 1% increasing of inbreeding coefficient. Linear and quadratic regressions of Maternal F were calculated 0.01 and -0.004, respectively. The significant deleterious effects of inbreeding on growth rate were reported by Akhtar *et al.* (2000); Sajjad-Khan *et al.* (2007); Santana *et al*. (2010); Maximini *et al.* (2011); Ghavi Hossein-Zadeh (2013). Regression coefficient by using simple linear regression for pre-weaning growth rate was estimate -0.0001 by Akhtar *et al.* (2000). Maximi *et al.* (2011) reported that the losing of average daily gain in German blackhead meat sheep by using quadratic regression of individual F was 0.63 grams per 1% increasing of inbreeding coefficient. In other species Santana *et al.* (2010) reported that the quadratic regression coefficient of weight gain from weaning to 18 months of age in Nellore cattle was significantly (P<0.001) -496.10. Considering the breed, species and methodical differences different response to inbreeding is logical.

KR_{0-3}

Table 2 suggests that there is no significant difference between individual inbreeding levels. KR_{0-3} was ranged 0.017-0.018 among the population studied. According to table 5 linear regression of individual and maternal F was estimated significantly 0.001 and 0.0002, respectively. KR_{0-3} was not affected significantly by the quadratic effects of individual and maternal F. Van Wyk *et al.* (1993) reported the linear regression of individual and maternal F for kleiber ratio from birth to weaning in Elsenburg Dormer sheep -0.0002 and -0.0001, respectively. The individual regression coefficient of kleiber ratio using linear algorithm for KR_{0-3} (birth to weaning) and KR_{3-6} (weaning to 6-

month) in Iranian Moghani sheep were reported 0.014 and 0.009, respectively (Ghavi Hossein-Zadeh, 2013).

Body measurements

Table 5 shows the positive (P<0.05) effects of linear regression and negative effects of quadratic regression of both individual and maternal F on HW, HR and BL. Heart girth was not affected significantly by linear nor quadratic effects of individual and maternal F. Table 2 shows that HW, HR and BL was affected positively (P<0.05) by the passive inbreeding and negatively by the active one. Linear regression coefficients of individual F for HW, HR and BL were estimated 9.46, 11.76 and 18.10, respectively. The quadratic regression coefficients of individual F suggested that the losing of three mentioned traits was 4.31, 6.90 and 3.83 cm, respectively per 1% increasing of individual active F (Table 5). Regarding maternal active F the quadratic regression coefficients of HW, HR and BL were estimated -0.75, -1.05 and -5.16, respectively. Because of a high genetic correlation between growth and body measurement traits the losing of body measurements due to the active inbreeding may result in decreasing of mass body weight, growth rate and feed conversion efficiency. In general the animals with a large body size have an earlier sexual maturation (Salako, 2006). Regarding this fact the high levels of individual and maternal F may delay the sexual maturation of individuals. The deleterious effects of inbreeding on the body measurement traits have been reported in humans (Paddaiah and Madhavi, 2001) and horses (Gomez *et al.* 2009). To our knowledge there has been no report that has estimated the effects of inbreeding on the body measurement traits in sheep.

Greasy fleece weight traits

Table 3 shows that the individual inbreeding levels more than 25% significantly (P<0.05) result to the losing of GFW1. Quadratic regression coefficient of individual F for GFW1 was estimated significantly (P<0.001) -0.007, but linear regression coefficient of individual F, linear and quadratic regression coefficients of maternal F were not significantly different from zero. Due to the high value of wool production in the commercial aspects of a flock holder, high inbreeding coefficients may result in economic loses. GFW2 was affected positively by the passive individual and maternal F (<6.25) and negatively by the active individual and maternal F (>6.25). The linear and quadratic regression coefficients of individual F for GFW2 were estimated 1.14 and -0.40, respectively (Table 5). The results of the present study showed that the fleece weight of Makooei sheep in the maturing age (18 months of age) were more sensitive to the high levels of inbreeding than other breeds such as Elsenburg Dormer Sheep stud (Van Wyk*et*

al. 2009). This finding strengthened the advantages of passive inbreeding coefficient hypothesis. In other words individual and maternal F in the low ranges may be a useful approach to gathering the beneficial genes resulting in the promotion of the population. In a report by Ercanbrack and Knight (1991) the linear individual F had a harmful effect on fleece weight whereas the quadratic one was estimated non-significantly. In Hissardale sheep the linear regression coefficient of pre-mature fleece weight was estimated -0.0002 per 1% increasing of individual inbreeding coefficient (Akhtar *et al.* 2000).

Reproductive traits
Conception rate
The mean values of studied traits in inbred and non-inbred population are summarized in Table 2. Apparently the conception rate of inbred ewes with an inbreeding coefficient lower than 6.25% was higher than that of non-inbred ones. Concerning a significance level of 5% only the groups 4 $(12.5 \leq F < 18.75)$ and 5 $(F \geq 25)$ were negatively different from other groups (Table 2).

Therefore the lower inbreeding coefficients (or passive inbreeding) were not need to be considered as a deleterious effect on CR. The linear and quadratic regression coefficients of CR were estimated 0.55 and -0.22 per 0.01 changes in ewe F, respectively (Table 5). Quadratic equation clearly supported the positively linear and negatively quadratic effects of ewe F on CR (Table 5). The deleterious effects of inbreeding coefficients on the reproductive traits have been reported by Ercanbrack and Knight, (1991); Van Wyk *et al.* (1993); Boujenane and Chami, (1997); Akhtar *et al.* (2000); Mandal *et al.* (2005); Swanepoel *et al.* (2007). Ercanbrack and Knight (1991) demonstrated the non-significant effects of quadratic regression of CR, but the linear regression coefficients of CR for Rombouillet, Targhee and Columbia sheep were estimated -0.23, -0.01 and -0.09, respectively.

Gestation period
In the present study regression coefficients of gestation period were not significantly different from zero (Table 5). Also table 2 shows that there were no significant differences between five groups of ewe F. There are reports which show the significant effect of inbreeding in increasing the gestation period in other species such as cattle (Rollins *et al.* 1956) and pig (Farkas *et al.* 2007).

Number of lambs born
NLB as a criterion of the litter size at birth was affected negatively (P<0.01) by the linear and positively (not significantly) by the quadratic effects of ewe F. The linear and quadratic regression coefficients of NLB were calculated-

0.29 and 0.16, respectively (Table 5). In Texel, Shropshire and Oxford Down the linear regression coefficients of NLB were reported -0.032, -0.019 and -0.03, respectively (Norberg and Sorensen, 2007).

Boujenane and Chami (1997) reported non-significant effects of inbreeding coefficient of litter size at birth. Linear regression nor quadratic regression coefficient were significantly estimated for NLB in Elsenburg Dormer sheep stud (Van Wyk *et al.* 1993).

Number of lambs alive at weaning
For NLAW however table 2 proposes no significant differences between five groups studied but regarding table 5, inbred ewes produced lambs whose mortality increased linearly along with the increasing of the ewe's inbreeding. The results of present study in general were in agreement with those of (Ercanbrack and Knight, 1991; Van Wyk *et al.* 1993; Boujenane and Chami, 1997).

Litter mean weight per lamb born and weaned
LMWLB as a criterion of mass lambs weight produced by the ewe was decreased significantly (P<0.01) by 0.63 kg per 0.01 change in the ewe's inbreeding. The quadratic regression coefficient of ewe F for LMWLB was estimated significantly (P<0.01) -0.63.

Table 2 and Table 5 coordinately show that LMWLW were not affected by different levels of ewe inbreeding coefficients. The linear and quadratic regression coefficient for litter mean weight at weaning (LMWLW) were calculated (not significantly) -0.43 and 0.27, respectively. These findings were in agreement with those of Boujenane and Chami (1997). Linear regression coefficient of Sardi sheep for litter weight at 90 days of age was estimated -0.01 (Boujenane and Chami, 1997).

CONCLUSION

Despite the low level of inbreeding in Makooei sheep in this study, in general it was shown that inbreeding had significant effects on the studied traits. The results revealed that the low levels of individual or maternal F, (lower than 6.25%) can be considered as a reliable measure in gathering the promoting genes in the studied population. Inbreeding level of the flock can be maintained in a non-harmful level by using an acceptable number of males and females and/or by preventing of close relative matings. Compared to quadratic regression results, estimation of inbreeding depression based on linear regression may lead to wrong decisions about the genetic structure of the flock. To have an appropriate estimate of the deleterious effects of the inbreeding, both the individual and maternal F should be evaluated in the population.

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