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LINEAR AND QUADRATIC EFFECTS OF INDIVIDUAL AND EWE INBREEDING ON GREASY FLEECE WEIGHT AND REPRODUCTIVE TRAITS OF MAKUIE SHEEP BREED

S. JAFARI

Department of Animal Science, Faculty of Agriculture, University of Urmia, Urmia, Iran
West Azerbaijan Jihad-Agriculture Organization, Makuie Sheep Breeding Station, Maku, Iran

ABSTRACT

A pedigree file consisting of 5860 individuals, 167 sires and 1582 dams collected at Makuie 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: greasy fleece weight at 6 months of age, greasy fleece weight at 18 months of age, conception rate, gestation length, number of lambs born, number of lambs alive at weaning, litter mean weight per lamb born and litter mean weight per lamb weaned. 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 ewe 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 an appropriate model for greasy fleece weight at 6 months of age. Quadratic regression coefficients of greasy fleece weight at 6 months of age and greasy fleece weight at 18 months of age were determined as significant ($P<0.001$) - 0.007 and - 0.40, respectively per 0.01 change in the individual F. The reproductive traits were studied basing on the ewe inbreeding coefficient. Number of lambs born was affected negatively ($P<0.01$) by the linear effect of ewe F. The lambs produced by the Inbred ewes had significantly ($P<0.05$) more survival ability from birth to weaning than those produced by the non-inbred ones. The significant quadratic regression coefficient of conception rate was determined (- 0.22; $P<0.05$). Significant quadratic regression coefficient ($P<0.01$) of litter mean weight per lamb born was determined (- 0.63 per 0.01 change in the ewe inbreeding coefficient). Gestation length and litter mean weight per lamb weaned were not affected significantly by linear or quadratic effects of ewe F. Therefore, inbreeding should be avoided, except for purposes of genetic breeding, whose main objective is the fixation of certain alleles in the population.

Key words: passive inbreeding depression; active inbreeding depression; greasy fleece weight; reproductive traits

INTRODUCTION

More than 20 indigenous sheep breeds are reared in Iran. Makuie 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). Makuie 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, what is the result of small effective population size (inbreeding 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,

Correspondence: E-mail: Jafarishoja@yahoo.com
Shoja Jafari, West Azerbaijan Jihad-Agriculture Organization, Makuie Sheep Breeding Station, 58616-85961 Maku, Iran
Tel.: +984623228406 Fax: +984624222602

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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.

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 the studied traits and its influences on breeding decisions, present study was aimed to determine the effect of inbreeding on fleece (greasy fleece weight at 6 months of age and greasy weight at 18 months of age) and reproductive traits (conception rate, gestation length, number of lambs born, number of lambs alive at weaning, litter mean weight per lamb born and litter mean weight per lamb weaned) in Makuie sheep.

MATERIAL AND METHODS

The breeding flock

Makuie sheep has 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 Makuie sheep importance in Azerbaijan region economy, in 1986 the Makuie sheep breeding station (MSBS) was established in the city of Maku, Western Azerbaijan, in Iran. The main goals of MSBS were protection and improvement of this sheep breed. Base animals of MSBS were provided from the flock holders of the region. All ewes were bred to rams for the first time at an average of 18 months. The age distribution of the ewes is 18 month (parity 1) to 84 months (parity 7). Averagely 16 rams and 181 ewes have been included in the breeding program per breeding year. Estrus synchronization was carried out in the flock with a progesterone-releasing intra vaginal sponge (CIDR). The ewes were then bred either by an artificial insemination in the first cycle of estrus or using controlled rams. Flushing and equine chorion gonadotrophin (ECG) injection at CIDR removal was applied since 2000 year to increase the litter size. The ewes were kept in the flock for a maximum of 7 lambings. The rams were kept for 5 breeding seasons. In a closed flock, such as MSBS, the excessive use of superior individuals, such as breeding rams or ewes, to make the faster genetic progress could quickly result in an increase in the level of inbreeding.

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 into two main groups. Greasy fleece weight traits were: greasy fleece weight at 6 months of age (GFW1) and greasy fleece weight at 18 months of age (GFW2). 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 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). The inbreeding coefficients were categorized into five classes according to Queiroz *et al.* (2000).

Statistical analysis

All known relationships among the animals were used to compute inbreeding coefficients by using the Pedigree program (2000) according to Wright's formula:

$$F_X = \left[\left(\tfrac{1}{2}\right)^{n_1 + n_2 + 1} (1 + F_A)\right]$$

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 basing on the sex ratio using $N_e = \frac{4N_mN_f}{N_m + N_f}$ (Falconer and Mackay, 1996), where N_m is the number of males and N_f is 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 program (2005), as well as statistical analysis to determine the significance of fixed effects on the traits.

Table 1: Pedigree structure of Makuie 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	4.610	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; SE, standard error

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 into appropriate models, as described by Meyer (1992).

The linear forms of six models were:

Model I: $Y_{ijklmn} = \mu + YR_i + SX_j + BT_k + AD_l + an_m + b_{1xijklmn} + b_2x^2_{ijklm} + e_{ijklmn}$

Model II: $Y_{ijklmno} = \mu + YR_i + SX_j + BT_k + AD_l + an_m + pe_n + b_1x_{ijklmno} + b_2x^2_{ijklmno} + e_{ijklmno}$

Model III: $Y_{ijklmno} = \mu + YR_i + SX_j + BT_k + AD_l + an_m + m_n + b_1x_{ijklmno} + b_2x^2_{ijklmno} + e_{ijklmno}$
($r_{am} = 0$)

Model IV: $Y_{ijklmno} = \mu + YR_i + SX_j + BT_k + AD_l + an_m + m_n + b_1x_{ijklmno} + b_2x^2_{ijklmno} + e_{ijklmno}$
($r_{am} \neq 0$)

Model V: $Y_{ijklmnop} = \mu + YR_i + SX_j + BT_k + AD_l + an_m + pe_n + m_o + b_1x_{ijklmnop} + b_2x^2_{ijklmnop} + e_{ijklmnop}$
($r_{am} = 0$)

Model VI: $Y_{ijklmnop} = \mu + YR_i + SX_j + BT_k + AD_l + an_m + pe_n + m_o + b_1x_{ijklmnop} + b_2x^2_{ijklmnop} + e_{ijklmnop}$
($r_{am} \neq 0$),

where $Y_{ijkl....}$ each observation on traits under study; μ, overall mean of population; YR_i, 24 levels, fixed effect of the 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, 7 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; $x_{ijkl...}$, individual or ewe inbreeding coefficient of *ijklmnop*-th individual included as co-variable ; b_1 and b_2 are linear and quadratic individual or ewe F regression coefficients, respectively; $e_{ijklmnop}$, random error associated with *ijklmnop*-th observation.

In model I, the direct additive genetic was considered as the random effects; in addition to fixed and random effects an individual or ewe inbreeding coefficient was fitted as linear or quadratic covariate. 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. In Model V, the direct additive genetic, maternal genetic and maternal permanent environments were considered as the random effects; in addition to fixed and random effects an individual or ewe inbreeding coefficient was fitted as linear or quadratic covariate. 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 (x^2), then its degree of freedom is differentiation between number of parameters of alternative model and null models. Statistical significance for models set at 5 % probability level. If the LRT value was greater than a critical value from a x^2 distribution with an appropriate degree of freedom (*df*), it can be concluded that the additional random effect has 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 an appropriate model. Some genetic parameters including direct heritability (h^2), maternal heritability (m^2) and variance ratio due to permanent environmental component (C^2) were done using DFREML program (Meyer, 1989).

RESULTS AND DISCUSSION

Inbreeding

A major part of inbreeding in the 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 is 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 mating of close relatives occurred, but the number of these matings was 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) and Oravcová and Krupa (2011).

According to Figure 1, an increasing trend of the mean inbreeding (both individual and ewe) is observable over the 24 years. The maximum individual and ewe F were observed in 1999 and 2002, respectively. The individual F was peaked again in 2013. The mean individual F and ewe 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 vs. 0.33 % estimated for individual inbreeding coefficient (Table 4). The maximum value of N_e 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. In a closed flock, such as Valachian sheep, N_e was estimated to be 20.6 animals vs. 1.69 % estimated for the individual inbreeding of the whole population

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

Traits	Groups of F									
	F = 0		0 < F < 6.25		6.25 ≤ F < 12.5		12.5 ≤ F < 18.75		F ≥ 25	
	% animal	Mean	% animal	Mean	% animal	Mean	% animal	Mean	% animal	Mean
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}

Differences between two levels of the same factor with different letter are significant at P<0.05 based on Duncan's test; 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

(Oravcová and Krupa, 2011). Therefore, the inbreeding can be avoided 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), where 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 size may vary quite widely.

The correlation between individual and ewe inbreeding coefficient was estimated as 0.15. The mean value of this correlation was reported to be 0.10 in Texel, Shropshire and Oxford Down sheep (Norberg and Sorensen, 2007). This value establishes a separation between the individual and ewe 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, the 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. 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

Table 3: Descriptive statistics for inbreeding coefficients for the studied population of Makuie 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

Table 4: Number of lambs and distribution into 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; GI, generation interval

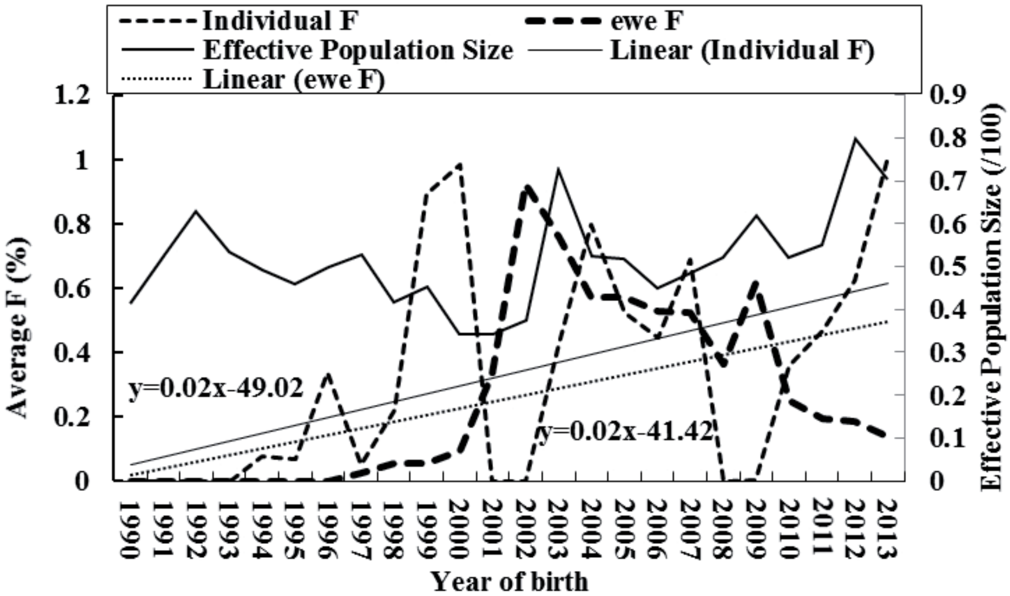

Fig. 1: Average individual and ewe F (%) of population and effective population size by year of birth

Table 5: Likelihood values of six different models for studied traits (the appropriate models are in bold faced)

Traits	MF	h^2	C^2	Log- likelihood values					
				Model I	Model II	Model III	Model IV	Model V	Model VI
GFW1 (kg)	II	0.20	0.06	1466.74	**1470.88**	1466.74	1466.74	1466.74	1466.74
GFW2 (kg)	I	0.22	-	**231.21**	231.21	231.21	231.21	231.21	231.21
CR (%)	I	0.07	-	**716.80**	716.80	716.80	716.80	716.80	716.80
GL (day)	I	0.08	-	**-998.62**	-998.62	-998.62	-998.62	-998.62	-998.62
NLB	I	0.03	-	**1199.97**	1200.78	1199.97	1199.97	1199.97	1199.97
NLAW	I	0.03	-	**676.51**	678.04	676.51	676.51	676.51	676.51
LMLB (kg)	I	0.20	-	**109.61**	109.61	109.61	109.61	109.61	109.61
LMLW (kg)	I	0.12	-	**-1550.32**	-1550.32	-1550.32	-1550.32	-1550.32	-1550.32

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; h^2, direct heritability; C^2, variance ratio due to permanent environmental component

levels could be attributed to the declining population size and the ratio of males to females over the studied 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 GFW1 was the model II. Although the model I was selected for 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

Table 6: Linear and quadratic regression coefficients of individual and ewe F of studied traits for a 0.01 change in inbreeding

Traits	MF	Fixed effects (mean square)				Inbreeding coefficient				Random effects	
						Individual F		ewe F			
		YR	SX	BT	AD	b_1 (S.E)	b_2 (S.E)	b_1 (S.E)	b_2 (S.E)	h^2	C^2
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	-

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 based on the log-likelihood ratio test; 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; C^2, variance ratio due to permanent environmental component; *, Significant at 0.05 probability level; **, significant at 0.01 probability level; ***, significant at 0.001 probability level

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 permanent environment (Safari *et al.*, 2005).

Greasy fleece weight traits

Table 2 shows that the individual inbreeding level at the value more than 25 % results in significant (P<0.05) loss of GFW1. Estimated quadratic regression coefficient of individual F for GFW1 was significantly different from zero (P<0.001; - 0.007), whilst linear regression coefficient of individual F did not significantly differ from zero. Due to the high value of wool production in the commercial aspects of a flock holder, high inbreeding coefficients may be resulted in the economic loses. GFW2 was affected positively by the passive individual F (<6.25) and negatively by the active individual F (>6.25). The linear and quadratic regression coefficients of individual F for GFW2 were estimated at 1.14 and - 0.40, respectively (Table 6). The results of the present study showed that the fleece weight of Makuie sheep at the mature age (18 months of age) was more influenced by the high levels of inbreeding than other breeds i.e. Elsenburg Dormer Sheep stud (Van Wyk *et al.*, 2009). This finding strengthened the advantages of the hypothesis of passive inbreeding coefficient. In the other words, individual F at the low ranges may be a useful approach to accumulate the beneficial genes resulting in the promotion of the population. In the report of Ercanbrack and Knight (1991) the linear individual F had a harmful effect on fleece weight, whereas the quadratic ones were estimated to be non-significant. In Hissardale sheep, the linear regression coefficient of pre-mature fleece weight was estimated to be - 0.0002 per 1 % increasing of individual inbreeding coefficient (Akhtar *et al*., 2000).

Reproductive traits

Conception rate

The mean values of studied traits in the 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≤F<18.75) and 5 (F≥25) were negatively differed from other groups (Table 2). Therefore, the lower inbreeding coefficients (or passive inbreeding) may not be considered as a deleterious effect on CR. The linear and quadratic regression coefficients of CR were estimated to be 0.55 and - 0.22 per 0.01 changes in ewe F, respectively (Table 6). The deleterious effects of inbreeding 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 effect of quadratic regression of CR, but the linear regression coefficients of CR for Rombouillet, Targhee and Columbia sheep were estimated to be - 0.23, - 0.01 and - 0.09, respectively.

Gestation period

In the present study regression coefficients for gestation period were not significantly differed from zero (Table 6). Also, table 2 shows that there were no significant differences between five ewe´s groups for F value. There are reports, which show the significant effect of inbreeding on the increase in the gestation period in other species i.e. 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´s F. The linear and quadratic regression coefficients of NLB were calculated to be - 0.29 and 0.16, respectively (Table 6). In Texel, Shropshire and Oxford Down the linear regression coefficients of NLB were reported to be - 0.032, - 0.019 and - 0.03, respectively (Norberg and Sorensen, 2007). Boujenane and Chami (1997) reported non-significant effect of inbreeding coefficient for litter size at birth. Neither linear regression nor quadratic regression coefficients were significant for NLB in Elsenburg Dormer sheep stud (Van Wyk *et al.*, 1993).

Number of lambs alive at weaning

For NLAW, however, table 2 demonstrates no significant differences between five groups studied. However, regarding table 6, 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) and 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 as significant (P<0.01) - 0.63.

Table 2 and Table 6 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) to be - 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 at - 0.01 (Boujenane and Chami, 1997).

CONCLUSION

Despite the low level of inbreeding in Makuie sheep in this study, in general it was showed that inbreeding had significant effects on the studied traits. The results revealed that the low levels of individual or ewe 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 ewe F should be evaluated in the population.

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