

The comparison of standard and fully recursive multivariate models for genetic evaluation of growth traits in Markhoz goat: predictive ability of models and ranking of animals

Animal Research Paper

Cite this article: Razmkabir M, Mokhtari M, Mahmoudi P, Rashidi A (2020). The comparison of standard and fully recursive multivariate models for genetic evaluation of growth traits in Markhoz goat: predictive ability of models and ranking of animals. *The Journal of Agricultural Science* **158**, 511–517. <https://doi.org/10.1017/S0021859620000830>



Received: 13 March 2020
Revised: 26 August 2020
Accepted: 25 September 2020
First published online: 23 October 2020

Key words:

Body weight; causal structure; Markhoz goat; structural equation model

Author for correspondence:

Mohammad Razmkabir,
E-mail: m.razmkabir@uok.ac.ir

Mohammad Razmkabir¹ , Morteza Mokhtari², Peyman Mahmoudi¹
and Amir Rashidi¹ 

¹Department of Animal Science, Faculty of Agriculture, University of Kurdistan, Sanandaj, Iran and ²Department of Animal Science, Faculty of Agriculture, University of Jiroft, P.O. Box 364, Jiroft, Iran

Abstract

Data of 2780 Markhoz kids originated from 1216 dams and 211 sires during 1993–2016 in Markhoz Goat Breeding Station, located in Sanandaj, Iran, were used. Traits investigated were body weights at birth, weaning, six-month age [six months weight (6MW)], nine-month age and yearling age [yearling weight (YW)]. Two considered multivariate models including standard multivariate model (SMM) and fully recursive multivariate model (FRM) were compared using deviance information criterion (DIC) and predictive ability measures including mean square of error (MSE) and Pearson's correlation coefficient between the observed and predicted values ($r(y, \hat{y})$) of records. Spearman's rank correlation coefficients between posterior means of direct genetic effects of the studied traits of kids under SMM and FRM were also calculated across all, 50, 10 and 1% top-ranked animals. In general, FRM performed better than SMM in terms of lower DIC and MSE and also higher $r(y, \hat{y})$. For all traits, the lowest MSE and the highest $r(y, \hat{y})$ were obtained under FRM. All structural coefficients estimated under FRM were statistically significant except for that of 6MW on YW. Comparisons of Spearman's rank correlations between posterior means of direct genetic effects of kids for growth traits under SMM and FRM revealed that taking the causal relationships among the studied growth traits of Markhoz goat into account may cause considerable re-ranking for the animals in terms of estimated breeding values, especially for the top-ranked animals. It may be concluded that FRM had more plausibility over SMM for genetic evaluation of the studied growth traits in Markhoz goat.

Introduction

Live body weight at different ages has decisive effects on the profitability of breeding enterprises. Therefore, these traits may be considered as selection criteria for developing efficient breeding programmes (Tosh and Kemp 1994). Selection of the best animals for body weight recorded at different ages to be parents of the next generation is a possible way for increasing meat production (Boujenane and Kansari 2002).

Rosa *et al.* (2011) have pointed out that in any breeding programme dealing with multiple traits, genetic evaluation has great importance for studying potential causal relationships among the traits. In the classical breeding programmes, breeding values of the selected candidates are predicted using standard mixed models [standard multivariate models (SMMs)], in which the existed potential causal relationships among the traits are ignored (Valente *et al.* 2013). Gianola and Sorensen (2004) developed the theory of quantitative genetics to become suitable for situations in which causal relationships exist between the phenotypes in a multivariate system.

Structural equation models (SEMs) enable fitting and studying cause-and-effect relationships between the traits (Wright, 1934) and were first introduced in genetics by Wright (1921) but have been ignored in quantitative genetics for many years. The work of Gianola and Sorensen (2004) stimulated the application of SEMs in animal breeding and genetics (Lopez de Maturana *et al.* 2010; Valente *et al.* 2010; Inoue *et al.* 2016; Mokhtari *et al.* 2018). Genetic parameters pertaining to SEMs can be useful for modelling biological relationships among the phenotypes (Valente *et al.* 2010). Furthermore, considering the high computational demands, fitting SEMs in the model is more parsimonious than SMMs, due to assumed uncorrelated residual effects. A number of studies have applied mixed-effects SEMs in the animal breeding context (Lopez de Maturana *et al.* 2010; Mokhtari *et al.* 2018; Amou Posht-e Masari *et al.* 2019).

Despite the advances in agricultural methods in developing countries, the number of goats has increased worldwide during the last few decades (Abadi *et al.* 2011; Shamsalddini *et al.* 2016). About 96% of goat's meat and milk are produced in developing countries, whereas only 4% are found in developed countries (Esmaili *et al.* 2019). Goat production is one of the major sources of income for farmers in the arid and semi-arid regions of the world (Barazandeh *et al.* 2012). Increasing meat, milk and fibre production of goats is not out of reach for farmers by using accurate and precise selection programmes (Moghbeli *et al.* 2013). Markhoz goat is one of the most important indigenous goat breeds in Iran. The breed is mainly kept by local flock holders in a wide range of forest mountain habitats in the region of Kurdistan, north-west of Iran. Markhoz goats are small-sized with a wide range in coat colour, varying from white to black (Rashidi *et al.* 2015). Many researchers have undertaken several studies on genetic evaluation of growth traits in Markhoz goat (Rashidi *et al.* 2008, 2011) and other goat breeds (Maghsoudi *et al.* 2009; Gholizadeh *et al.* 2010; Mohammadi *et al.* 2012); however, these studies have not considered possible causal relationships.

To the best of our knowledge, there is only one report on genetic evaluation of growth traits in breeds of goat considering possible causal relationships among them. Mokhtari *et al.* (2018) compared the SMM, which ignores the possible causal effects among the traits, with the recursive multivariate model (RMM), a type of SEM, which handles the existence of causal relationships among the traits, in terms of the predictive ability of models and the estimates of genetic parameters of growth traits in Raeini Cashmere goat. They concluded that RMM was more plausible for the genetic evaluation of growth traits in Raeini Cashmere goat in terms of better predictive ability over SMM. The importance of considering causal relationships among the traits for the accurate ranking of animals was documented (Amou Posht-e Masari *et al.* 2019).

Therefore, the objectives of the present research were to compare SMM and fully recursive multivariate model (FRM) in terms of their predictive ability. Furthermore, the effect of different mathematical models on the ranking of the animals based on their predicted breeding values was also examined.

Materials and methods

Flock management and the studied traits

The data set and pedigree information used in the present study were collected from 1993 to 2016 in Markhoz goat Breeding Station located in Sanandaj, Kurdistan province, north-western part of Iran. The herd was reared under a semi-intensive production system, in which goats were grazed on natural pastures in spring and were fed by a standard ration in other seasons of the year. The period of mating started in October and lasted until November, and the kidding season was from February to March. Does were first exposed to the bucks approximately at 18 months of age. Annually, 20–30 bucks were randomly allocated to mate with about 10 or 15 does each, with sire identification recorded. Some of the sires were used for two or three mating seasons. New-born kids were weighed and ear-tagged after birth time and allowed to remain with their dam for a week. One week after birth, the kids were separated from their dams and suckled twice a day until 3–4 months of age. All kids weaned on the same day (Rashidi *et al.* 2011).

The studied characteristics were body weight traits including birth weight (BW), weaning weight (WW), six months weight

Table 1. Descriptive statistics for the studied traits

Item	Traits (kg)				
	BW	WW	6MW	9MW	YW
Mean	2.6	16	18	21	25
SD	0.46	4.2	4.3	5.1	6.8
Min.	1.2	5	6	7	8
Max.	4.5	31	35	39	48
C.V. (%)	17.9	27	24	24	27
No. of records	2780	2780	2780	2780	2780
No. of sires	211	211	211	211	211
No. of dams	1216	1216	1216	1216	1216

BW, birth weight; WW, weaning weight; 6MW, six months weight; 9MW, nine months weight; YW, yearling weight.

(6MW), nine months weight (9MW) and yearling weight (YW). Animals with body weights outside of the range of mean $\pm 3 \times$ SD have been excluded from the data set. The structure and summary of the data set used are presented in Table 1.

Statistical analyses

Investigating the importance of maternal effects on the studied traits

In mammalian species, growth traits especially in early life are determined not only by the animal's own additive genetic merit but also by maternal effects. The maternal effects mainly denote those related to the milk production of dam and its mothering ability (Roy *et al.* 2008). Previous studies confirmed the importance of including maternal effects in genetic evaluation of growth traits in several goat breeds (Roy *et al.* 2008; Rashidi *et al.* 2011). Therefore, for studying the role of maternal effects on the genetic evaluation of the studied traits a restricted maximum likelihood procedure under average information algorithm, applying DMU programme (Madsen *et al.* 2014), was used and nine models including different combinations of direct additive effects, maternal additive genetic, maternal permanent environmental and maternal temporary environmental, were tested. The considered models (in matrix notation) are as below:

$y = X_b + Z_a + e$		Model 1
$y = X_b + Z_a + Z_{pe} + e$		Model 2
$y = X_b + Z_a + Z_m + e$	Cov(a, m) = 0	Model 3
$y = X_b + Z_a + Z_m + e$	Cov(a, m) = Aσ_{am}	Model 4
$y = X_b + Z_a + Z_m + Z_{pe} + e$	Cov(a, m) = 0	Model 5
$y = X_b + Z_a + Z_m + Z_{pe} + e$	Cov(a, m) = Aσ_{am}	Model 6
$y = X_b + Z_a + Z_{pe} + Z_1 + e$		Model 7
$y = X_b + Z_a + Z_m + Z_{pe} + Z_1 + e$	Cov(a, m) = 0	Model 8
$y = X_b + Z_a + Z_m + Z_{pe} + Z_1 + e$	Cov(a, m) = Aσ_{am}	Model 9

where y is a vector of records for the studied traits; b , a , m , pe , 1 and e are vectors of fixed, direct genetic, maternal genetic, maternal permanent environmental, maternal temporary

environmental (common litter effects) and the residual effects, respectively. The matrices of X , Z_a , Z_m , Z_{pe} , and Z_l are design ones associating corresponding effects to a vector of y . Also, A is the numerator relationship matrix and σ_{am} denotes covariance between additive and maternal effects. Common fixed effects included in the models for the studied traits were the sex of kids in 2 classes (male and female), dam age at lambing in 6 classes (2–7 years old), birth year in 23 classes (1993–2016) and birth type in 3 classes (single, twin and triplet). Interactions among fixed effects were also fitted. Age of kids at weaning, at six months, at nine months, and at yearling body weight weighing (in days) was considered as a linear covariate for WW, 6MW, 9MW, and YW, respectively. Significance testing of fixed effects and least square analyses were carried out using the general linear model procedure of the SAS software (SAS 2004). The interactions between considered fixed effects were not significant and therefore dropped out.

The Akaike’s information criterion (AIC) was applied for determining the most appropriate model among tested models (Akaike 1974):

$$AIC_i = -2 \log L_i + 2P_i$$

where $\log L_i$ is the maximized log-likelihood and P_i is the number of parameters fitted for model i . In each case, the model with the lowest AIC was considered as the best model. The AIC values under the considered animal models are given in Table 2, with the most appropriate model in boldface for each trait.

Statistical inference

After the selection of the most suitable model of genetic analysis for the studied traits, Bayesian Markov Chain Monte Carlo (MCMC) implementation was carried out applying the GIBBS2F90 programme of Misztal *et al.* (2002), which implements Gibbs sampling to evaluate the posterior density of the parameter estimates. The length of the chain and the burn-in period were examined by visual inspection of the trace plots of posterior samples of the parameters in several preliminary analyses. For each model, 100 000 iterations were run and posterior samples from each chain were thinned considering thinning intervals of 10 iterations after discarding the first 10 000 iterations as burn-in. Hence, 9000 samples were considered for computing features of the posterior distribution. Posterior analyses for calculating posterior means and posterior standard deviations (PSDs) were carried out applying the POSTGIBBSF90 programme of Misztal *et al.* (2002).

It was assumed that the direct additive and maternal additive genetic effects followed a multivariate normal distribution, a priori, with a null mean vector and a (co)variance matrix $G \otimes A$, where G and A are the genetic (co)variance matrix and numerator relationship matrix among animals, respectively. Furthermore, it was assumed that the vector of residual effects followed a multivariate normal distribution with a null mean vector and (co)variance matrix $R \otimes I_n$, where I_n is an identity matrix and R is the residual (co)variance matrix; \otimes shows the Kronecker product. Multivariate normal distribution was also assumed for maternal permanent environmental and maternal temporary environmental effects so that their fully conditional distributions were also multivariate normal. The prior distribution of the genetic (G), maternal permanent environmental (Pe) and maternal temporary environmental (L) (co)variance matrices were follow inverted

Table 2. AIC values from univariate analysis for the studied traits with the best model in bold

Model ^a	Traits				
	BW	WW	6MW	9MW	YW
Model 1	–2415	9169	9415	10 086	11 390
Model 2	–2460	9147	9401	10 084	11 391
Model 3	–2445	9155	9407	10 087	11 394
Model 4	–2441	9159	9410	10 090	11 397
Model 5	–2458	9150	9404	10 090	11 394
Model 6	–2455	9153	9407	10 093	11 397
Model 7	–2534	9150	9403	10 090	11 393
Model 8	–2532	9153	9406	10 093	11 396
Model 9	–2529	9157	9409	10 096	11 400

BW, birth weight; WW, weaning weight; 6MW, six months weight; 9MW, nine months weight; YW, yearling weight.

^aModel 1 included direct additive and residual effects; Model 2 included direct additive, maternal permanent environmental and residual effects; Model 3 included direct additive, maternal additive and residual effects; Model 4 is similar to Model 3, but a covariance between direct and maternal additive effects was assumed; Model 5 included direct additive, maternal additive, maternal permanent environmental and residual effects; Model 6 is similar to Model 5, but a covariance between direct and maternal additive effects was assumed; Model 7 included direct additive, maternal permanent environmental, maternal temporary environmental and residual effects; Model 8 included direct additive, maternal additive, maternal permanent environmental, maternal temporary environmental and residual effects; Model 9 is similar to Model 8, but a covariance between direct and maternal additive effects was assumed. The best model is shown in bold.

Wishart distribution so that their fully conditional posterior distributions were also inverted Wishart (Sorensen and Gianola 2002). The SEMs are not identifiable at the likelihood level due to the presence of extra parameters, including structural coefficients. For achieving identification, it was assumed that residual correlations in the system were uncorrelated. In other words, in SEMs, R was assumed to be a diagonal matrix for the identification purposes.

Lopez de Maturana *et al.* (2007) pointed out that the method described by Gianola and Sorensen (2004) for incorporating causal effects in quantitative genetics is not straightforward enough to perform in a general manner and showed that recursive models could be handled by fitting parent trait as a covariate for other trait(s) while genetic correlations between traits are considered in multivariate analyses. In this case, the parent trait denotes trait which causally influences other trait(s). Therefore, this methodology was applied in the present study. Detailed information and the theoretical background about the methodology used in the present study for fitting recursive models are given by Lopez de Maturana *et al.* (2007).

Model comparisons

The SMM and FRM were compared by applying deviance information criterion (DIC), predictive ability measures, and Spearman’s rank correlations between posterior means of genetic effects under SMM and FRM. The DIC takes the trade-off between model goodness-of-fit and the corresponding complexity of model into account (Bouwman *et al.* 2014). A model with smaller DIC values is better supported by the data.

For assessing the predictive ability of the tested models (SMM and FRM), the dataset was randomly partitioned five times into two sets including the training set (50% of data set) and testing

set (retained 50% data set). 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 assessed by PREDICTF90 programme of Misztal *et al.* (2002) and compared applying two measures. The first measure was the mean square of error (MSE) as follow:

$$\text{MSE} = \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{n}$$

where, y_i and \hat{y}_i represent the i th observed and predicted record for each trait in the testing data set, respectively, and n is the number of records. The second measure was the Pearson correlation between observed and predicted values ($r(y, \hat{y})$) in the testing data set. The MSE and $r(y, \hat{y})$ values were calculated five times, and the average of obtained results was used as the final value. The lower MSE and higher $r(y, \hat{y})$ indicate the superiority of the model.

The SMM and FRM were also compared using Spearman's rank correlations between the posterior means of genetic effects for all, 50% top-ranked, 10% top-ranked and 1% top-ranked animals. For this purpose, breeding values (equivalent to the SMM) were estimated as (Konig *et al.* 2008):

$$\mathbf{BV}^* = \mathbf{A}^{-1}\mathbf{BV}$$

where \mathbf{BV} is a vector of breeding values estimated under FRM. The matrix \mathbf{A} is the structural coefficients matrix, in which diagonal elements are filled with 1 and the off-diagonal elements are determined based on the causal relationships between the traits. Structural coefficients are in fact a kind of regression coefficient, which are estimated by fitting SEMs (Gianola and Sorensen 2004). The matrix of structural coefficients with five traits under a FRM, which is used in the present study, is as follows:

$$\mathbf{A}_{5 \times 5} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ -\lambda_{21} & 1 & 0 & 0 & 0 \\ -\lambda_{31} & -\lambda_{32} & 1 & 0 & 0 \\ -\lambda_{41} & -\lambda_{42} & -\lambda_{43} & 1 & 0 \\ -\lambda_{51} & -\lambda_{52} & -\lambda_{53} & -\lambda_{54} & 1 \end{bmatrix}$$

where the first trait affects second, third, fourth, and fifth traits, the second trait affects the third, fourth, and fifth traits, the third trait affects fourth and fifth traits, and eventually, the fourth trait has a causal effect on the fifth trait.

Results

Direct additive genetic and maternal additive genetic effects, without considering covariance between them, and maternal permanent environmental effects (Model 5) were random sources of variation for BW. Model 2, in which direct additive genetic effects and maternal permanent environmental effects were significant random effects, determined as the best one for WW, 6MW and 9MW traits. Maternal effects had no influencing effects on YW.

The outcome of comparisons between SMM and FRM based on DIC is presented in Table 3. The lower DIC was obtained under FRM than SMM. The SMM and FRM were also compared in terms of the predictive ability of models based on the average MSE and average Pearson's correlation coefficient between observed and predicted records ($r(y, \hat{y})$) of the traits under these

Table 3. DIC values from the different multivariate studied models

Model	DIC
SMM	35 661
FRM	35 167

SMM, standard multivariate model; FRM, fully recursive multivariate model.

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

Traits	Model			
	SMM		FRM	
	MSE	$r(y, \hat{y})$	MSE	$r(y, \hat{y})$
BW	0.176	0.456	0.174	0.471
WW	11.4	0.593	10.8	0.635
6MW	12.5	0.564	6.1	0.794
9MW	17.6	0.581	7.5	0.769
YW	24.5	0.665	12.4	0.849

BW, birth weight; WW, weaning weight; 6MW, six months weight; 9MW, nine months weight; YW, yearling weight; SMM, standard multivariate model; FRM, fully recursive multivariate model; MSE, mean square of error, $r(y, \hat{y})$ = Pearson correlation between observed and predicted values.

models (Table 4). For all the studied traits, the lowest MSE and the highest $r(y, \hat{y})$ values were obtained under FRM, which was more pronounced for 6MW, 9MW and YW than BW and WW.

Applying FRM features of posterior means and PSDs for structural coefficients among the studied body weight traits of Markhoz goat are presented in Table 5. All the estimated structural coefficients were positive and highly significant, except for that of 6MW on YW. Considering the causal structure considered under FRM (Fig. 1) among the studied body weight traits of Markhoz goat, BW had direct causal effects on all other studied traits the estimated direct causal effects of BW on WW, 6MW, 9MW and YW were 1.24, 0.79, 0.87 and 0.50, respectively. In other words, each 1 kg increase in BW of Markhoz kids will increase WW, 6MW, MW and YW as 1.24, 0.79, 0.87 and 0.50 kg, respectively. Direct causal effects of WW on 6MW, 9MW and YW were 0.65, 0.22 and 0.16, respectively.

Spearman's rank correlations between posterior means of direct genetic effects within the studied traits applying SMM and FRM for the whole animals, 50, 10 and 1% of top-ranked animals are shown in Table 6. The highest Spearman's rank correlation (1.00) between posterior means of direct genetic effects was obtained for BW. Rankings of the ten top-ranked animals for the trait studied based on the posterior direct genetic effects under SMM and FRM are shown in Table 7. Substantial changes were observed in the rank of the ten top-rank animals especially for 6MW, 9MW and YW. For example, for YW, the best animal when applying SMM was ranked as the rank of 231 under FRM.

Discussion

Statistical comparisons between SMM and FRM

Mokhtari *et al.* (2018) compared RMM and SMM for genetic evaluation of early growth traits in Raeini Cashmere goat including BW, WW and 6MW in terms of DIC, MSE and $r(y, \hat{y})$ and

Table 5. Posterior means \pm PSD for the structural coefficients under the fully recursive multivariate (FRM) model

Traits	Mean \pm PSD ^a
BW-WW	1.2 \pm 0.27
BW-6MW	0.8 \pm 0.19
BW-9MW	0.9 \pm 0.19
BW-YW	0.5 \pm 0.28
WW-6MW	0.7 \pm 0.03
WW-9MW	0.2 \pm 0.03
WW-YW	0.2 \pm 0.04
6-9MW	0.6 \pm 0.03
6MW-YW	0.0 \pm 0.04
9MW-YW	0.7 \pm 0.04

BW, birth weight; WW, weaning weight; 6MW, six months weight; 9MW, nine months weight; YW, yearling weight; PSD, posterior standard deviation.

^a99% HPD intervals did not include zero.

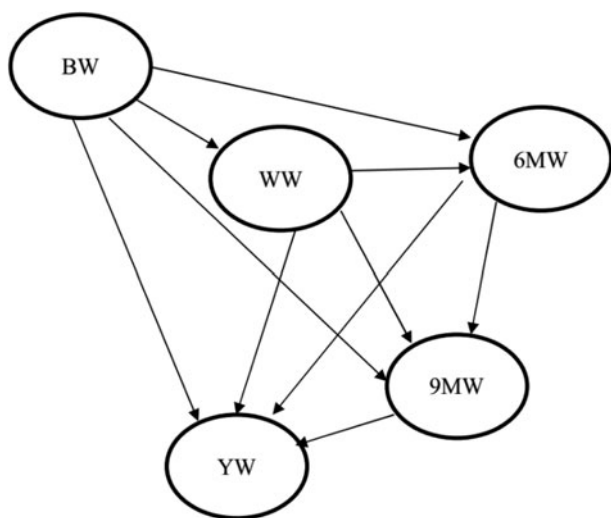


Fig. 1. Multivariate fully recursive model considered among the studied growth traits in Markhoz goat (BW, birth weight; WW, weaning weight; 6MW, six months weight; 9MW, nine months weight; YW, yearling weight).

Table 6. Spearman’s rank correlations of posterior means of direct genetic effects for studied growth traits in Markhoz goat under the standard multivariate (SMM) and fully recursive multivariate (FRM) models

Traits	All animals	50% top-ranked	10% top-ranked	1% top-ranked
BW	1.000**	1.000**	1.000**	1.000**
WW	0.994**	0.977**	0.940**	0.837**
6MW	0.945**	0.841**	0.762**	0.550**
9MW	0.925**	0.808**	0.670**	0.205 ^{ns}
YW	0.892**	0.740**	0.548**	0.190 ^{ns}

BW, birth weight; WW, weaning weight; 6MW, six months weight; 9MW, nine months weight; YW, yearling weight.

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

found lower DIC, lower MSE and higher $r(y, \hat{y})$ (for WW and 6MW) under RMM than the SMM one. They concluded that considering causal relationships among the studied growth traits in Raeini goat may provide a better explanation for biological relationships among the studied traits. Amou Posht-e Masari *et al.* (2019) compared three multivariate models including SMM, temporal RMM and FRM for genetic evaluation of growth traits in Lori-Bakhtiari sheep breed, temporal RMM favoured over other models in terms of lower DIC.

In a previous study, Lopez de Maturana *et al.* (2010) considered causal relationships among calving traits including gestation length (as parent trait), calving difficulty and stillbirth in first-parity US Holsteins under three RMMs and compared them with the SMM in terms of mean square error and Pearson’s correlation coefficient between predicted and observed records. They generally concluded that models included causal relationships performed better than SMM by lower mean square error and higher Pearson correlation coefficient between predicted and observed records.

Structural coefficients

In the present study, any improvement in BW had positive causal effects on the other body weight traits in Markhoz goat. Mokhtari *et al.* (2018) reported direct causal effects of BW on WW and on 6MW of Raeini Cashmere kids as 1.94 and 2.48 kg, respectively, which were higher than the corresponding values estimated in the present study. Mioc *et al.* (2011) studied the BW and WW of Croatian multicoloured goat kids and reported that kids with higher BW have higher WW, also. Valente *et al.* (2013) pointed out that the genetic effects from SMM and SEM have different meanings, while the SMM represent overall genetic effects that included all direct and indirect (which mediating by other traits) effects on each trait and SEM represent only direct effects (which not mediating by other traits in the causal network). Overall effects may be partitioned into direct and indirect ones by applying SEM (Valente *et al.* 2013). As shown in Fig. 1, BW had indirect causal effects on 6MW (mediated via WW), on 9MW (mediated via WW and 6MW) and YW (mediated via WW, 6MW and 9MW). The indirect causal effect of BW on 6MW was calculated as the product direct causal effects of BW on WW (1.24), WW on 6MW (0.65) which was 0.806. The overall causal effects of BW on 6MW are the summation of direct (0.79) and indirect (0.806) causal effects, which is equal to 1.596. In general, each 1 kg increase in BW of Markhoz kids will increase 6MW as 1.1596 kg. The overall causal effect (direct and indirect) of BW on 6MW of Raeini Cashmere goat was obtained as 4.48 kg by Mokhtari *et al.* (2018) which was higher than the corresponding value obtained in the present study. Considering the same manner, the overall effects of BW on 9MW and YW were calculated as 1.337 and 0.832 kg, respectively.

It may be concluded that any increase in WW of Markhoz kids significantly will increase 6MW, 9MW and YW. Mokhtari *et al.* (2018) studied causal relationships among early growth traits in Raeini Cashmere goat by fitting a FRM. They estimated direct causal recursive effects of WW on 6MW as 1.03 kg which was higher than the corresponding value obtained in the present study. WW had indirect causal effects on 9MW (mediated via 6MW) and on YW (mediated via 6MW and 9MW), which were calculated as 0.38 and 0.27 kg, respectively. Overall causal effects of WW on 9MW and YW were obtained as 0.60 and 0.43 kg, respectively. Direct causal effects of 0.58 and 0.71 kg

Table 7. Rank comparison of ten top-ranked animals based on posterior means of genetic effects under the standard multivariate (SMM) and fully recursive multivariate (FRM) models

Ranking for trait										
BW		WW		6MW		9MW		YW		
SMM	FRM	SMM	FRM	SMM	FRM	SMM	FRM	SMM	FRM	
1	1	1	2	1	32	1	10	1		231
2	2	2	3	2	13	2	17	2		12
3	3	3	1	3	1	3	3	3		9
4	4	4	4	4	7	4	5	4		43
5	5	5	6	5	62	5	2	5		57
6	6	6	14	6	95	6	24	6		128
7	7	7	5	7	23	7	17	7		46
8	8	8	20	8	43	8	38	8		10
9	9	9	12	9	4	9	62	9		90
10	10	10	11	10	65	10	13	10		100

BW, birth weight; WW, weaning weight; 6MW, six months weight; 9MW, nine months weight; YW, yearling weight.

were obtained from 6MW on 9MW and from 9MW on YW, respectively. The indirect causal effect of 6MW on YW (mediated via 9MW) was calculated as 0.411. No significant direct causal effect was observed from 6MW on YW.

Ranking of animals under SMM and FRM

Considering causal relationships among the studied growth traits of Markhoz goat had no impact on posterior means of direct genetic effects of BW. In the fully recursive model considered among growth traits of Markhoz goat (Fig. 1) BW is considered as a parent trait, which influenced all other traits but not influenced by the others. The obtained Spearman's rank correlation between posterior means of direct genetic effects of BW may be explained partly by such a causal structure. When 50% and 10% of top-ranked animals were considered, the lowest Spearman's rank correlations were obtained for YW (Table 6). There were substantial changes for rank correlations between posterior means of genetic effects under SMM and FRM for 1% top-ranked animals, except for BW. Spearman's rank correlations between posterior means of direct genetic effects for 9MW and YW were not statistically significant ($P > 0.05$); implied substantial re-ranking of animals under SMM and FRM. Therefore, this underlies the importance of model choice in breeding value estimation and it may be concluded that accounting for causal relationships among the studied growth traits in Markhoz goat may have beneficial effects for accurate predicting of breeding values and correspondingly accurate ranking of top-ranked animals. König *et al.* (2008) studied causal relationships between claw disorders and milk yield in Holstein cows via recursive models and reported changes in the ranking of top-ranked sires under SMM and TRM. Amou Posht-e Masari *et al.* (2019) reported re-ranking of the top-ranked animal for 6MW of Lori-Bakhtiari lambs under SMM and temporal recursive model.

In conclusion, inferring relationships among the studied growth traits in Markhoz could help to identify the development of the growth process from birth to yearling age. Furthermore, FRM showed more superiority over SMM in terms of lower

MSE and higher Pearson's correlation coefficient between observed and predicted records of the studied growth traits. Furthermore, for fitting FRM, the residual correlations among the traits studied were set zero, which reduced the number of parameters to be estimated (15 residual correlations were not estimated under FRM). On the other hand, FRM included extra parameters over SMM as structural coefficients (10 structural coefficients were estimated in the present study). It may be concluded that the FRM is a more parsimonious model than the corresponding SMM which reduces computational demands in a multivariate genetic evaluation context. Comparisons of rank correlations between posterior means of direct genetic effects for the studied growth traits under SMM and FRM revealed that taking the causal relationships among the studied growth traits of Markhoz goat into account may cause considerable re-ranking for the animals, especially top-ranked ones, in terms of the estimated breeding values.

In conclusion, the present study revealed that causal effects had more statistical advantages than ignoring them for accurate genetic evaluation of the studied growth traits in Markhoz goat in terms of predictive ability of models and ranking of animals.

Financial support. This research received no specific grant from any funding agency, commercial or not-for-profit sectors.

Conflicts of interest. The authors certify that there are no conflicts of interest among authors and between authors and other people and organizations.

Ethical standards. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

References

- Abadi MRM, Askari N, Baghizadeh A and Esmailzadeh AK (2011) A directed search around caprine candidate loci provided evidence for microsatellites linkage to growth and cashmere yield in Rayini goats. *Small Ruminant Research* **81**, 146–151.
- Akaike H (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19**, 716–723.

- Amou Posht-e Masari H, Hafezian SH, Abdollahi-Arpanahi R, Mokhtari MS RMG and Taheri Yeganeh A** (2019) The comparison of alternative models for genetic evaluation of growth traits in Lori-Bakhtiari sheep: implications on predictive ability and ranking of animals. *Small Ruminant Research* **173**, 59–64.
- Barazandeh A, Moghbeli SM, Vatankhah M and Mohammadabadi MR** (2012) Estimating non-genetic and genetic parameters of pre-weaning growth traits in Raini Cashmere goat. *Tropical Animal Health and Production* **44**, 811–817.
- Boujenane I and Kansari J** (2002) Estimates of (co)variances due to direct and maternal effects for body weights in Timahdite sheep. *Animal Science* **74**, 409–414.
- Bouwman AC, Valente BD, Janss LLG, Bovenhuis H and Rosa GJM** (2014) Exploring causal networks of bovine milk fatty acids in a multivariate mixed model context. *Genetics Selection Evolution* **46**, 2.
- Esmaili AVN, Esmailizadeh Koshkooieh A, Aytolahi AM, Mohammadabadi MR, Babenko OI, Bushtruk M, Tkachenko S, Stavetska R and Klopenko N** (2019) Comparison of genetic diversity of leptin gene between wild goat and domestic goat breeds in Iran. *Malaysian Applied Biology* **48**, 85–93.
- Gholizadeh M, Rahimi Mianji G, Hashemi M and Hafezian H** (2010) Genetic parameter estimates for birth and weaning weights in Raeini goats. *Czech Journal of Animal Science* **55**, 30–36.
- Gianola D and Sorensen D** (2004) Quantitative genetic models for describing simultaneous and recursive relationships between phenotypes. *Genetics* **167**, 1407–1424.
- Inoue K, Valente BD, Shoji N, Honda T, Oyama K and Rosa GJM** (2016) Inferring phenotypic causal structures among meat quality traits and the application of a structural equation model in Japanese black cattle. *Journal of Animal Science* **94**, 4133–4142.
- Konig S, Wu XL, Gianola D, Heringstad B and Simianer H** (2008) Exploration of relationships between claw disorders and milk yield in Holstein cows via recursive linear and threshold models. *Journal of Dairy Science* **91**, 395–406.
- Lopez de Maturana E, Legarra A, Varona L and Ugarte E** (2007) Analysis of fertility and dystocia in Holsteins using recursive models to handle censored and categorical data. *Journal of Dairy Science* **90**, 2012–2024.
- Lopez de Maturana E, de los Campos G, Wu XL, Gianola D, Weigel KA and Rosa GJM** (2010) Modeling relationships between calving traits: a comparison between standard and recursive mixed models. *Genetics Selection Evolution* **42**, 1.
- Madsen P, Jensen J, Labouriau R, Christensen OF and Sahana G** (2014) DMU – a package for analyzing multivariate mixed models in quantitative genetics and genomics. *Proceedings of the 10th World Congress on Genetics Applied to Livestock Production, Vancouver, Canada*.
- Maghsoudi A, Vaez Torshizi R and Safi Jahanshahi A** (2009) Estimates of (co)variance components for productive and composite reproductive traits in Iranian Cashmere goats. *Livestock Science* **126**, 162–167.
- Mioc B, Susic V, Antunovic Z, Prpic Z, Vnucec I and Kasap A** (2011) Study on birth weight and pre-weaning growth of Croatian multicolored goat kids. *Veterinarski Arhiv* **81**, 339–347.
- Misztal I, Tsuruta S, Strabel T, Auvray B, Druet T and Lee D** (2002) BLUPF90 and related programs (BGF90). *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production, Montpellier, France*.
- Moghbeli SM, Barazandeh A, Vatankhah M and Mohammadabadi MR** (2013) Genetics and non-genetics parameters of body weight for post-weaning traits in Raini Cashmere goats. *Tropical Animal Health and Production* **45**, 1519–1524.
- Mohammadi H, Moradi Shahrehabak M and Moradi Shahrehabak H** (2012) Genetic parameter estimates for growth traits and prolificacy in Raeini Cashmere goats. *Tropical Animal Health and Production* **44**, 1213–1220.
- Mokhtari MS, Moghbeli Damaneh M and Abdollahi Arpanahi R** (2018) The application of recursive multivariate model for genetic evaluation of early growth traits in Raeini Chasmere goat: a comparison with standard multivariate model. *Small Ruminant Research* **165**, 54–61.
- Rashidi A, Sheikhhamedi M, Rostamzadeh J and Shrestha JNB** (2008) Genetic parameter estimates of body weight at different ages and yearling fleece weight in Markhoz goats. *Asian-Australian Journal of Animal Science* **21**, 1395–1403.
- Rashidi A, Bishop SC and Matika O** (2011) Genetic parameter estimates for pre-weaning performance and reproduction traits in Markhoz goats. *Small Ruminant Research* **100**, 100–106.
- Rashidi A, Mokhtari M and Gutierrez JP** (2015) Pedigree analysis and inbreeding effects on early growth traits and greasy fleece weight in Markhoz goat. *Small Ruminant Research* **124**, 1–8.
- Rosa GJM, Valente BD, de los Campos G, Wu XL, Gianola D and Silva MA** (2011) Inferring causal phenotype networks using structural equation models. *Genetics Selection Evolution* **43**, 6.
- Roy R, Mandal A and Notter D** (2008) Estimates of (co) variance components due to direct and maternal effects for body weights in Jamunapari goats. *Animal* **20**, 354–359.
- SAS (Statistical Analysis System)** (2004) *SAS Users' Guide, Version 9.1*. Cary, North Carolina, USA: SAS Institute Inc.
- Shamsalddini S, Mohammadabadi MR and Esmailizadeh AK** (2016) Polymorphism of the prolactin gene and its effect on fiber traits in goat. *Russian Journal of Genetics* **52**, 405–408.
- Sorensen DA and Gianola D** (2002) *Likelihood, Bayesian and MCMC Methods in Quantitative Genetics*. New York, 175 Fifth Avenue, New York: Springer-Verlag Inc.
- Tosh JJ and Kemp RA** (1994) Estimation of variance components for lamb weights in three sheep populations. *Journal of Animal Science* **72**, 1184–1190.
- Valente BD, Rosa GJM, de los Campos G, Gianola D and Silva MA** (2010) Searching for recursive causal structures in multivariate quantitative genetics mixed models. *Genetics* **185**, 633–644.
- Valente BD, Rosa GJM, Gianola D, Wu XL and Weigel K** (2013) Is structural equation modeling advantageous for the genetic improvement of multiple traits? *Genetics* **194**, 561–572.
- Wright S** (1921) Correlation and causation. *Journal of Agricultural Research* **20**, 557–585.
- Wright S** (1934) An analysis of variability in number of digits in an inbred strain of guinea pigs. *Genetics* **19**, 506–536.