Genetic parameter estimates of body weight traits in Iran-Black sheep

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Abstract The objective of the current study was to estimate the genetic parameters for body weight traits at different ages in Iran-Black sheep. Data collected during a 24-year period (1984-2008) on body weight were used to model the growth trajectory and estimate genetic parameters. Studied traits were birth weight (BW), weaning weight at 3 months of age (WW), 6 months weight (6MW), 9 months weight (9MW) and yearling weight (YW). Genetic parameters were estimated using the restricted maximum likelihood (REML) procedure under univariate and multivariate animal models. Random effects were explored by fitting additive direct genetic effects, maternal additive genetic effects, maternal permanent environmental effects, the covariance between direct and maternal genetic effects and common litter effects in twelve different models for analysis of each trait. Direct heritabilities estimated for BW, WW, 6MW, 9MW and YW were 0.02, 0.14, 0.16, 0.25 and 0.34, respectively. Maternal additive genetic variance had significant effects on the expression of body weights from birth to six months of age; resulting in values of 0.24, 0.02 and 0.09 for maternal heritability of BW, WW and 6MW, respectively. Maternal permanent environmental effects were only significant for BW, WW and 9MW leading to estimates of 0.09, 0.13 and 0.08 for maternal permanent environmental variance as a proportion of phenotypic variance (c^2) for these traits, respectively. The magnitude of the ratio of common litter variance to phenotypic variance (l^2) was 0.24 and 0.13 for BW and 6MW, respectively. The present study showed the importance of inclusion of maternal effects in designing appropriate breeding programs for genetic improvement in Iran-Black lambs for body weight.

Keywords: heritability, genetic correlation, growth traits, sheep.

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Introduction

Iran-Black sheep is a composite breed, synthesized from the cross between Baluchi and Chios sheep in Iran. This breed is well adapted to the dry and harsh conditions. Development of a new breed of sheep is a suitable tool for faster genetic improvement and increasing the efficiency of a production system. Body weight of lambs at different ages has deterministic effects on the profitability of sheep breeding enterprises. Selection of the best animals, based on breeding values for body weight traits at different ages, might increase meat production. However, this requires accurate estimates of genetic parameters for economic traits. Thus, estimation of (co)variance components is the perquisite for designing breeding programs and genetic improvement systems. Heritability of a trait is not a constant parameter and is different between breeds and for each breed during different generations. Several genetic parameters have been estimated for body weight traits in native Iranian sheep breeds (Yazdi et al., 1997; Miraei-Ashtiani et al., 2007; Rashidi et al., 2008; Mokhtari et al., 2008; Mohammadi et al., 2010; Jafaroghli et al., 2010; Mohammadi et al., 2011), but, there is no published report on the estimation of genetic parameters for body weight traits in this composite sheep breed in Iran. Therefore, the main objective of the present study was to estimate (co)variance components and corresponding genetic parameters for live weights of Iran-Black sheep at various ages.

Materials and methods

Flock history, management and data collection

The breeding project commenced in the Sheep Breeding Station of Abbasabad, located in Khorasan Razavi province, north-east of Iran, aimed at improving the litter size, weaning weight, wool quality, and tolerance to harsh and unfavorable environmental conditions in Baluchi sheep. The project was started in 1975, and performance recording in 1984. The genetic composition of Iran-Black sheep was 50% Baluchi and 50% Chios gene pool. During the breeding season, late August to late October; maiden ewes at approximately 18-month of age were exposed to fertile rams. The ewes in heat were detected by teaser rams. Annually, 10-12 rams were randomly allocated to mate with about 20-25 ewes per ram, with sire identification recorded. Ewes were kept in the flock for a maximum of 7 parities (until 8 years of age) and rams for a 2 or 3 mating seasons. Annually, 20% and 40%, of ewes and rams were replaced, respectively. Lambing occurred in late January to late March. Newborn lambs were ear-tagged and weighed. The ewes and their lambs were kept in separate pens for a few days depending on litter size and rearing ability of the ewe. Lambs were fed on natural pastures, mainly Festuca and Poa, and reared together until weaning; approximately at three months of age. The lambs were weaned on the same day, but not necessarily at the same age. During spring and summer, the sheep had access to the available pasture and in autumn they grazed on wheat and barley stubble. The lambs were kept indoors and stall- fed during winter. Supplementary feeding was offered during winter and late pregnancy, consisting of a ration composed of wheat and barley straw, alfalfa hay, dry sugar beet pulp and concentrate.

Data used in the present study were collected during a 24-year period from 1984 to 2008. The studied traits were body weights of the lambs at birth (BW), 3 months of age as weaning weight (WW), 6 months of age (6MW), 9 months of age (9MW) and yearling age (YW). The structure and descriptive statistics are presented in Table 1.

Statistical analysis

Preliminary analyses were performed, using the general linear model (GLM) procedure of SAS (SAS Institute, 1989), to determine the significance of the fixed effects to be included in the operational model for each trait. The significant fixed effects in the analytical model were lamb gender (male or female), year of birth in 24 classes (1984–2008), dam age at lambing in 7 classes (2 to 8 years old), birth type in 4 classes (single, twin, triplet and quadruplet) and lamb age at 3, 6, 9 and 12 months (in days) as a linear covariate for WW, 6MW, 9MW and YW, respectively. The interactions between fixed effects were not significant and therefore excluded from the models.

(Co)variance components and the corresponding genetic parameters were obtained by the restricted maximum likelihood (REML) procedure, using a derivative free approach under twelve univariate animal models using WOMBAT software (Meyer, 2010). The tested models in matrix notation were:

$y = Xb+Z_a a+e$		Model 1
$y = Xb+Z_a a+Z_c c+e$		Model 2
$y = Xb+Z_a a+Z_m m+e$	Cov (a,m) = 0	Model 3
$y = Xb+Z_a a+Z_m m+e$	Cov (a,m) = $A\sigma_{am}$	Model 4
$y = Xb+Z_a a+Z_m m+Z_c c+e$	Cov (a,m) = 0	Model 5
$y = Xb+Z_a a+Z_m m+Z_c c+e$	Cov (a,m) = $A\sigma_{am}$	Model 6
$y = Xb+Z_a a+Z_l l+e$		Model 7
$y = Xb+Z_a a+Z_c c+Z_l l+e$		Model 8
$y = Xb+Z_a a+Z_m m+Z_l l+e$	Cov (a,m) = 0	Model 9
$y = Xb+Z_a a+Z_m m+Z_l l+e$	Cov (a,m) = $A\sigma_{am}$	Model 10
$y = Xb+Z_a a+Z_m m+Z_c c+Z_l l+e$	Cov (a,m) = 0	Model 11
$y = Xb+Z_a a+Z_m m+Z_c c+Z_l l+e$	Cov (a,m) = $A\sigma_{am}$	Model 12

where y is a vector of observations on the trait; b, a, m, c, l and e are vectors of fixed, direct genetic, maternal genetic, maternal permanent environmental, common litter and the residual effects, respectively; X, Z_a, Z_m, Z_c and Z_l are design matrices relating observations to the fixed, direct additive genetic, maternal additive genetic, maternal permanent environmental and common litter effects, respectively.

It was assumed that direct additive genetic, maternal additive genetic, maternal permanent environmental, common litter and residual effects to be normally distributed with mean of zero and variance of $A\sigma^2_a$, $A\sigma^2_m$, $I_d\sigma^2_c$, $I_l\sigma^2_l$ and $I_n\sigma^2_e$, respectively; where, σ^2_a, σ^2_m, σ^2_c, σ^2_l and σ^2_e are direct additive genetic, maternal additive genetic, maternal permanent environmental (half sibs across years), common litter (full sibs within year) and the residual variance components, respectively. "A" is the additive numerator relationship matrix, I_d, I_l and I_n are identity matrices that have order equal to the number of the dams, litters and number of the records, respectively, and σ_{am} refers to the covariance between direct genetic and maternal additive genetic effects.

The Akaike information criterion (AIC) was used to determine the most appropriate model for estimating the (co)variance components for each trait (Akaike, 1974):

$$AIC_i = -2 \log L_i + 2 p_i \quad (1)$$

where, log L_i is the maximized log likelihood of the model at convergence and p_i is the number of parameters obtained from each model; model with the lowest AIC was chosen as the most appropriate model. Total heritability was estimated according to Willham (1972):

$$h^2 t = \sigma^2_a + 0.5\sigma^2_m + 1.5\sigma^2_{a,m}/\sigma^2_P \quad (2)$$

Table 1. Summary of descriptive statistics for the studied traits

Traits [a]	No. of records (lambs)	Mean (kg)	S.D. [b] (kg)	No. of dams	No. of sires	Average no. of records per dam	Average no. of records per sire	No. of dams with records	No. of sires with records
BW	4962	3.65	0.83	1194	100	4.15	49.62	1042	85
WW	3962	20.83	5.16	1071	95	3.70	41.70	912	79
6MW	3389	30.23	6.12	1015	94	3.34	36.05	856	80
9MW	2942	33.33	5.76	969	93	3.03	31.63	820	80
YW	2714	39.30	6.97	948	93	2.86	29.18	799	80

Maternal repeatability across year for ewe performance (tm) was calculated as follows:

$$t_m = 1/4\sigma^2_a + \sigma^2_m + c^2 + (m\, r_{a,m}h) \quad (3)$$

Genetic and phenotypic correlations were estimated using multivariate analysis, applying the most appropriate models based on the univariate analyses. The fixed effects included in the multivariate animal model were those significant in univariate analyses. When the value of -2 log likelihood variance in the AIREML function was below 10^{-8}; it was assumed that convergence had been achieved.

Results and discussion

Fixed effects

Approximately 20.2 % of the lambs deceased from birth to weaning age. Frequencies of single, twin, triplet and quadruplet birth were 31.0%, 58.0%, 8.8% and 2.2%, respectively. The least squares means (± SE) of BW, WW, 6MW, 9MW and YW were 3.33 ± 0.03, 19.72 ± 0.23, 29.12 ± 0.30, 31.95 ± 0.29 and 37.75 ± 0.31, respectively. All body weight traits were significantly influenced by lamb gender, type of birth, age of dam and year of birth ($P < 0.01$). Lamb age, as a covariate, significantly impacted on WW, 6MW, 9MW and YW.

Model comparison

Model comparison for determination of the most appropriate model for each trait was done using AIC test (Table 2). The most appropriate model for BW was the model containing the direct additive genetic, maternal additive genetic, maternal permanent environmental and common litter effects, ignoring the covariance between direct additive and maternal additive genetic effects (Model 11). The most appropriate model for WW was similar to that of BW, ignoring common litter effects (Model 5). The most suitable model for 6MW was the model containing the direct additive genetic, maternal additive genetic and common litter effects without taking into account the covariance between direct additive and maternal additive genetic effects (Model 9). Model 2, with the direct additive genetic and maternal permanent

Table 2. AIC values a for studied traits under different models with the best model in bold face

Models	Traits[b] BW	WW	6MW	9MW	YW
Model 1	579.38	3774.93	42.76	21.55	**0.00**
Model 2	209.88	703.20	17.07	**0.00**	1.87
Model 3	187.06	727.32	23.63	12.34	6.48
Model 4	189.01	715.95	15.90	6.64	4.54
Model 5	171.73	**0.00**	18.00	1.998	3.87
Model 6	173.22	5.29	13.29	1.69	1.71
Model 7	230.20	766.39	20.32	22.33	8.95
Model 8	37.24	707.75	7.02	6.68	7.77
Model 9	6.52	1012.66	**0.00**	17.27	10.96
Model 10	5.77	1004.22	9.00	9.83	3.55
Model 11	**0.00**	987.06	7.45	8.68	9.77
Model 12	0.55	985.24	2.45	8.41	7.48

[a] As deviations from the model with the lowest AIC value.
[b] For trait abbreviations see footnote to Table 1.

Table 3. Genetic parameter estimate [a] for studied traits fitting the most appropriate model

Trait [b]	Model	$h^2_a \pm S.E.$	$h^2_m \pm S.E.$	$c^2 \pm S.E.$	$l^2 \pm S.E.$	h^2t	t_m	σ^2_P
BW	11	0.02 ± 0.01	0.24 ± 0.04	0.09 ± 0.03	0.24 ± 0.02	0.14	0.34	0.49
WW	7	0.14 ± 0.04	0.02 ± 0.02	0.13 ± 0.02	-	0.15	0.19	16 59
6MW	9	0.16 ± 0.05	0.09 ± 0.02	-	0.13 ± 0.02	0.20	0.13	25.72
9MW	2	0.25 ± 0.05	-	0.08 ± 0.02	-	0.25	0.13	21.99
YW	1	0.34 ± 0.04	-	-	-	0.34	0.09	28.38

[a] h^2_a: direct heritability; h^2_m: maternal heritability; c^2: ratio of maternal permanent environmental effects to phenotypic variance; l^2: ratio of common litter effects to phenotypic variance; *S.E.*: standard error; h^2t: total heritability = (h^2_a +0.5 h^2_m +1.5σa,m) / σ^2_P ; tm = (1/4 h^2_a + h^2_m + c^2+m r_{am} h), σ^2_P: phenotypic variance

[b] For trait abbreviations see footnote to Table 1

environmental effects as significant random effects, was the most suitable model for 9MW. Maternal effects had no effect on YW, resulting in selection of the simplest model, which included direct additive genetic effects as the sole random effects for YW.

Estimates of genetic parameters under univariate analysis

Genetic parameter estimates, based on the best model under univariate analyses, are presented in Table 3. Direct heritability values were low (BW) to moderate (YW), with estimates increasing with age. Birth weight had a moderate maternal heritability but the value of maternal heritability for WW and 6MW was low. The maternal environmental components were low for BW, WW, 6MW and 9MW. Litter effects were moderate for BW and low for 6MW.

Direct heritability estimates increased by age, implying greater expression of animals own genetic potential with the advancement of age (Yazdi et al., 1997). Estimation of direct heritability depends on model of analysis and ignoring maternal effects, probably resulting in an overestimation of variance components and corresponding genetic parameters (Duguma et al., 2002).

Birth weight is a trait of potential economic importance due to its influence on lamb survival and preweaning growth rate and promotion of economic success in any sheep breeding system (Al-Shorepy, 2001). The low estimated direct heritability for BW was in agreement with that published by Jafaroghli et al. (2010). This result showed that a slow genetic progress may be obtained for this trait by selection. Such low direct heritability is possibly due to the inclusion of maternal effects in the selected model.

The estimated direct heritability values for WW and 6MW were similar in magnitude. Estimated values for direct heritability of WW were in agreement with other estimates (Miraei-Ashtiani et al., 2007; Gowane et al., 2010; Mohammadi et al., 2011), and that for 6MW is in agreement with result reported by Vatankhah and Talebi (2008) in Lori-Bakhtiari sheep and Abegaz et al. (2005) in Horro sheep.

There is little information regarding genetic parameters of 9MW in the literature and the published values are mainly related to Iranian native sheep breeds (Miraei-Ashtiani et al., 2007; Mokhtari et al., 2008; Mohammadi et al., 2010). A moderate estimate of 0.25 was obtained for direct heritability of 9MW that falls within the range of 0.03 in Kermani sheep (Mokhtari et al., 2008) to 0.59 in Afrino sheep (Snyman et al., 1995).

The direct heritability estimate for YW was within the range of reported values, from 0.10 (Miraei-Ashtiani et al., 2007) to 0.58 (Snyman et al., 1995). At yearling age, maternal effects disappeared and direct heritability reached its maximum value. Therefore, YW may be an appropriate selection criterion for improving growth performance of Iran-Black sheep. Moderate direct heritability obtained for 9MW and YW traits implies that there is a potential for accurate selection for these traits in Iran-Black sheep. Riggio et al. (2008) estimated the genetic parameters of the body weight in Scottish Blackface sheep and concluded that measuring live body weight on older lambs would increase the accuracy of selection.

As expected, maternal effects constituted a sizeable source of variation in BW, most likely reflecting the differences in the uterine environment and the quality and capacity of the uterine space for fetal growth (Gowane et al., 2010). The estimated value of maternal heritability for BW was in agreement with the estimates of Rashidi et al. (2008) in Kermani sheep and Eskandarinassab et al. (2010) in Afshari sheep. Lower estimates were also reported by Matika et al. (2003) and Mohmmadi et al. (2010). In the present study, maternal heritability estimate was greater than the direct heritability; although, opposite results were also reported (Snyman et al., 1995; Matika et al., 2003). In a review, Safari et al. (2005) reported weighted means of maternal heritability estimates for BW of wool, dual-purpose and meat breeds of sheep as 0.21, 0.18 and 0.24, respectively. Such estimates are in general agreement with the values estimated in the present study.

Maternal heritability estimates for WW and 6MW were smaller than those of direct ones. The importance of maternal effects from birth to weaning was reported by several authors (Snyman et al., 1995; Yazdi et al., 1997; Gowane et al., 2010, Rashidi et al., 2011). The results showed that maternal genetic effects had negligible influence on WW in Iran-Black sheep; the impact of maternal effects on WW was mainly due to maternal permanent environmental effects. Estimate of maternal heritability for WW agreed with those published earlier (Ligda et al., 2000; Vatankhah and Talebi, 2008). Higher estimates were also reported by Snyman et al. (1995) and Miraei-Ashtiani et al. (2007). Maternal heritability of 6MW was low but unexpectedly higher than that of WW. Decreased maternal effects of the dam on body weight of lambs from birth to later stages of growth was expected. Such decrease was also found by Yazdi et al. (1997) in Baluchi sheep.

Maternal genetic effects had low impact on studied traits, expect on BW. A carry-over effect of maternal effects was found after weaning until 9 months of age. Poor pasture quality may prevent expression of the genetic potential of the dams for providing adequate quantity of milk for their lambs. Post-weaning period of Iran-Black lambs begins at the end of spring, late in June; when feed supplement and pasture quality and quantity are not enough to meet nutritional requirements of the lambs. Under such environmental conditions a favorable maternal environment at pre-weaning period will negatively affect post-weaning lamb growth because large lambs will encounter more difficulties in satisfying their nutritional requirements, and lambs which hold back due to low milk production of their dams experience compensatory growth after weaning (Yazdi et al., 1997). Therefore, the expression of maternal ability of the dams could be masked.

The estimated value of c^2 for BW was in agreement with that reported by van Wyk et al. (2003) in the Elsenburg Dormer sheep stud. Mousa et al. (1999) reported estimates of 0.09 and 0.12 for c^2 of BW and WW (at 7 weeks of age) in a composite terminal sire breed, respectively. They concluded that suckling lambs are still dependent on their dams, whereas at post-weaning time body weight is only minimally affected by maternal effects.

Our estimate on c^2 at 9MW was similar to those reported by Miraei-Ashtiani et al. (2007) in Sangsari sheep and by Mokhtari et al. (2008) in Kermani sheep. Gowane et al. (2010) reported a low value of c^2 for 9MW in Malpura sheep. Maternal effects denote the mothering ability for milk production as well as intrauterine conditions and may be partitioned into genetic and non-genetic portions (Maniatis and Pollott, 2002).

The estimated value of l^2 at BW was in agreement with that reported by van Wyk et al. (2003). Common litter effects disappeared after birth and emerged again at 6 months of age; resulting in a value of 0.13 for l^2 at 6MW which was in general agreement with the estimate of Abegaz et al. (2005) in Horro sheep.

Safari et al. (2005) pointed out that where multiple births are relatively common, as was the case for Iran-Black sheep, partitioning maternal environmental effects into across year effect (maternal permanent environmental) and litter effect (within year common environmental effect specified to the litter) is of paramount importance in terms of breeding. They also reported that for traits affected by maternal effects, the interpretation of genetic parameters under animal model is mainly dependent on data structure and the analytical model used. Based on our results, accurate genetic evaluation of growth traits in Iran-Black sheep requires adopting a model that contains direct, maternal genetic and maternal environmental and common litter effects.

Total heritability estimates (h^2_t) for the studied traits increased with age, ranging from 0.14 for BW to 0.34 for YW, but the values for maternal across year repeatability for ewe performance (t_m) decreased and varied from 0.34 for BW to 0.09 for YW. Total heritability estimates are sensitive to the model fitted (Gowane et al., 2010). Abegaz et al. (2005) stated that total heritability is of breeding importance when maternal effects are important in the expression of animal performance. The obtained estimates of t_m for BW and WW were in general agreement with those reported by Gowane et al. (2010) in Malpura sheep. Such moderate estimates suggested the scope of improvement in BW and WW through mass selection. The obtained values for t_m at post-weaning body weights were generally higher than those estimated by Gowane et al. (2010).

Correlation estimates

Estimates of correlation among body weight traits at different ages are presented in Table 4. Direct additive genetic correlations were positive and ranged from 0.15 for WW-YW to 0.98 for 6MW-9MW. Birth weight (BW) had high direct genetic correlations with other body weight measures, ranging from 0.91 (BW-6MW and BW-YW) to 0.95 (BW-9MW), expect with WW. A moderate value was estimated for direct genetic correlation of BW-WW. Low to moderate direct genetic correlations was found for WW with post-weaning body weights. Similar to those reported by Gowane et al. (2010), direct genetic

Table 4. Correlation estimates among body weight traits at different ages

Trait1-Trait2 [a]	r_a	r_p	r_m	r_c	r_l	r_e
BW-WW	0.38±0.08	0.12±0.02	0.58±0.07	0.21±0.17	-	0.35±0.03
BW-6MW	0.91±0.06	0.28±0.01	0.73±0.18	-	-0.07±0.01	0.35±0.04
BW-9MW	0.95±0.04	0.28±0.02	-	0.82±0.15	-	0.31±0.03
BW-YW	0.91±0.05	0.26±0.01	-	-	-	0.16±0.08
WW-6MW	0.25±0.07	0.20±0.02	0.98±0.12	-	-	0.51±0.03
WW-9MW	0.34±0.06	0.60±0.02	-	0.56±0.21	-	0.71±0.04
WW-YW	0.15±0.11	0.41±0.02	-	-	-	0.45±0.03
6MW-9MW	0.98±0.01	0.79±0.01	-	-	-	0.87±0.02
6MW-YW	0.91±0.01	0.75±0.01	-	-	-	0.73±0.03
9MW-YW	0.35±0.04	0.81±0.01	-	-	-	0.79±0.04

$r_{a:}$ direct genetic correlation; $r_{p:}$ phenotypic correlation; $r_{m:}$ maternal genetic correlation r_c: maternal permanent environmental correlations; r_l: common litter effect correlation $r_{e:}$ environmental correlation

[a] For trait abbreviations see footnote to Table 1

correlations for 6MW-9MW and 6MW-YW were high and near unity but that found between 9MW and YW was moderate. Estimated direct genetic correlations among body weights were generally in agreement with those reported by others (Mirae-Ashtiani et al., 2007; Mohammadi et al., 2010). Positive direct genetic correlations among body weights suggested that genetic factors that influence body weights at different ages were the same. High estimated direct genetic correlations of 6MW with 9MW and YW were also found by Gowane et al. (2010); implying that animals with higher 6MW would tend to be above average in genetic merit for 9MW and YW.

Maternal genetic correlation estimates among BW, WW and 6MW were high; indicating that maternal additive genetic effects, which favor the growth of fetus, could have some beneficial effect on post-natal growth traits. In other words, body weight from birth to 6 months of age is largely influenced by similar genes of the dam in terms of maternal genetic effects. Estimated positive and moderate to high maternal permanent environmental correlations for BW-WW, BW-9MW and WW-9MW were in agreement with the estimates of Gowane et al. (2010). Such positive and high estimates imply that good management conditions and favorable maternal behavior would have a positive influence on body weight of lambs at birth, weaning and 9 months of age (Gowane et al., 2010).

Similar to estimates of Safari et al. (2005), phenotypic correlation estimates among the studied traits were positive and generally lower than those of direct genetic correlations. There were positive and moderate to high environmental correlations among the studied traits. Estimated environmental correlations were in agreement with those reported by Yazdi et al. (1997) and Mohammadi et al. (2010). Positive genetic (direct and/or maternal), phenotypic and environmental correlations among body weight traits indicated that there was no genetic, anatonistic phenotypic and environmental relationship among these traits. Therefore, selection for any of these body weights will bring about positive response to selection in terms of genetic and phenotypic values.

Conclusions

Results of the present study showed the importance of maternal and common litter effects on the statistical models considered for estimation of (co) variance component and genetic parameters of growth traits, especially for pre-weaning ones. Exclusion of maternal and common litter effects in models resulted in upward biased estimates for genetic parameters. Direct post-weaning heritability estimates were at least moderate for body weights in Iran-Black sheep. While YW was not influenced by maternal effects, but maternal effects were found to be important on lamb body weights from birth to 9 months of age, and should be considered in the genetic evaluation of this breed. It seems that YW is an appropriate selection criterion for use in improvement of growth performance in Iran-Black lambs through selection. Favorable and moderate to high genetic correlations among body weights suggested that such a selection strategy might improve all traits.

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