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The comparison of standard multiple-trait and structural equation modeling approaches for the estimation of genetic and phenotypic parameters of growth traits in Arman sheep

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Abstract The current investigation was performed to compare the performance of standard multivariate and structural equation models for the estimation of genetic parameters of growth traits in Arman sheep. Data were collected on 2194 Arman lambs in 13 years (1999 to 2012) at Abbasabad Sheep Breeding Station, Khorasan Razavi province, north-eastern Iran. The studied growth traits were body weight at birth (BWT), weaning (WWT), six months (6MWT), nine months (9MWT), and yearling weight (YWT). The predictive abilities of three multivariate animal models comprising standard (SMM), temporal recursive (TRM), and fully recursive (FRM) models were evaluated by applying two statistical criteria including the mean square of error (MSE) and Pearson's correlation coefficient between the observed and predicted records ($r(y,\hat{y})$). In general, TRM performed better than SMM and FRM. The lowest MSE and the highest $r(y,\hat{y})$ were found under TRM. All posterior means for the structural coefficients were statistically significant. Spearman's rank correlation coefficients between the estimated breeding values for the body weight traits were also computed across all, 50% top-ranked, and 10% top-ranked animals. Comparisons of these correlations between posterior means of estimated breeding values of individuals for the growth traits under SMM and TRM revealed that taking the causal relationships among these traits into account could result in significant re-ranking of the animals according to the estimated breeding values; showing that TRM had more advantage over SMM for the estimation of genetic parameters and the breeding values of the studied traits in Arman sheep.

Keywords: animal model, body weight, causal relationship, predictive ability, sheep

Introduction

Arman sheep breed was synthesized in 1975 by crossing four sheep breeds namely Baluchi and Ghezel (two Iranian local breeds) and Chios and Suffolk (two exotic breeds) in Abbasabad Breeding Station, located in Khorasan Razavi province, north-east Iran while the main purpose was enhancing litter size, meat production and resistance to prevalent harsh environmental circumstances in the region (Mokhtari et al., 2013). Body weights at different ages are important traits in domestic species including sheep and goats which affect the profitability of the production systems. Therefore, growth traits should be considered when developing breeding programs for these species (Tosh and Kemp, 1994). The genetic selection of superior individuals for body weight traits is an applied procedure for increasing meat production (Boujenane and Kansari, 2002). Accurate breeding value estimates obtained by multivariate animal models are required for designing an efficient selection program for domestic animals.

The structural equation model (SEM) (Wright, 1921) is a multivariate method that enables evaluation of the causal relationships among traits. Gianola and Sorensen (2004) developed models to describe situations in which cause-and-effect relationships stand among the traits in a multiple-trait system. Rosa et al. (2011) pointed out that in any multivariate genetic selection scheme, evaluating possible cause-and-effect relationships among the phenotypes is essential. Fitting SEM is more parsimonious than standard multivariate models (SMM) in terms of computational demands because uncorrelated residual covariances were supposed to fit SEM (Rosa et al., 2011). By applying SEM, the existence of cause-and-effect relationships among growth traits has been documented in Lori-Bakhtiari (Amou Posht-e Masari et al., 2019), Kurdi (Mohammadi et al., 2020), Kermani (Mokhtari et al., 2020), and Moghani (Jafaroghli et al., 2021) sheep breeds. These studies have shown the advantage of SEM over SMM by considering the predictive ability of models and the accurate estimation of breeding values of animals.

The estimates of genetic parameters for the growth traits of Arman sheep by using SMM, while causal relationships among the traits ignored, were previously reported by Mokhtari et al. (2013). Thus, the main purpose of the current investigation was to analyze some body weight traits of Arman sheep by using two SEM-based multivariate models and compare outcomes with SMM. The influence of the existence of cause-and-effect relationships in the genetic analysis model on the ranking of the individuals based on their estimated breeding values was also evaluated.

Materials and methods

Data collection and flock management

Data and genealogical information employed in the current investigation were gathered from 1999 to 2012, at Abbasabad Sheep Breeding Station, Khorasan Razavi province, north-eastern Iran. The pedigree structure of the studied population of Arman sheep is shown in Table 1. In the station, animals were reared under a conventional breeding method similar to local flocks. The breeding season lasts from late August to late October and consequently, lambing happens late in January to late March. Maiden Arman ewes were allocated to fertile rams at about 18 months of age at a ratio of 20-25 ewes per ram. To avoid inbreeding, rams were exposed rotationally to each group of ewes. The ewes and their newborn lambs were kept in separate pens for a few days. During the pre-weaning period, the lambs were creep-fed and grazed on the pastures. Lambs were weaned at about 3 months of age. During spring and summer, the lambs were grazed on pastures, and in the autumn they were grazed on wheat and barley stubbles. During winter, the lambs were kept indoors and hand-fed.

Table 1. Pedigree structure of the studied population of Arman sheep

Item	Numbers
Individuals in total	2421
Inbreds in total	731
Sires in total	68
Dams in total	649
Individuals with progeny	717
Individuals with no progeny	1704
Founders	227
Individuals with both parents known	2194
Individuals with both parents unknown	227
Individuals with one parent unknown	0
Average inbreeding coefficients (%)	1.65
Average inbreeding coefficients in the inbreds (%)	5.48
Maximum of inbreeding coefficients (%)	26.56
Minimum of inbreeding coefficients (%)	0.39

Traits

The studied traits were birth weight (BWT), weaning weight (WWT), six months weight (6MWT), nine months weight (9MWT), and yearling weight (YWT). The available records were monitored and screened several times and lambs with incorrect information on body weights, birth date, and pedigree information were deleted from the data set. Furthermore, animals with body weights beyond the range of mean ±3× S.D. were removed from the dataset. A description of the dataset is presented in Table 2.

Table 2. Descriptive statistics for the studied traits in Arman sheep

Item	Traits (kg) ¥				
	BWT	WWT	6MWT	9MWT	YWT
Mean	3.95	21.65	32.54	35.67	41.85
S.D.	0.85	5.53	6.78	6.14	7.54
Min.	1.50	6.00	10.00	15.00	16.00
Max.	7.20	40.00	56.00	57.00	65.00
C.V. (%)	21.52	25.54	20.83	17.21	18.01

¥BWT: birth weight; WWT: weaning weight; 6MWT: Six-month weight; 9MWT: Nine-month weight; YWT: Yearling weight

Statistical analyses

The impact of maternal effects on the estimation of variance components of the traits was evaluated. Models containing various combinations of direct additive genetic, maternal additive genetic, maternal permanent, and maternal temporary environmental or litter (dam within a year) effects were fitted to the studied growth traits. The tested models were as follows:

$y = Xb + Z_1a + e$		**Model 1**
$y = Xb + Z_1a + Z_2pe + e$		**Model 2**
$y = Xb + Z_1a + Z_3m + e$	**Cov (a,m) = 0**	**Model 3**
$y = Xb + Z_1a + Z_3m + e$	**Cov (a,m) = $A\sigma_{am}$**	**Model 4**
$y = Xb + Z_1a + Z_2pe + Z_4l + e$		**Model 5**
$y = Xb + Z_1a + Z_2pe + Z_3m + e$	**Cov (a,m) = 0**	**Model 6**
$y = Xb + Z_1a + Z_2pe + Z_3m + e$	**Cov (a,m) = $A\sigma_{am}$**	**Model 7**
$y = Xb + Z_1a + Z_2pe + Z_3m + Z_4l + e$	**Cov (a,m) = 0**	**Model 8**
$y = Xb + Z_1a + Z_2pe + Z_3m + Z_4l + e$	**Cov (a,m) = $A\sigma_{am}$**	**Model 9**

where, **y** denotes the vector of measurements for the studied traits; **b**, **a**, **m**, **pe**, **l**, and **e** imply the vectors of fixed (sex, birth type, dam age, and birth year of lambs), direct additive genetic, maternal additive genetic, maternal permanent environmental, maternal temporary environmental (litter), and the residual effects, respectively. The matrices of **X**, **Z_1**, **Z_2**, **Z_3**, and **Z_4**, are design matrices relating corresponding effects to vector **y**. It was assumed **a** ~ N (0, $\mathbf{A}\sigma_a^2$), **m** ~ N (0, $\mathbf{A}\sigma_m^2$), **pe** ~ N (0, $\boldsymbol{I_{pe}}\sigma_{pe}^2$), **l** ~ N (0, $\boldsymbol{I_l}\sigma_l^2$) and **e** ~ N (0, $\boldsymbol{I_n}\sigma_e^2$). **A** is the numerator relationship matrix, and σ_{am} shows covariance between direct additive and maternal additive genetic effects. **I_{pe}**, **I_l**, and **I_n** are identity matrices of appropriate dimensions. Furthermore, σ_a^2, σ_m^2, σ_{pe}^2, σ_l^2 and σ_e^2 are direct additive genetic, maternal additive genetic, maternal permanent environmental, maternal temporary environmental (litter), and residual variances, respectively. The Bayesian Information Criterion (BIC) (Schwarz, 1978) was used to determine the most appropriate univariate animal model among the tested ones. For each trait, the model with the lowest BIC was chosen as the best model. Genetic analyses were performed by applying the WOMBAT software (Meyer, 2013). After the determination of the best univariate animal model for traits, three types of multiple-trait models comprising of SMM, temporal recursive multivariate (TRM), and fully recursive multivariate (FRM) were applied. Schematic presentations of TRM and FRM models are shown in Figures 1 and 2, respectively. By taking the full model considered in the present study (model 9) into account, the SEM-based multivariate model is shown in matrix notation as below:

$$\Lambda y_i = X_i b_i + Z_{1i} a + Z_{2i}\, pe + Z_{3i} m + Z_{4i} l + e_i \qquad \textbf{Cov (a,m) = } \mathbf{A}\boldsymbol{\sigma}_{\mathbf{am}}$$

The matrix **Λ** is the structural coefficients matrix, in which diagonal elements are replaced with 1 and the off-diagonal elements are specified according to the cause-and-effect relationships between the phenotypes. Structural coefficients were types of regression coefficients, which are estimated by using SEM (Gianola and Sorensen, 2004). By considering five traits, the matrix of structural coefficients under FRM was:

$$\boldsymbol{\Lambda}_{5\times5} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ -\boldsymbol{\lambda}_{21} & 1 & 0 & 0 & 0 \\ -\boldsymbol{\lambda}_{31} & -\boldsymbol{\lambda}_{32} & 1 & 0 & 0 \\ -\boldsymbol{\lambda}_{41} & -\boldsymbol{\lambda}_{42} & -\boldsymbol{\lambda}_{43} & 1 & 0 \\ -\boldsymbol{\lambda}_{51} & -\boldsymbol{\lambda}_{52} & -\boldsymbol{\lambda}_{53} & -\boldsymbol{\lambda}_{54} & 1 \end{bmatrix}$$

where, the first trait influences causally the second, third, fourth, and fifth traits, the second trait influences causally the third, fourth, and fifth traits, the third trait influences causally the fourth and fifth traits, and eventually, the fourth trait has a causal effect on the fifth trait. By considering five traits, the matrix of structural coefficients under a TRM was:

$$\boldsymbol{\Lambda}_{5\times5} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ -\boldsymbol{\lambda}_{21} & 1 & 0 & 0 & 0 \\ 0 & -\boldsymbol{\lambda}_{32} & 1 & 0 & 0 \\ 0 & 0 & -\boldsymbol{\lambda}_{43} & 1 & 0 \\ 0 & 0 & 0 & -\boldsymbol{\lambda}_{54} & 1 \end{bmatrix}$$

where, the first trait influences causally the second, the second trait influences causally the third, and so on. Other components of the model are as described earlier. The SEMs are not identifiable at the likelihood level because of the existence of extra parameters such as structural coefficients. To achieve identification, it was supposed that residual correlations in the system were uncorrelated. In other words, the variance-covariance matrix of residuals (**R)** in SEM, was supposed to be a diagonal matrix. Furthermore, a multivariate normal distribution with a null mean vector and (co)variance matrix **R** ⊗ **I_n** was supposed for residual effects. Where **I_n** is an identity matrix and **R** is the residual (co)variance matrix; ⊗ denoting the Kronecker product.

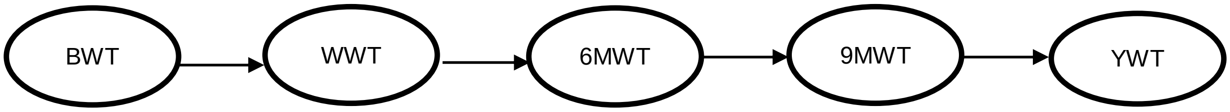

Figure 1. The temporal recursive model considered among the studied growth traits in Arman sheep (BWT: birth weight; WWT: weaning weight; 6MWT: Six-month weight; 9MWT: Nine-month weight; YWT: Yearling weight). Arrows show the direction of causal effects.

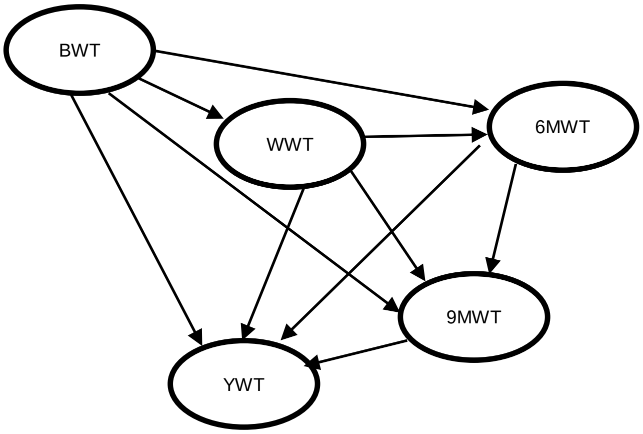

Figure 2. Multivariate fully recursive model considered among the studied growth traits in Arman sheep (BWT: birth weight; WWT: weaning weight; 6MWT: Six-month weight; 9MWT: Nine-month weight; YWT: Yearling weight). Arrows show the direction of causal effects.

Multivariate analyses were carried out via the Bayesian approach by using the GIBBS2F90 program of Mizstal et al. (2002). The chain length and the warming-up period were inspected by visual control of the trace plots of posterior samples of the parameters. The first 20,000 iteration samples were dropped out as a warming-up. For each multivariate model, 200,000 iterations were run and posterior samples from each chain were thinned considering thinning intervals of 20 iterations. Hence, 9,000 samples remained for computing features of the posterior means of variance and covariance components by using the POSTGIBBSF90 program of Mizstal et al. (2002).

Lopez de Maturana et al. (2007) showed that the SEM-based models are executed by fitting the parent trait as a covariate for another trait while genetic correlations between traits are included in multiple trait analyses. In this case, a trait considered as a parent one causally affects another trait. Therefore, the same methodology was used in the current investigation for fitting the SEM-based models (FRM and TRM).

Statistical measures for model comparisons

The SMM, TRM, and FRM were evaluated by applying the predictive ability criteria and Spearman's rank correlations between posterior means of the genetic effects under SMM and FRM. To evaluate the predictive ability of SMM, TRM, and FRM, the dataset was randomly partitioned five times into two sets including the training set (50% of the dataset) and the testing set (retained 50% of the dataset). Then, solutions for all fixed and random effects of the training set were estimated and used to predict body weight records in the testing set. The predictive ability of the models was evaluated by the PREDICTF90 program (Mizstal et al., 2002) and compared by using two statistical criteria, i.e., the mean square of error (MSE) and the Pearson correlation coefficient between the observed and predicted values ($r(y,\hat{y})$) in the testing set. The MSE and $r(y,\hat{y})$ values were computed five times and averaged. The lower the average MSE and the higher the average $r(y,\hat{y})$ value imply the superiority of the model.

System parameters

The parameters estimated by applying SEM are called system parameters and their interpretation is different from the corresponding parameters estimated by SMM (Gianola and Sorensen, 2004). Therefore, further transformation is required for comparison of the parameters estimated under SEM and SMM by applying the following formulas (Gianola and Sorensen, 2004):

$$\mathbf{G}^* = \boldsymbol{\Lambda}^{-1}\mathbf{G}\boldsymbol{\Lambda}'^{-1}$$

$$\mathbf{M}^* = \boldsymbol{\Lambda}^{-1}\mathbf{M}\boldsymbol{\Lambda}'^{-1}$$

$$\mathbf{PE}^* = \boldsymbol{\Lambda}^{-1}\mathbf{PE}\boldsymbol{\Lambda}'^{-1}$$

$$\mathbf{L}^* = \boldsymbol{\Lambda}^{-1}\mathbf{L}\boldsymbol{\Lambda}'^{-1}$$

$$\mathbf{R}^* = \boldsymbol{\Lambda}^{-1}\mathbf{R}\boldsymbol{\Lambda}'^{-1}$$

and $\mathbf{P}^* = \boldsymbol{\Lambda}^{-1}\mathbf{P}\boldsymbol{\Lambda}'^{-1}$.

The matrices $\mathbf{G}^*$, $\mathbf{M}^*$, $\mathbf{PE}^*$, $\mathbf{L}^*$, $\mathbf{R}^*$, and $\mathbf{P}^*$ are (co)variance matrices for direct additive genetic, maternal additive genetic, maternal permanent environmental, maternal temporary environmental, residual, and phenotypic effects, respectively. Firstly, these effects were estimated by SEM and then transformed into their SMM equivalents. $\mathbf{R}^*$ is a matrix with non-zero off-diagonal elements.

The effect of models (SMM and FRM) on the ranking of animals based on estimated direct breeding values was also evaluated by applying Spearman's rank correlations between the posterior means of the genetic effects for all, 50% top-ranked, and 10% top-ranked animals. Initially, the breeding values (equivalent to the SMM) were estimated by applying the following formula (Konig et al., 2008):

$$\mathbf{BV}^* = \boldsymbol{\Lambda}^{-1}\,\mathbf{BV}$$

where, **BV** is the vector of estimated breeding values under SEM.

Results and discussion

The importance of maternal effects

The BIC values obtained by fitting nine univariate animal models for all traits are presented in Table 3. Based on these values, the model that included the direct additive genetic, maternal permanent environmental, and maternal temporary environmental (litter) effects (model 5) was the best model for BWT and WWT. For 6MWT, 9MWT, and YWT the model with the direct additive genetic effects (model 1) was determined as the most appropriate model. The importance of including the maternal effects in the model used for the estimation of the genetic parameters of the body weight traits has been well demonstrated in Lori-Bakhtiari (Amou Posht-e Masari et al., 2019), Kermani (Mokhtari et al., 2020), and Kurdi (Mohammadi et al., 2020) sheep breeds.

Table 3. BIC values for the studied traits in Arman sheep breed under different models

Model	Traits ¥				
	BWT	WWT	6MWT	9MWT	YWT
Model 1	842.378	6667.316	**6433.99**	**5349.106**	**5413.972**
Model 2	843.676	6668.76	6434.56	5355.898	5420.694
Model 3	849.95	6673.27	6438.208	5354.506	5420.686
Model 4	857.58	6679.058	6444.606	5361.19	5427.526
Model 5	**814.524**	**6662.938**	6438.394	5362.748	5426.41
Model 6	852.062	6676.188	6441.792	5361.632	5427.664
Model 7	860.328	6683.386	6448.408	5368.318	5434.32
Model 8	824.182	6670.366	6445.598	5368.616	5433.38
Model 9	831.398	6677.65	6452.254	5375.292	5440.062

¥BWT: birth weight; WWT: weaning weight; 6MWT: Six-month weight; 9MWT: Nine-month weight; YWT: Yearling weight

The best model is shown in boldface.

The predictive ability of the SMM, TRM, and FRM

As shown in Table 4, the SMM, TRM, and FRM were evaluated in terms of the predictive ability of models evaluated by using the average mean square of error (MSE) and average Pearson's correlation coefficient between real and predicted records (r(y,$\hat{y}$)) of traits. For all the traits, FRM and TRM had lower MSE and higher r(y,$\hat{y}$) values than SMM: TRM provided lower MSE and higher r(y,$\hat{y}$) than FRM, and was ranked as the top multivariate model in the present study. Therefore, the causal structure (Figure 1) is appropriate for describing the causal relationships among the body weight traits studied in Arman sheep. The excellence of the model containing this causal structure (TRM) was previously reported by Amou Posht-e Masari et al. (2019) in Lori-Bakhtiari sheep, Mokhtari et al. (2020) in Kermani sheep, and Jafaroghli et al. (2021) in Moghani sheep breeds. Amou Posht-e Masari et al. (2019) pointed out that taking causal relationships among the growth traits in Lori-Bakhtiari sheep into account for genetic analysis of these traits may provide a better description of biological relations among them than that obtained under SMM.

Table 4. The predictive ability for the studied traits under the different multivariate studied models

Traits ¥	Model ¥¥					
	SMM		TRM		FRM	
	¥¥¥ MSE	¥¥¥ r(y,$\hat{y}$)	¥¥¥ MSE	¥¥¥ r(y,$\hat{y}$)	¥¥¥ MSE	¥¥¥ r(y,$\hat{y}$)
BWT	0.29	0.76	0.26	0.80	0.28	0.77
WWT	8.97	0.81	7.63	0.84	7.92	0.83
6MWT	18.94	0.73	10.71	0.86	11.20	0.85
9MWT	19.31	0.71	7.44	0.90	8.45	0.88
YWT	25.46	0.75	9.55	0.91	12.02	0.89

¥ BWT: birth weight; WWT: weaning weight; 6MWT: Six-month weight; 9MWT: Nine-month weight; YWT: Yearling weight

¥¥ SMM: Standard multivariate model, FRM: Fully recursive multivariate model, TRM: Temporal recursive multivariate model

¥¥¥ MSE: mean square error, r(y,$\hat{y}$)= Pearson correlation between observed and predicted values

Structural coefficients

The features of posterior means for the structural coefficients among growth traits of Arman sheep, estimated by applying TRM, with 99% highest posterior density (HPD) intervals are shown in Table 5. All estimated structural coefficients were positive and statistically significant (99% of HPD intervals did not include zero). The BWT of Arman lambs had a direct causal effect of 1.88 on WWT, implying that about 1.88 kg increase in WWT will be anticipated per kg increase in BWT. The estimated values for direct causal effects of WWT on 6MWT (0.81), 6MWT on 9MWT (0.81), and 9MWT on YWT (0.77) were statistically significant (99% of HPD intervals did not include zero). This means, 0.81 kg increase in 6MWT, 0.81 kg increase in 9MWT, and 0.77 kg increase in YWT will be anticipated per one kg increase in WWT, 6MWT, and 9MWT, respectively. In general, any increase in BWT (as a parent trait) had favorable causal influences on the other studied growth traits in Arman sheep. Jafaroghli et al. (2021) investigated the causal relations among quarterly-recorded body weights from birth to yearling age of Moghani sheep using TRM and reported causal effects of BWT on WWT, of WWT on 6MWT, of 6MWT on 9MWT, and of 9MWT on YWT as 1.19, 0.67, 0.72, 0.71 kg, respectively. In another study, Mohammadi et al. (2020) estimated the causal effects of BWT on WWT, WWT on 6MWT, 6MWT on 9MWT, and 9MWT on YWT of Kurdi lambs as 1.478, 0.737, 0.776, and 0.929 kg, respectively.

Valente et al. (2013) stated that the genetic effects estimated under SMM and SEM are distinct concepts, while SMM shows the overall genetic effects that include the direct and indirect components of each trait: SEM enables partitioning of the overall effects into direct (which is not mediated by other traits in the causal network) and indirect (which mediating by other traits in the causal network) effects. As presented in Figure 1, BWT of Arman lambs had an indirect causal effect on 6MWT (mediated via WWT), on 9MWT (mediated via WWT and 6MWT), and on YWT (mediated via WWT, 6MWT, and 9MWT). The causal effect of BWT on

6MWT, mediated via WWT, was computed as the product of direct causal effects of BWT on WWT (1.88) and WWT on 6MWT (0.81) which is 1.52. Mokhtari et al. (2020) reported the indirect causal effect of BWT on 6MWT (mediated via WWT) of Kermani lambs as 0.77 which is lower than the corresponding value obtained in the present study. A value of 1.312 was reported for the causal influence of BWT on 6MWT (mediated through WWT) in Kurdi lambs (Mohammadi et al., 2020) which is higher than the corresponding value in the current research.

By using a similar method, the causal influences of BWT on 9MWT (mediated via both WWT and 6MWT) and on YWT (mediated via all WWT, 6MWT, and 9MWT) were 1.23 and 0.95, respectively. By applying the TRM, Jafaroghli et al. (2021) obtained estimates of 0.574 and 0.407 for indirect causal effects of BWT on 9MWT and YWT of Moghani lambs, respectively. By applying the TRM, Mohammadi et al. (2020) estimated coefficients of 0.845 and 0.785 for the indirect causal influences of BWT on 9MWT and indirect causal effects of BWT on YWT in Kurdi sheep, respectively which are higher than the corresponding values in the current research. The causal effects of WWT on 9MWT (mediated through 6MWT) and on YWT (mediated through 6MWT and 9MWT) of Arman sheep were estimated as 0.656 and 0.505, respectively, implying that any increase in WWT significantly would increase 6MWT, 9MWT, and YWT. In Kurdi sheep, Mohammadi et al. (2020) obtained estimates of 0.572 and 0.531 for the indirect causal influences of WWT on 9MWT and the indirect causal influences of WWT on YWT respectively. The causal impact of 6MWT on YWT in Arman lambs (mediated by 9MWT) was 0.624. The indirect causal effect of 6MWT on YWT (which was mediated via 9MWT) were 0.511 and 0.721 in Moghani (Jafaroghli et al., 2021) and Kurdi (Mohammadi et al., 2020) sheep breeds, respectively.

Table 5. Posterior means ± posterior standard deviation (PSD) for the structural coefficients under TRM

Traits ¥	Mean ± PSD ¥¥	99% HPD interval ¥¥
BWT-WWT	1.88±0.30	1.11-2.65
WWT-6MWT	0.81±0.04	0.71-0.91
6MWT-9MWT	0.81±0.03	0.73-0.89
9MWT-YWT	0.77±0.04	0.67-0.87

¥BWT: birth weight; WWT: weaning weight; 6MWT: Six-month weight; 9MWT: Nine-month weight; YWT: Yearling weight

¥¥ PSD: Posterior Standard Deviation, 99% HPD intervals did not include zero.

Genetic parameter estimates

The features of posterior means for the direct heritability (h^{2}), the ratio of permanent maternal variance to phenotypic variance (pe^{2}), and the ratio of temporary maternal environmental variance to phenotypic variance (l^{2}) under TRM are presented in Table 6. All estimates were statistically significant (95% of HPD intervals did not include zero).

Direct heritability estimates were low values of 0.17, 0.17, 0.23, 0.15, and 0.19 for BWT, WWT, 6MWT, 9MWT, and YWT, respectively, implying low direct additive genetic variability and greater importance of the non-additive genetic and environmental factors for these traits in Arman sheep. Mohammadi et al. (2020) reported direct heritability estimates of 0.21, 0.38, 0.24, 0.23, and 0.31 for BWT, WWT, 6MWT, 9MWT, and YWT in Kurdi sheep, respectively, which are relatively higher than the corresponding values in the present study. In Sanjabi sheep, Mohammadi et al. (2010) estimated values of 0.09, 0.15, 0.09, 0.19, and 0.11 for direct heritability of BWT, WWT, 6MWT, 9MWT, and YWT, respectively, which are generally lower than the corresponding values in the current study.

Maternal permanent and maternal temporary environmental effects were found to be important only for BWT and WWT in Arman lambs with maternal temporary environmental effects being more important than maternal permanent environmental ones. In the present study, a high value of 70% was obtained for multiple-birth rate in Arman sheep which necessitates considering the maternal temporary environmental effects in the model used for genetic evaluation of BWT and WWT. Amou Posht-e Masari et al. (2018) reported pe^{2} estimates of 0.10 and 0.14 for BWT and WWT in the Iranian Lori-Bakhtiari sheep breed, respectively, under a temporal recursive multivariate model: these values are higher than the corresponding posterior means of the estimated values for BWT (0.02) and WWT (0.04) in the present study. Abegaz et al. (2005) estimated values of 0.51 and 0.11 for l^{2} in Horro sheep which are higher than the l^{2} estimates of 0.10 (for BWT) and 0.08 for WWT in Arman sheep.

Table 6. Posterior means ± posterior standard deviation (PSD) for the direct heritability (h^2), the ratio of permanent maternal (pe^2) and/or temporary maternal (l^2) environmental variance to phenotypic variance estimates for the studied traits of the traits under TRM

Traits ¥	h^2 ± PSD	pe^2 ± PSD	l^2 ± PSD
BWT	0.17±0.05	0.02±0.01	0.10±0.05
WWT	0.17±0.04	0.04±0.02	0.08±0.04
6MWT	0.23±0.06	-	-
9MWT	0.15±0.05	-	-
YWT	0.19±0.06	-	-

¥BWT: birth weight; WWT: weaning weight; 6MWT: Six-month weight; 9MWT: Nine-month weight; YWT: Yearling weight

The features of posterior means ± posterior standard deviation (PSD) for direct additive genetic, phenotypic, and residual correlation estimates of the studied body weight traits in Arman sheep, under TRM, are shown in Table 7. All estimated correlations among body weight traits were significant (95% HPD intervals did not include zero). Direct additive genetic correlations were positive and medium to high, ranging from 0.51 (for BWT-YWT) to 0.84 (for BWT-WWT). Phenotypic correlations varied from 0.24 (BWT-9MWT) to 0.73 (for both 6MWT-9MWT and (9MWT-YWT) and residual correlations from 0.11 (BWT-YWT) to 0.73 (6MWT-9MWT). Posterior means for the direct additive genetic correlations were higher than those of the corresponding phenotypic and residual ones. Such a trend was also reported by Abegaz et al. (2005) in Horro and by Mohammadi et al. (2020) in Kurdi sheep. The existence of positive phenotypic and direct genetic correlations among the studied body weight traits denotes that improvement in any of the traits would result in positive direct genetic and phenotypic gains for others. The estimated values for direct genetic, phenotypic, and residual correlations of the body weight traits in Arman sheep are in the range of those reported by Mohammadi et al. (2020) in Kurdi sheep.

Table 7. Posterior means ± posterior standard deviation (PSD) for direct genetic (r_g), phenotypic (r_p), and residual correlation (r_e) estimates for the studied traits under TRM.

Traits ¥	r_g ± PSD	r_p ± PSD	r_e ± PSD
BWT-WWT	0.84±0.07	0.39±0.05	0.33±0.02
BWT-6MWT	0.81±0.10	0.31±0.04	0.20±0.01
BWT-9MWT	0.73±0.15	0.24±0.04	0.16±0.01
BWT-YWT	0.51±0.06	0.26±0.04	0.11±0.01
WWT-6MWT	0.59±0.02	0.59±0.03	0.61±0.02
WWT-9MWT	0.64±0.17	0.48±0.03	0.48±0.01
WWT-YWT	0.61±0.06	0.54±0.04	0.43±0.02
6MWT-9MWT	0.74±0.13	0.73±0.02	0.73±0.01
6MWT-YWT	0.71±0.09	0.72±0.04	0.55±0.01
9MWT-YWT	0.79±0.20	0.73±0.03	0.71±0.01

¥BWT: birth weight; WWT: weaning weight; 6MWT: Six-month weight; 9MWT: Nine-month weight; YWT: Yearling weight

Ranking of the estimated breeding values

Spearman's rank correlations between posterior means of the estimated breeding values across the investigated body weight traits under SMM and TRM for all, 50% of top-ranked, and 10% of top-ranked animals are presented in Table 8. In general, a decreasing pattern was found for Spearman’s rank correlations between the breeding values estimated by SMM and TRM. Thus, causal relationships among the body weight traits should be included in the model used for genetic evaluation of these traits in Arman sheep because ignoring them may result in an inaccurate ranking of lambs. Similar trends were also observed by Jafaroghli et al. (2020) for Spearman's rank correlations between the posterior means of estimated breeding values of body weight traits in Moghani sheep under SMM and TRM.

In the present study, the highest Spearman's rank correlations between posterior means of direct genetic effects were found for BWT. It means that taking the causal relations among the studied growth traits of Arman sheep into account had a negligible influence on the estimated breeding values for lamb BW. In the present study, when TRM was fitted (Figure 1), BWT was regarded as the parent trait, which influenced others but was not influenced by the subsequent traits. The Spearman's rank correlations between posterior means of the estimated breeding values of BWT may be justified to some extent by such causal structure.

There were considerable changes in rank correlations between posterior means of the estimated breeding values under SMM and TRM for other traits, especially in 50% and 10% top-ranked animals; implying an important re-ranking of animals for WWT, 6MWT, 9MWT, and YWT under SMM and TRM. As a result, accounting for causal relationships among the studied growth traits in Arman sheep may have crucial effects on the accurate prediction of the breeding values and consequently accurate ranking of animals based on their estimated breeding values. Similar patterns in the re-ranking of animals under SEM-based models were also found in Lori-Bakhtiari sheep (Amou Posht-e Masari et al., 2019), in Kermani sheep (Mokhtari et al., 2020), and in Moghani sheep (Jafaroghli et al., 2021) breeds.

Table 8. Spearman's rank correlations of posterior means of direct genetic effects for studied growth traits of Arman sheep under SMM and FRM

Traits ¥	All animals	50% top-ranked	10% top-ranked
BWT	0.99 **	0.97 **	0.93 **
WWT	0.73 **	0.57 **	0.44 **
6MWT	0.77 **	0.60 **	0.54 **
9MWT	0.86 **	0.71 **	0.47 **
YWT	0.87 **	0.71 **	0.50 **

¥BWT: birth weight; WWT: weaning weight; 6MWT: Six-month weight; 9MWT: Nine-month weight; YWT: Yearling weight

**: P-value <0.01, ns: P-value <0.05

Conclusions

In the present investigation, three multiple-trait models comprising of SMM, FRM, and TRM models were evaluated for estimating the genetic parameters of growth traits in Arman lambs. By employing the predictive ability measures in model comparison, TRM was superior to SMM and FRM. Positive and statistically significant direct causal effects were found from BWT on WWT, WWT on 6MWT, 6MWT on 9MWT, and 9MWT on YWT. Comparisons of Spearman's rank correlations between posterior means of the estimated breeding values for growth traits under SMM and TRM showed that incorporating the cause-and-effect relations among growth traits in the model used for estimating the genetic parameters and breeding values could impose important re-ranking for these animals.

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