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RESEARCH ARTICLE

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Genetic parameters of live body weight, body measurements, greasy fleece weight, and reproduction traits in Makuie sheep breed

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Abstract

Genetic parameters of production and reproduction traits were estimated using 39,926 records from 5,860 individual progenies of 163 sires and 1,558 dams. The data were collected at Makuie Sheep Breeding and Raising Station (Maku, Iran) from 1989 through 2013. Nineteen traits were classified in four main groups: a) live body weight traits, b) body measurement traits, c) greasy fleece weight traits, and d) reproduction traits. Year of birth, lamb sex, age of dam, and birth type were considered as fixed effects in the animal model. Four different animal models that are differentiated by including or excluding maternal effects were fitted for each trait. The Akaike information criterion was used to determine the most appropriate model for each trait. Parameters were overestimated substantially when maternal effects, either genetic or environmental, were ignored from the models. By ignoring the maternal effects, the traits could be classified into three main groups: body live weight traits with high heritability (0.34-0.46), body measurement and greasy fleece weight traits with medium heritability (0.11-0.27) and reproduction traits with low heritability (0.03-0.20). The genetic correlations among the traits ranged from-0.41 to 0.99. The estimated genetic parameters may be used to set up short/long term breeding program for the selection purpose of Makuie sheep breed.

Additional key words: animal model; production traits; direct and maternal effects; heritability.

Introduction

Makuie is a breed of sheep native to Iran which is mainly found in the West Azerbaijan province. Its population is approximately 2.7 million. This breed has adapted to cold and highland environments; it has a fat-tail and medium-sized body. The animals are white in color with black rings around their eyes, nose, and feet (Jafari *et al*., 2012). They are raised primarily for meat and wool production. Their wool is coarse and is used for carpet weaving.

In order to promote and support the Makuie breed, the Makuie Sheep Breeding and Raising Station (MSBRS) was established at the city of Maku, West Azerbaijan, Iran in 1986. The base animals were purchased from regional flock holders. On average, 16 rams and 181 ewes have been considered in the breeding program every year. Estrus synchronization with a progesterone-releasing intra vaginal (CIDR) is carried out in the flock. Ewes are then bred either by artificial insemination (in the first cycle of estrus) or with controlled rams. Flushing and an equine chorion gonadotrophin (ECG) injection at CIDR

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Abbreviations used: AIC (Akaike information criterion); BL (body length); BW (birth weight); CIDR (intravaginal progesterone release device for controlled breeding); CR (conception rate); CV (coefficient of variation); DF (derivative free); ECG (equine chorion gonadotrophin); GFW (greasy fleece weight); GL (gestation length); HG (heart girth); HR (height at rump); HW (height at wither); LMWLB (litter mean weight per lamb born); LMWLW (litter mean weight per lamb weaned); MSBRS (Makuie Sheep Breeding and Raising Station); NLAW (number of lambs alive at weaning); NLB (number of lambs born); NLBA (number of lambs born alive); REML (restricted maximum likelihood); SE (sampling error); WW (weaning weight); YW (yearling weight); 6MW (6-months weight); 9MW (9-months weight).

removal time are applied to increase litter size. Ewes and rams are kept in the flock for a maximum of six parity and five breeding seasons, respectively. The dams' minimum and maximum ages at lambing are 18 and 72 months, respectively. Lambing occurs once in a year, and it starts early in the second month of winter (late January). During the pre-weaning period, lambs have access to mother's milk, and they are fed ad-lib amounts of creep feed from 15 days of age. They are weaned at 90 ± 5 days of age.

Estimating genetic parameters of local breeds is important not only for conservation purposes, but also for defining breeding objectives and programs. Live body weight, body measurements, greasy fleece weight, and reproduction traits are influenced by the individual direct genetics and the environment under which the animal is raised, as well as by the maternal genetics and the maternal environment effects (Matika *et al*., 2003). Then, implementing a full model that includes all of these effects may provide an accurate estimate of genetic parameters for the trait. Additionally, body measurements other than weight describe an individual or population more completely than conventional methods such as weighing and grading (Salako, 2006a), and these biometric characteristics or linear measurements could be used as indirect criteria of live-body weight in many domestic animals.

Reproduction traits are more complex traits that are influenced by different components including an animal's direct genetic effect and many environmental factors such as puberty, ovulation, estrus, fertilization, embryo implantation, pregnancy, parturition, lactation, and mothering ability (Snowder, 2008). Each component is controlled by direct genetic effects (Safari *et al*., 2005), but expressions of the genetic effects are affected largely by environmental factors such as season, climatic conditions, management, health, nutrition, ram to ewe breeding ratio, ewe parity, and ram libido and fertility. Because of gene-environment interaction, the genetic improvement of reproduction traits is very complicated (Snowder, 2008).

To set up an optimum design for the selection of programs, the estimation of genetic parameters for production and reproduction traits using animal models is one of the initial steps. Although the Makuie sheep population has been under selection for the last 25 years, to our knowledge, there are only a few reports on genetic estimation of production and reproduction traits of this sheep breed. The objectives of the present study are to estimate genetic parameters of production and reproduction traits and to reveal any association between these traits using bivariate analyses.

Material and methods

Genetic parameters of production and reproduction traits were estimated using 39926 records of 5860 individuals yielded from 163 sires and 1558 dams over 25 years (Table 1). The pedigree structure of the Makuie sheep breed was built up by using the pedigree program (Pedigree© 2000, vers. 1.01, Animal Science Research Institute, Department of Animal Genetic and Breeding, Karaj, Iran). The records were collected at MSBRS from 1989 through 2013. The 19 considered traits were classified into four main groups:

— Live body weight traits included birth weight (BW), weaning weight (WW, at 3-months of age), 6-month weight (6MW), 9-month weight (9MW), and yearling weight (YW).

— Body measurement traits consisted of height at wither (HW), height at rump (HR), body length (BL), and heart girth (HG) which were recorded simultaneously with yearling weight.

— Greasy fleece weight traits comprised greasy fleece weight at 16 months of age (GFW1), greasy fleece weight at 28 months of age (GFW2), and greasy fleece weight at 40 months of age (GFW3).

Table 1. Pedigree structure of the individuals used in the analysis

Item	Number
Animals in total	5860
Inbred animals	559
Sires in total	163
Dams in total	1558
Animals with progeny	1749
Animals without progeny	4111
Base animals	
Sires	99
Dams	434
Without progeny	12
Non base animals	
Sires	68
Dams	1148
Grand parents	
Grand sires	140
Grand dams	804
Great grand parents	
Great grand sires	590
Great grand dams	110

— Finally, the reproduction traits were conception rate (CR: with a code of 1 being ewe accepted the ram and 0 being ewe did not accept the ram), gestation length (GL), number of lambs born (NLB: number of fully-formed lambs born per ewe at lambing), number of lambs born alive (NLBA: number of lambs alive at day 1 of age), number of lambs alive at weaning (NLAW: number of lambs alive at weaning, reared both by the ewe and in the nursery), litter mean weight per lamb born (LMWLB: average weight of lambs at birth from the same parity), and litter mean weight per lamb weaned (LMWLW: average weight of lambs at weaning from the same parity).

Variance and covariance components of the traits were estimated based on animal model using a derivate-free (DF) restricted maximum likelihood (REML) algorithm (Meyer, 1989). Year of birth, sex of lamb, age of dam, and birth type with 25, 2, 6, and 3 levels, respectively, were considered as fixed effects in the models. For reproduction traits, year of breeding, parity of dam, sex of lamb, and type of lambing with, 25, 6, 2, and 3 levels, respectively, were considered as fixed effects in the models. Four different univariate models were fitted for each trait, and they were different in the accounting for different random effects. The basic model (I) had an individual additive genetic effect; then, maternal genetic, permanent environmental, and both effects of maternal genetic and maternal environment were added to the basic model in Model II, Model III, and Model IV, respectively, as described by Meyer (1992).

The linear forms of the four fitted models were:

Model I: $Y_{ijklmn} = \mu + YR_i + SX_j + BT_k + AD_l + AN_m + e_{ijklmn}$
Model II: $Y_{ijklmno} = \mu + YR_i + SX_j + BT_k + AD_l + AN_m + PE_n + e_{ijklmno}$
Model III: $Y_{ijklmno} = \mu + YR_i + SX_j + BT_k + AD_l + AN_m + M_n + e_{ijklmno}$
Model IV: $Y_{ijklmnop} = \mu + YR_i + SX_j + BT_k + AD_l + AN_m + PE_n + M_o + e_{ijklmnop}$

where $Y_{ijkl...}$ = each observation of an underlying trait belongs to its appropriate group; m = overall mean of population; YR_i = fixed effect of i^{th} birth year; SX_j = fixed effect of sex; BT_k = fixed effect of birth type; AD_l = fixed effect of dam age at lambing (or dam parity); AN_m = random effect of individual additive genetic effect of animal m; PE_n = random effect of permanent maternal environment; M_n = maternal genetic effect; $e_{ijkl...}$ = residual random effect of each observation. The GLM procedure of SAS (SAS, 2005) software was used to test the significance ($p < 0.05$) of the fixed effects to be considered in the animal models.

Direct heritability (h^2), maternal heritability (m^2), and variance ratio due to permanent environmental component (c^2) were estimated based on the fitted model. Akaike information criterion (AIC) (Akaike, 1974) was used to determine the most appropriate model as: $AIC_i = -2 \log L_i + 2 p_i$, where: $\log L_i$ is the maximized log likelihood of model i at convergence and p_i is the number of parameters estimated from each model; the model with the smallest AIC was chosen as the most appropriate model.

Genetic and phenotypic correlations between traits were estimated using series of bivariate models using model I.

Results and discussion

Descriptive statistics

Number of records, mean of the traits, sampling errors (SE), coefficient of variation (CV), and maximum and minimum values of records are presented in Table 2. CV as a criterion of variation was categorized into three groups: low (0-10%), medium (10-20%), and high (≥20%). Among the studied traits the lowest CV was observed for traits related to body measurements (4.70-6.56%) and GL (1.35%). Body live weight traits and reproduction traits (NLB, NLBA, LMWLB, and LMWLW) presented medium CV values (11.8-18.76%) while greasy fleece weight traits, CR, and NLAW had the highest CV values (25.43-36.49%). The relatively low CV value estimates suggest small variance among animals, more uniformity of traits, minor changes in traits by environmental qualifications, better response to selection, and other unknown factors (Salako, 2006b). The lower CVs for body measurement traits were also reported by other researchers (Fourie *et al.,* 2002; Ermias & Rege, 2003; Alfolayan *et al*., 2006; Salako, 2006b).

Fixed effects

Fixed effects along with their significance levels for each trait are presented in Table 3. The effect of birth year was significant on body live weight traits ($p < 0.05$), body measurement traits ($p < 0.001$), and GFW1 ($p < 0.05$). The significant effect of year of birth on some traits could be due to differences in management system, feed availability, disease, and climatic

Table 2. Descriptive statistics of body live weight, body measurement, greasy fleece weight, and reproduction traits of the Makuie sheep breed

Trait[x]	No. of records	Mean ± SE[y]	CV[z] (%)	Minimum	Maximum
Body live weight traits					
BW (kg)	5163	4.31± 0.60	11.80	2.00	6.50
WW (kg)	4882	19.73± 3.77	14.62	9.20	34.50
6MW (kg)	3848	27.40± 4.94	13.63	12.70	49.00
9MW (kg)	3116	28.50± 4.64	12.40	17.00	46.50
YW (kg)	2264	33.16± 5.82	12.50	18.40	59.00
Body measurement traits					
HW (kg)	2264	63.36± 4.64	4.95	48.00	76.00
HR (cm)	2264	64.81± 4.63	4.70	49.00	77.00
BL (cm)	2264	51.00± 4.83	5.90	36.00	66.00
HG (cm)	2264	81.96± 6.97	6.56	47.00	105.00
Greasy fleece weight traits					
GFW1 (kg)	2198	1.21± 0.38	25.43	0.50	3.00
GFW2 (kg)	1002	1.67± 0.52	27.63	0.80	5.00
GFW3 (kg)	1033	1.67± 0.52	26.32	0.80	3.80
Reproduction traits					
CR (%)	1242	0.88± 0.32	36.49	0.00	1.00
GL (days)	819	149.27± 2.07	1.35	142.00	157.00
NLB	1077	1.03± 0.19	17.72	1.00	3.00
NLBA	1079	1.03± 0.20	18.76	0.00	3.00
NLAW	1079	0.97± 0.32	31.25	0.00	3.00
LMWLB (kg)	1077	4.13± 0.56	12.70	1.60	6.00
LMWLW (kg)	991	19.22± 3.50	15.04	9.50	30.40

[x] BW, birth weight; WW, weaning weight; 6MW, 6 months weight; 9MW, 9 months weight; YW, yearling weight; HW, height at wither; HR, height at rump; BL, body length; HG, heart girth; GFW1, GFW2, GFW3, greasy fleece weight at 16, 28 and 40 months of age, respectively; CR, conception rate; GL, gestation length; NLB, number of lambs born; NLBA, number of lambs born alive; NLAW, number of lambs alive at weaning; LMWLB, litter mean weight per lamb born; LMWLW, litter mean weight per lamb weaned. [y] SE, sampling error. [z] CV, coefficient of variation.

condition (rate of rainfall, humidity, and temperature) that affect the quality and quantity of pasture forage and raising systems in different years. The significant effect of breeding years ($p < 0.05$) on reproduction traits can be attributed to differences in forage availability, management systems, photoperiod, and hormone changes (Zhang *et al*., 2009). These results were consistent with a report on Sabi sheep by Matika *et al*. (2003).

The effect of dam age was significant ($p < 0.05$) on body live weight traits, body measurement traits (HW, HR, and BL), GFW1, and GFW3. Young ewes tended to produce lighter lambs. Primiparous ewes are not at their mature weight and complement their growth in addition to fetus growth, and that could have affected lamb weight. It is well-known that mothering ability (*e.g.,* milk yield) increases with parity, and older ewes are usually larger in body size and produce more milk. The same results have been reported by El Fadili *et al*. (2000) on the Moroccan Timahdit breed of sheep. Ewe parity had no significant effect on CR, whereas it significantly affected ($p < 0.001$) the other reproduction traits. Ewe parity had a significant effect ($p < 0.001$) on GL. In accordance with the report of Sezenler *et al*. (2011) for Kivircik, Sakiz and Gokceada breeds of sheep, ewe parity had a significant ($p < 0.05$) on NLB. The mean of NLB in ewes in parity six was 16% more than that of primiparous ewes. Lamb mortality at birth was significantly affected ($p < 0.001$) by ewe parity. Smith (1977) reported that yearling ewes had lambs with smaller birth weights, less vigor, and higher mortality rates than older ewes.

Table 3. Analysis of variance of fixed effects fitted for body live weight, body measurement, greasy fleece weight and reproduction traits of the Makuie sheep breed

Traits[x]	Fixed effects				
	Year of birth	Age of dam	Sex of lamb	Birth type	R-square
Body live weight traits					
BW	0.0001	0.0001	0.0001	0.0001	0.30
WW	0.0007	0.0001	0.0001	0.0001	0.20
6MW	0.0001	0.0018	0.0001	0.0001	0.15
9MW	0.0098	0.0080	0.0001	0.0001	0.15
YW	0.0471	0.0016	0.0001	0.0001	0.36
Body measurement traits					
HW	0.0001	0.0004	0.0001	0.0001	0.29
HR	0.0001	0.0004	0.0001	0.0001	0.32
BL	0.0001	0.0466	0.0001	0.019	0.40
HG	0.0001	0.2825	0.0001	0.0056	0.12
Greasy fleece weight traits					
GFW1	0.0001	0.0276	0.0001	0.2680	0.15
GFW2	0.0780	0.3458	0.0001	0.2589	0.04
GFW3	0.3064	0.0003	< 0.0001	0.0574	0.14
	Year of breeding	**Parity of the ewe**	**Sex of lamb born**	**Type of lambing**	**R-square**
Reproduction traits					
CR	0.0445	0.2242	—	—	0.02
GL	0.0293	0.0001	0.0004	0.9768	0.07
NLB	0.0348	0.0001	0.6979	0.0001	0.05
NLBA	0.0433	0.0001	0.5344	0.0001	0.06
NLAW	0.0259	0.0001	0.0199	0.0001	0.08
LMWLB	0.0001	0.0001	0.0001	0.0001	0.27
LMWLW	0.0005	0.0001	0.0001	0.0001	0.10

[x] For traits, see Table 2.

Physiological characteristics and endocrinal system (type and quantity of hormone secretion, especially sex hormones) can explain the significant influences ($p < 0.001$) of sex of lamb on body live weight traits, body measurement traits, and greasy fleece weight traits. Significant effects of lamb sex on body live weight traits have been reported in various sheep breeds (Mokhtari *et al*., 2008; Aghaali-Gamasaee *et al*., 2010). The significance of lamb sex on body measurement traits was similar to that reported by Kunene *et al*. (2007) for the Zulu breed of sheep. Among reproduction traits, GL, NLAW, LMWLB, and LMWLW were significantly affected ($p < 0.05$) by the sex of lamb born. Gestation length in the ewes carrying female lambs was slightly shorter than those carrying male lambs. The mean value of GL in ewes carrying female lambs was 149 days, whereas in ewes carrying male lambs it was 150 days. These findings were in agreement with those reported by Brown (2007). NLAW, as a criterion of mortality of lambs from birth to weaning, was affected significantly ($p < 0.05$) by the sex of the lamb. In accordance with Southey *et al*. (2001) and Mandal *et al.* (2007), lamb mortality was greater among males than females in the period of birth to weaning.

The significant effect of birth type ($p < 0.05$) on body live weight and body measurement traits can be due to limited uterine space during pregnancy, nutrition of dams especially during late pregnancy (regardless of twin or triple pregnant dams), and competition for suckling between multiple birth lambs during the birth to weaning period. The greasy fleece weight traits were

Table 4. Genetic parameter estimates of live body weight, body measurement, greasy fleece weight and reproduction traits

Trait[x]	MF[y]	Model fitted[z]											
		Model I			Model II			Model III			Model IV		
		$h^2 \pm$ SE	c^2	m^2	$h^2 \pm$ SE	$c^2 \pm$ SE	m^2	$h^2 \pm$ SE	c^2	$m^2 \pm$ SE	$h^2 \pm$ SE	c^2	$m^2 \pm$ SE
BW	II	0.35±0.03	—	—	0.27±0.03	0.10±0.02	—	0.20±0.03	—	0.15±0.04	0.20±0.03	0.07	0.09±0.04
WW	II	0.41±0.04	—	—	0.23±0.04	0.15±0.02	—	0.20±0.04	—	0.20±0.05	0.20±0.04	0.15	0.04±0.05
6MW	II	0.46±0.04	—	—	0.41±0.04	0.07±0.02	—	0.20±0.04	—	0.26±0.06	0.20±0.04	0.07	0.21±0.069
9MW	II	0.43±0.04	—	—	0.40±0.04	0.05±0.05	—	0.20±0.04	—	0.23±0.07	0.20±0.04	0.05	0.19±0.07
YW	II	0.34±0.05	—	—	0.31±0.05	0.04±0.02	—	0.20±0.05	—	0.14±0.03	0.20±0.05	0.04	0.11±0.03
HW	I	0.20±0.05	—	—	0.18±0.05	0.03±0.03	—	0.10±0.05	—	0.10±0.04	0.18±0.05	0.03	0.00±0.00
HR	II	0.25±0.05	—	—	0.21±0.05	0.05±0.03	—	0.10±0.05	—	0.15±0.04	0.20±0.05	0.05	0.01±0.04
BL	II	0.11±0.03	—	—	0.09±0.03	0.06±0.03	—	0.10±0.03	—	0.01±0.03	0.09±0.03	0.06	0.00±0.00
HG	II	0.18±0.04	—	—	0.15±0.04	0.05±0.03	—	0.10±0.04	—	0.06±0.03	0.15±0.04	0.05	0.00±0.00
GFW1	II	0.27±0.08	—	—	0.22±0.08	0.07±0.06	—	0.10±0.08	—	0.17±0.09	0.20±0.08	0.07	0.01±0.01
GFW2	I	0.20±0.08	—	—	0.20±0.08	0.00±0.06	—	0.10±0.08	—	0.10±0.10	0.20±0.08	0.00	0.00±0.00
GFW3	I	0.22±0.08	—	—	0.22±0.08	0.00±0.07	—	0.10±0.08	—	0.12±0.07	0.20±0.08	0.00	0.02±0.07
CR	I	0.07±0.07	—	—	0.07±0.07	0.00±0.03	—	0.07±0.07	—	0.00±0.02	0.07±0.07	0.00	0.00±0.02
GL	I	0.08±0.07	—	—	0.08±0.07	0.00±0.07	—	0.08±0.07	—	0.00±0.05	0.08±0.07	0.00	0.00±0.05
NLB	I	0.03±0.08	—	—	0.02±0.08	0.07±0.05	—	0.03±0.08	—	0.00±0.04	0.02±0.08	0.07	0.00±0.04
NLBA	I	0.04±0.08	—	—	0.04±0.08	0.07±0.05	—	0.04±0.08	—	0.00±0.04	0.04±0.08	0.70	0.00±0.04
NLAW	I	0.03±0.08	—	—	0.02±0.08	0.10±0.06	—	0.03±0.08	—	0.00±0.03	0.02±0.08	0.10	0.00±0.03
LMWLB	I	0.20±0.06	—	—	0.20±0.06	0.00±0.02	—	0.10±0.06	—	0.10±0.06	0.20±0.06	0.00	0.00±0.06
LMWLW	I	0.12±0.05	—	—	0.12±0.05	0.00±0.03	—	0.10±0.05	—	0.02±0.02	0.12±0.05	0.00	0.00±0.02

[x] For traits, see Table 2. [y] MF, model fitted. [z] h^2, direct heritability; SE, sampling error; c^2, variance ratio due to permanent environmental component; m^2, maternal heritability.

not significantly affected by birth type. NLBA (as a criterion of lamb mortality in the first 24 hours of life) and NLAW (as a criterion of lamb mortality from birth to weaning) were significantly affected ($p < 0.001$) by type of lambing. The high mortality in twins and triplets may be explained by the fact that they have a lower energy balance than singletons (Skalski, 2003). Moreover, it also takes the ewe dam a longer time to lick and dry 2 or 3 lambs. Furthermore, the milk requirement of twins or triplets is higher than that of a single lamb, and starvation is more likely among them. The type of lambing significantly affected ($p < 0.001$) LMWLB and LMWLW; litter mean weight was lower in twins and triplets than for singles.

Heritability estimates

Body live weight traits

Estimated genetic parameters for the traits are summarized in Table 4. The estimates of direct heritability for body live weight traits were high, ranging from 0.34 to 0.46. The results of model selection based on AIC showed that the direct additive genetic, maternal permanent environment, and residual effects were notable sources of variations in the body live weight traits. Maternal permanent environment, which is the so-called dam-lamb association (Khan *et al.*, 2006), such as the uterus environment, amount of milk production, milk composition and udder conditions, significantly influenced the BW, WW, 6MW, 9MW, and YW traits. Four to fifteen percent of the variance in live body weight traits is due to maternal permanent environment. The results were in accordance with the results of Safari *et al*. (2005). The notable estimates of c^2, especially for BW and WW (0.10 and 0.15, respectively), suggest the maternal permanent environment effect on phenotypic variation among young animals should be considered.

Direct heritability estimation of BW using model I was higher than that of other breeds such as Dorper (Neser *et al*., 2001). However, h^2 was decreased to 0.27 from 0.35 using model II. The c^2 value of 0.10 indicated that one notable phenotypic variation of BW is due to the maternal permanent environment which was lower than that reported by other researchers (Neser

Table 5. Akaike information criterion (AIC) values for each model applied for the traits in Makuie sheep

Trait[x]	Model I	Model II	Model III	Model IV
BW	–2681.58	**–2721.66**	–2679.58	–2719.66
WW	14715.72	**14609.64**	14717.72	14611.64
6MW	13489.56	**13468.4**	13491.56	13470.4
9MW	10646.66	**10642.12**	10648.66	10644.12
YW	8550.76	**8549.28**	8552.76	8551.28
HW	**6074.38**	6074.98	6076.38	6076.98
HR	5937.84	**5936.72**	5939.84	5938.72
BL	5957.58	**5955.96**	5959.58	5957.96
HG	8015.48	**8014.58**	8017.48	8016.58
GFW1	–2931.48	**–2937.76**	–2929.48	–2935.76
GFW2	**–460.42**	–458.42	–458.42	–456.42
GFW3	**–562.7**	–560.7	–560.7	–558.7
CR	**–1431.6**	–1429.6	–1429.6	–1427.6
GL	**1999.24**	2001.24	2001.24	2003.24
NLB	**–2397.94**	–2397.56	–2395.94	–2395.56
NLBA	**–2290.92**	–2290.38	–2288.92	–2288.38
NLAW	–1351.02	**–1352.08**	–1349.02	–1350.08
LMWLB	**–217.22**	–215.22	–215.22	–213.22
LMWLW	**3102.64**	3104.64	3104.64	3106.64

[x] For traits, see Table 2. The best models are shown in bold.

et al., 2001) (Table 4). Considering the direct and maternal genetic effects simultaneously in the same model (model IV), the h^2, c^2, and m^2 of BW were estimated to be 0.20, 0.07, and 0.09, respectively.

The estimates of h^2 and c^2 for weaning weight using model II were 0.23 and 0.15, respectively; this was in agreement with the results of other researchers such as Mandal *et al*. (2006). The high value of c^2 for weaning weight suggests the importance of the permanent maternal environment.

Among the studied traits, the highest h^2 was estimated for 6MW. For the traits 6MW, 9MW, and YW, the permanent maternal environment effect was gradually decreased. Instead, the direct and maternal genetic effects were notable parts of the phenotypic variation for the aforementioned traits. In a study on the Sangsari sheep, another Iranian fat-tailed breed, the estimates of h^2 and c^2 for 6MW were higher than our estimates (Miraei-Ashtiani *et al*., 2007). Parameter estimates in different populations were strongly influenced by the number of progenies per dam and the number of mothers with records (Matiatis & Pollott, 2003).

Our estimates of h^2 and c^2 for 9MW were in the range of values estimated for the Kermani breed of sheep (Mokhtari *et al*., 2008). As in the estimates of 6MW, the effect of maternal permanent environment was reduced, whereas the maternal genetic was considerably more than direct genetics and permanent maternal environment (Table 4). The estimates of h^2, c^2, and m^2 for YW were in the range of those reported by Komlosi (2008).

Body measurement traits

HR was observed to be higher by 1.45 cm than HW, and it could be proposed as an advantage of the Makuie sheep due to its raising conditions and breed characteristics (Table 2). Such breeds are more suitable for mountainous conditions than non-native breeds. More height in the rear part of the body may help the animal climb in the mountains. This finding is in accordance with the results of Cam *et al*. (2010) for the Turkish Karayaka sheep breed.

According to the direct heritability estimates, body measurement traits were classified as traits with medium heritability (from 0.11 to 0.25). Based on the AIC test, Model II was recognized as the most appropriate model for HR, BL, and HG. Regarding the selected model, 5-6% of the total phenotypic variation was due to the maternal permanent environment, and 15-21% was due to the direct additive genetic. Model I was selected for HW (Table 4 and Table 5). These findings revealed that there was no significant reason to consider the maternal effects in these traits analysis as notable sources of phenotypic variation. The results were in accordance with the reports of Mandal *et al*. (2010) for body measurement traits at 12 months of age in the Muzzafarnegri breed of sheep.

Greasy fleece weight traits

Considering Model I, the direct heritability was estimated at 0.20 to 0.27 for greasy fleece weight traits (Table 4). GFW1 which was the record of younger individuals was more dependent upon maternal effects, especially maternal permanent environment. Maternal heritabilities for greasy fleece weight traits were estimated from 0.00 to 0.07 by using Model IV. Lee *et al*. (2000) reported an average heritability of 0.50 for greasy fleece weights of 1-, 2- and 3-year-old Rambouillet sheep.

Reproduction traits

The estimated genetic parameters for reproduction traits are summarized in Table 4. In accordance with the reports of Rosati *et al*. (2002) and Vatankhah *et al*. (2008), the heritability of reproduction traits ranged from 0.03 to 0.20. The mean value of direct heritability for CR on 18 estimates from different sheep breeds was 0.06 and 0.08 in reports by Fogarty (1995) and Safari *et al*. (2005), respectively. Low heritability for this trait may be due to the importance of random environmental factors and categorical expression of the trait (Matiatis & Pollott, 2003; Matika *et al*., 2003). The genetic progress for conception rate, based on traditional selection, would therefore be difficult due to the low heritability, even though CR has great economic importance. Both m^2 and c^2 for CR were estimated to be zero. The h^2 estimate of GL was lower than those reported by Zhang *et al*. (2009). A continuous trait with low heritability, such as GL, is affected largely by environmental factors (non-genetic factors), such as: year of breeding, season of breeding, ewe parity, lamb sex, type of lambing, and birth weight of lambs. Overall, the genetic parameter estimates in the present study were lower than those reported by Osinowo *et al*. (1993) and Babar (2008) for Yankasa and Lohi breeds of sheep, respectively. Table 4 shows that gestation length was not affected by the maternal effects. Considering all studied models, c^2 and m^2 for GL were estimated to be zero. The direct heritability, maternal heritability, and variance ratios due to the permanent environment were estimated to be 0.00 to 0.07 (Table 4). The results were similar to those reported by Rosati *et al*. (2002) and Vatankhah *et al*. (2008). Therefore, there is a weak possibility for genetic progress in multiple births in the Makuie sheep breed by a traditional selection method. Similar to NLB, direct heritability estimates for NLBA and NLAW were actually low. In contrast with direct heritability, the c^2 values were relatively high. These results suggest that the importance of the maternal permanent environment effect on the viability of lambs in the first 24 hours of life and birth to weaning periods. The estimates of h^2 for LMWLB and LMWLW ranged from 0.12 to 0.20. Based on AIC criterion, Model I was selected as an appropriate model for these traits. Including the direct and maternal effects simultaneously in the same model or separately in different models, the direct heritability estimates were identical. Comparatively, the high estimates of h^2 suggest that LMWLB and LMWLW may be reliable enough to be included in selection programs. The genetic parameter estimates of the two last traits were in the range of those reported by Rosati *et al*. (2002) and Vatankhah *et al*. (2008).

Correlation estimates

Series of bivariate models were used to estimate correlations between traits (Table 6). Genetic and phenotypic correlations were relatively high (from 0.32 to 0.95) among live body weight traits. Favorable positive correlations were consistently estimated among the same group of traits (Table 6). Phenotypic correlations were generally slightly lower than the corresponding genetic correlations. Just as reported by Boujenane & Hazzab (2008), genetic and phenotypic correlations were higher in adjacent weights than in non-adjacent ones. The results of the present study were consistent with reports on Sangsari sheep (0.17 to 0.99) (Miraei-Ashtiani *et al*., 2007). Among body measurement traits, genetic correlations were estimated from 0.45 to 0.99. Genetic and phenotypic correlations between live body weight and body measurement traits were estimated to be moderate to high. The highest genetic and phenotypic correlations were observed between YW and HG. Therefore, body live weight can be predicted via body measurements in pasture as reported by Atta & El Khidir (2004). The

Table 6. Estimated genetic (above diagonal) and phenotypic (below diagonal) correlations using bivarite model

	BW	WW	6MW	9MW	YW	HW	HR	BL	HG	GFW1	GFW2	GFW3	CR	GL	NLB	NLBA	NLAW	LMWLB	LMWLW
BW		0.49±0.05	0.44±0.06	0.34±0.08	0.32±0.10	0.42±0.13	0.42±0.12	–0.04±0.18	0.35±0.14	0.01±0.11	–0.15±0.18	–0.06±0.17	0.00±0.18	0.56±0.25	–0.10±0.17	–0.10±0.17	–0.11±0.20	0.64±0.13	0.27±0.22
WW	0.30		0.95±0.02	0.92±0.02	0.83±0.04	0.76±0.08	0.74±0.08	0.72±0.10	0.78±0.07	0.24±0.10	–0.18±0.17	–0.31±0.19	0.18±0.17	0.46±0.28	0.09±0.16	0.10±0.16	0.09±0.19	0.42±0.16	0.91±0.12
6MW	0.23	0.69		0.92±0.02	0.77±0.05	0.53±0.10	0.57±0.09	0.71±0.10	0.67±0.08	0.08±0.10	–0.22±0.16	–0.22±0.18	0.12±0.16	0.23±0.27	0.02±0.15	0.03±0.15	–0.01±0.17	0.36±0.15	0.86±0.13
9MW	0.19	0.64	0.73		0.87±0.03	0.67±0.10	0.68±0.08	0.64±0.11	0.71±0.08	0.13±0.11	–0.15±0.17	–0.20±0.16	0.15±0.16	0.17±0.27	0.02±0.15	0.02±0.15	–0.03±0.17	0.04±0.14	0.89±0.11
YW	0.20	0.51	0.55	0.72		0.52±0.11	0.53±0.10	0.71±0.10	0.91±0.05	0.20±0.13	0.15±0.16	0.05±0.17	0.13±0.15	0.11±0.25	0.03±0.14	0.02±0.14	0.00±0.17	0.36±0.14	0.70±0.15
HW	0.16	0.33	0.33	0.41	0.41		0.99±0.01	0.45±0.16	0.54±0.13	0.01±0.15	–0.22±0.18	–0.17±0.26	0.26±0.23	0.28±0.57	–0.04±0.29	–0.04±0.29	–0.06±0.33	0.26±0.30	0.83±0.30
HR	0.19	0.37	0.36	0.44	0.45	0.91		0.60±0.13	0.58±0.11	0.13±0.14	–0.14±0.18	–0.11±0.24	0.28±0.21	–0.07±0.42	–0.02±0.24	–0.02±0.24	0.00±0.27	0.22±0.25	0.84±0.25
BL	0.13	0.31	0.32	0.37	0.40	0.41	0.46		0.57±0.14	0.17±0.19	–0.12±0.28	–0.08±0.32	0.10±0.28	0.25±0.46	–0.02±0.32	– 0.02±0.32	–0.01±0.37	0.11±0.34	0.15±0.52
HG	0.14	0.36	0.40	0.47	0.54	0.48	0.50	0.45		0.17±0.17	0.10±0.28	0.00±0.38	0.16±0.30	–0.07±0.42	0.00±0.29	0.00±0.29	–0.01±0.32	0.48±0.28	0.59±0.31
GFW1	0.04	0.12	0.15	0.21	0.30	0.15	0.17	0.14	0.23		0.40±0.19	0.31±0.20	0.20±0.20	–0.14±0.35	0.16±0.21	0.18±0.21	0.20±0.24	–0.19±0.23	0.04±0.28
GFW2	0.05	0.06	0.00	0.01	0.09	0.00	0.03	0.06	0.09	0.24		0.60±0.19	–0.20±0.20	0.11±0.35	0.00±0.22	0.05±0.22	–0.02±0.26	–0.41±0.22	–0.10±0.31
GFW3	0.07	0.05	0.02	0.00	0.04	0.02	0.03	–0.02	0.05	0.22	0.34		–0.03±0.21	–0.03±0.41	–0.08±0.20	–0.07±0.20	–0.11±0.20	–0.14±0.22	–0.22±0.30
CR	0.02	0.06	0.03	0.04	0.05	0.02	0.02	0.05	0.00	0.06	–0.27	–0.09		–	0.58±0.17	0.58±0.17	0.38±0.23	0.51±0.28	0.12±0.82
GL	0.10	–0.01	0.02	0.00	0.00	0.03	0.06	0.01	0.06	–0.07	–0.10	0.01	–		–0.09±0.32	–0.08±0.32	–0.05±0.20	0.51±0.25	–0.19±0.45
NLB	0.00	0.03	0.06	0.06	0.05	–0.02	–0.05	0.03	0.04	0.07	–0.03	0.00	0.73	–0.05		0.84±0.08	0.42±0.17	–0.22±0.18	–0.02±0.25
NLBA	0.00	0.03	0.06	0.06	0.04	–0.02	–0.05	0.03	0.03	0.07	–0.02	0.00	0.73	–0.04	0.89		0.44±0.16	–0.22±0.18	–0.02±0.25
NLAW	0.00	0.01	0.03	0.03	0.04	0.02	0.00	0.04	0.07	0.11	–0.06	–0.04	0.61	–0.02	0.60	0.62		–0.24±0.18	–0.01±0.24
LMWLB	0.17	0.11	0.12	0.14	0.17	0.15	0.17	0.12	0.17	0.00	–0.03	–0.04	0.86	0.28	–0.30	–0.30	–0.34		0.24±0.25
LMWLW	0.09	0.19	0.22	0.25	0.23	0.18	0.20	0.13	0.21	0.00	0.00	–0.10	0.63	0.05	–0.24	–0.24	–0.23	0.37	

For traits, see Table 2.

results are almost similar to the reports on Belgian blue du Main, Suffolk, and Texel sheep (Janssens & Vandepitte, 2004) and Yankasa lambs (Yakubu, 2010). Genetic correlations among greasy fleece weight traits were estimated from 0.31 to 0.60. Similar to the values reported by Safari & Fogarty (2003), the genetic correlation between live body weight and greasy fleece weight traits were estimated to be from –0.31 ± 0.15 to 0.24 ± 0.10. The results suggest that some traits from the two different categorical groups are influenced differently by genetic and environmental effects. The correlations (both genetic and phenotypic) generally increased with age from birth to yearling weight. However, regarding the higher values of sampling errors, most of the genetic correlation estimates are negligible or low, which means that there will be low correlated response to selection. Genetic correlations were highly positive between CR and other reproduction traits, which implies that selection based on CR may not be useful due to low heritability. It could, however, be a successful approach to progress in other reproduction traits due to the high genetic correlation. As reported by Osinowo *et al*. (1993), genetic and phenotypic correlations between GL and the traits related to litter size were negative. The genetic correlations between NLB, NLBA, and NLAW were highly favorable. Selection based on NLB may be a useful approach for genetic progress in NLBA and NLAW. As reported on Lor-Bakhtiari sheep by Vatankhah *et al*. (2008), the negative estimate of genetic and phenotypic correlations between NLB, NLBA, and NLAW with LMWLB and LMWLW were also expected, because a greater number of lambs in the litter would be associated with smaller weights of each lamb at birth and at weaning. Genetic and phenotypic correlations between LMWLB and LMWLW were 0.24 and 0.37, respectively. The genetic correlations between reproduction and live body weight traits were positive and moderate in magnitude, in agreement with reports by Safari *et al*. (2005). The genetic and phenotypic correlations between greasy fleece weight traits and reproduction traits were estimated to be generally small and negative. Investigation of genetic and phenotypic correlations between reproduction and greasy fleece weight traits revealed slightly antagonistic phenomena between the two groups of traits. The small and negative correlations are negligible, but the negative correlations between GFW3, LMWLB, and LMWLW imply that selection gain in GFW3 could be reduced due to decreases in LMWLB and LMWLW.

In summary, the outcomes of AIC indicate that a notable part of the phenotypic variance was due to the maternal permanent environment, especially in younger animals. Estimated genetic parameters in the present study suggest that there is a substantial additive genetic variability for all traits in the studied population. The classification of studied traits based on direct heritability revealed that live body weight, body measurements, and greasy fleece weight traits are suitable traits to include in selection programs. The reproduction traits, due to their overall low heritability, are not reliable enough to make genetic progress via a traditional selection program. The high genetic correlation between weaning weight and yearling weight indicates that sires could be selected at an earlier age in a selection program with emphasis on meat and body size. The highly favorable correlation between body measurements and live body weights suggests that the genetic progress is simultaneously possible in body measurements and live weight traits. The negative correlation estimates among some traits suggest that researchers should be aware of the unfavorable effects of selection based on only one group of traits.

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