



Inferring causal relationships among growth traits in Kermani sheep applying structural equation modeling

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Abstract Data on early growth traits of 1574 Kermani lambs, the offspring of 874 dams and 122 sires, were recorded between 1992 to 2010 at the Breeding Station of Kermani sheep breed in Shahr-e Babk city, Kerman province, Iran. The traits included the birth weight (BW), weaning weight (WW) and weight at six months of age (6MW). Preliminary investigations demonstrated the decisive effects of direct and maternal genetic influences on the expression of these traits. The data were used to adopt three models of genetic analysis. The first model was the standard multivariate model (SMM), which does not consider the causal relationships among the traits. The second model was the fully recursive multivariate model (FRM), which assumes the existence of causal influences of BW on WW and on 6MW, and the influence of WW on 6MW. The third model was the temporal recursive model (TRM), in which BW causally impacts on WW, and WW on 6MW. The Bayesian approach, via Gibbs sampling, was used for genetic analysis. The adopted models were compared considering the deviance information criterion (DIC) and mean square error of prediction (MSE) as criteria for assessing the predictive ability of the models. The DIC values revealed the superiority of TRM over FRM and SMM. Under the investigated multivariate models, the values of MSE were similar for BW but those obtained for WW and 6MW were the lowest under TRM. The causal effect of BW on WW and that of WW on 6MW were statistically significant estimates of 1.10 kg and 0.70 kg, respectively. Furthermore, accounting for causal relationships, the early growth traits in Kermani sheep may have advantageous impacts on prediction of the breeding values and consequently the accuracy of lamb ranking for selective breeding purposes. Generally, significant causal relationships were detected among the early body weight traits in Kermani sheep, and the superiority of TRM over other models showed the necessity of considering such causal influences in the genetic evaluation of these growth-related characteristics.

Keywords: body weight, maternal effects, predictive ability, recursive model

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Introduction

Structural equation modeling (SEM), an extension of multivariate regression model which allows studying and testing causal relationships between phenotypes,

was first presented in genetics by Wright (1921). The theory of quantitative genetics was developed by Gianola and Sorensen (2004) for describing conditions in

which causal relationships, including recursive and / or simultaneous ones, exist among the traits in a multivariate framework. The SEM methodology has been exploited in several species such as sheep (Amou Posht-e Masari et al., 2019), goat (Mokhtari et al., 2018) and dairy cows (Lopez de Maturana et al., 2010). Rosa et al. (2011) pointed out that the consideration of potential causal relationships among traits was of great importance for developing breeding program dealing with multiple-trait genetic evaluations.

Live body weights and growth rate at various ages are of great importance on the gainfulness of the breeding systems in small ruminants. Thus, these traits should be considered as selection criteria for constructing efficient selective programs (Tosh and Kemp, 1994). As pointed out by Boujenane and Kansari (2002), selection of the genetically superior animals for growth potential is a practicable method for enhancing meat production. In mammals, growth characteristics are mainly determined by the additive genetic effects and also by maternal ones, especially early in life. Rashidi et al. (2008) documented the significance of considering maternal components for the genetic assessment of early growth traits in Kermani sheep breed.

The potential existence of causal relationships among growth traits in Raeini Cashmere goats (Mokhtari et al., 2018) and Lori-Bakhtiari sheep (Amou Posht-e Masari et al., 2019) was investigated applying SEM, and the advantage of multi-trait models with causal relationships was confirmed over the standard multivariate models which didn't involve such causal relationships.

Kermani sheep, a medium-sized and dual-purpose (meat and wool) fat-tailed sheep breed, is the native of the south-eastern areas of Iran, and adapted to the arid and unfavorable environmental conditions in the region (Rashidi et al., 2008). There is no previous investigation for inferring potential causal relationships among early growth traits in Kermani lambs. Thus, the objective of the current study was to infer the causal structure among the early growth traits and testing the possible multivariate

animal models for the genetic assessment of these traits in Kermani lambs.

Materials and methods

Management of the flock at the breeding station

Management of the experimental flock was similar to that of nomadic flocks in the area. The Breeding Station of Kermani sheep is in Shahr-e Babak city, Kerman province, Iran. Kermani lambs were kept during the day on the nearby low quality pastures, and housed at night. Supplementary feeding was provided during the cold season and before mating. The season of breeding lasted from mid-August to mid-September with lambing at mid-January to mid-February, respectively. The ewes were bred at about 18 months of age, and lambs were weaned at about 3 months of age (75-105 days old). Generally, one fertile ram was assigned to 25-35 ewes. Lambs with outlier live body weights, i.e. outside the range of mean $\pm 2.5 \times S.D.$, were omitted from analysis.

Data and traits

Records on the body weight and genealogical information were derived from 1992 to 2010. The traits considered in the present study were early growth traits including the birth weight (BW), weaning weight (WW) and weight at six months of age (6MW). The structure of the edited data set is shown in Table 1.

Statistical analysis

The effect of maternal components on early growth traits

To study the significance of maternal components on the genetic assessment of the early growth traits in Kermani sheep a derivative-free algorithm restricted maximum likelihood (REML) procedure was used and various combinations of the direct and maternal components were evaluated under six univariate animal mo-

Table 1. Descriptive statistics for the live body weight traits in Kermani sheep

Item	Traits ¹		
	BW (kg)	WW (kg)	6MW (kg)
No. of records	1574	1574	1574
Mean	3.30	20.52	23.95
S.D.	0.48	4.39	4.62
Min.	1.60	9.50	12.00
Max.	4.8	36.00	42.50
No. of sires	122	122	122
No. of dams	874	874	874

¹BW: birth weight, WW: weaning weight, 6MW: weight at six months of age

dels using the WOMAT program (Meyer, 2007). The matrix notation of the models is shown below:

$y = Xb + Z_1a + e$		Model 1
$y = Xb + Z_1a + Z_3pe + e$		Model 2
$y = Xb + Z_1a + Z_2m + e$	$Cov(a,m) = 0$	Model 3
$y = Xb + Z_1a + Z_2m + e$	$Cov(a,m) = A\sigma_{am}$	Model 4
$y = Xb + Z_1a + Z_2m + Z_3pe + e$	$Cov(a,m) = 0$	Model 5
$y = Xb + Z_1a + Z_2m + Z_3pe + e$	$Cov(a,m) = A\sigma_{am}$	Model 6

where, y is a the vector of records for the considered growth traits; b , a , m , pe and e are vectors related to the fixed, direct genetic, maternal genetic, maternal permanent environmental and the residual components, respectively. The X , Z_a , Z_m and Z_l are design matrices associating these effects to y . Also, A is the matrix of numerator relationship and σ_{am} represents the covariance between direct and maternal components. The fixed effects fitted in the animal models were lamb sex (male and female), ewe age at lambing in 6 categories (2-7 years old), year of the birth of lamb in 18 categories (1992-2010) and birth type of lamb (single and twin). The corresponding interactions were also included in the primary analyses. The lamb age (in days) at three and six month's body weights was included as linear covariate for WW and 6MW, respectively. Significance testing of the fixed effects for inclusion in the models of the genetic analysis was performed by applying the general linear model (GLM) procedure (SAS, 2004). Interactions among the fixed effects were not significant and excluded from the final animal models. The best univariate model was selected based on the Bayesian Information Criterion (BIC; Gayawan and Ipinyomi, 2009).

The model with the lowest BIC was chosen as the best model for the genetic analysis of each trait.

The best model was then used in multivariate analyses accomplished under three models via the Bayesian approach. In the standard multivariate model (SMM), the likely existence of the causal relationships among growth traits were ignored. A fully recursive relationship among traits (FRM) was assumed in the second model. Under FRM, it was hypothesized that each trait could causally impact on the other subsequent traits (Figure 1).

The third model assumed a recursive temporal sequence among the traits (TRM). Under TRM, causal effects were assumed based on the sequential time of the traits (Figure 2), in which each trait is causally influenced by its prefix, only. The fixed and random effects, fitted in SMM, FRM and TRM, were the same. Lopez de Maturana et al. (2007) commented that the methodology developed by Gianola and Sorensen (2004) for incorporating the cause-and-effect relationships in genetic analyses is difficult to accomplish sufficiently, and demonstrated that recursive multivariate models could be handled by considering the parent trait as a co-variable for other trait(s) while simultaneously considering the genetic correlations among all traits involved in the genetic analysis. In SEM literature, the parent trait implies a trait which causally impacts on the other trait. For fitting TRM and FRM, the same method described by Lopez de Maturana et al. (2007) was performed. More details on this methodology and the relevant theoretical background were presented by Lopez de Maturana et al. (2007).

The Bayesian Markov Chain Monte Carlo execution

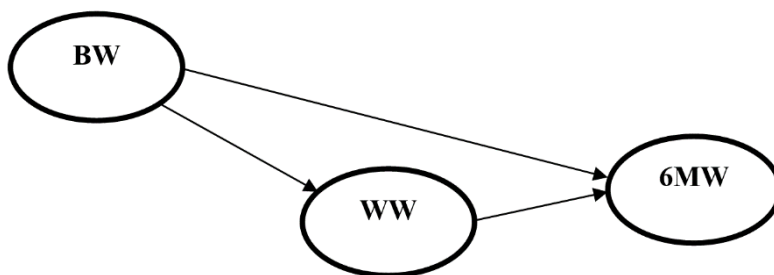


Figure 1. The multivariate fully recursive model considered among the studied growth traits in Kermani sheep (BW: birth weight, WW: weaning weight, 6MW: weight at six months of age).



Figure 2. The multivariate temporal recursive model considered among the studied growth traits in Kermani sheep (BW: birth weight; WW: weaning weight; 6MW: weight at six months of age)

was done applying the GIBBS2f90 (Mizstal et al., 2002). For each of the multivariate models (SMM, TRM and FRM), 200,000 iterations were run. The first 50,000 iterations were ignored as the warming-up period and the remaining posterior samples were thinned every 10 iterations. Post-Gibbs analyses were implemented by the POSTGIBBSF90 (Mizstal et al., 2002). Under post-Gibbs analysis, posterior means and posterior standard deviations of the genetic parameters were computed. Also, the convergence achievement checking was carried out.

The general form of an SEM-based multivariate animal model (the best model for each trait under univariate analyses) is as follows:

$$\Lambda \mathbf{y}_i = \mathbf{X}\mathbf{b}_i + \mathbf{Z}_1\mathbf{a}_i + \mathbf{Z}_2\mathbf{m}_i + \mathbf{e} \quad \text{Cov}(\mathbf{a},\mathbf{m}) = \mathbf{0}$$

In the Lambda matrix (Λ) which represents the structural coefficients, diagonal elements are shown as 1 and the off-diagonal ones are specified according to the magnitude and sign of the causal relationships among the traits. Under SMM, Λ is an identity matrix with the order equal to the number of traits. Structural coefficients are types of regression coefficients and estimated via fitting SEM (Gianola and Sorensen, 2004). Considering an FRM with three traits, the matrix of structural coefficients is as follows:

$$\Lambda = \begin{bmatrix} 1 & 0 & 0 \\ -\lambda_{21} & 1 & 0 \\ -\lambda_{31} & -\lambda_{32} & 1 \end{bmatrix}$$

where, the first trait causally impacts on the second and third traits, and the second trait on the third one. Considering a TRM with three traits, the matrix of structural coefficients is as follows:

$$\Lambda = \begin{bmatrix} 1 & 0 & 0 \\ -\lambda_{21} & 1 & 0 \\ 0 & -\lambda_{32} & 1 \end{bmatrix}$$

The deviance information criterion (DIC) was used for comparing the SMM, FRM and TRM. The model with the lowest DIC is regarded as the most suitable one. For evaluating the predictive ability of the SMM, FRM

and TRM, the data set was divided by random five times into two subsets included the training subset (50% of the data set) and testing subset (the retained 50% of the data set). Afterwards, by considering the training subsets, solutions for the fixed and random direct and maternal effects were estimated and applied for predicting the body weight records in the testing subsets. The predictive abilities of the SMM, FRM and TRM were evaluated using the PREDICTF90 (Mizstal et al., 2002), and compared by applying the mean square error of prediction (MSE) as:

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

where, y_i and \hat{y}_i refer to i^{th} observed and predicted body weights for any of the traits in the testing subset, n denotes the number of body weight records in the testing subset. The MSE was computed five times and averaged.

The Spearman's rank correlations between posterior means of the direct genetic effects were also calculated for both SMM and SEM. For this purpose, the estimates of breeding values under SEM were transformed into SMM equivalent by the following formula (Konig et al., 2008):

$$\mathbf{bv}^* = \Lambda^{-1} \mathbf{bv}$$

in which, \mathbf{bv} is the vector of system breeding values which was estimated under SEM.

Results and discussion

Model selection for genetic analysis

The BIC values from the univariate analyses for each trait are shown in Table 2. The most appropriate univariate model for BW, WW and 6MW contained the direct and maternal additive genetic effects by ignoring the covariance between them (Model 3). The decisive effect of the maternal components on the growth traits of sheep has been reported (Boujenane and Kansari, 2002;

Table 2. The BIC values from the univariate analysis of live body weight traits in Kermani lambs (the best model is shown in bold face)

Model	Traits ¹		
	BW	WW	6MW
Model 1	-1440.63	8455.48	6582.58
Model 2	-1457.74	8425.65	6581.56
Model 3	-1464.15	8422.32	6576.18
Model 4	-1457.61	8430.85	6584.11
Model 5	-1458.00	8427.99	6584.07
Model 6	-1451.60	8434.05	6591.62

¹BW: birth weight, WW: weaning weight, 6MW: weight at six months of age

Table 3. The DIC values from various multivariate models

Model ¹	DIC
SMM	12431.9928
FRM	12328.5159
TRM	12304.0707

¹SMM: Standard multivariate model, FRM: Fully recursive multivariate model, TRM: Temporal recursive multivariate model

Rashidi et al., 2008). Therefore, the maternal components should be considered in the models applied for the genetic evaluation of live body weight traits in Kermani lambs.

The DIC values obtained by fitting SMM, FRM and TRM are presented in Table 3. The FRM and TRM models were superior to the SMM one, and among the tested multivariate models, TRM was the most appropriate one for multivariate genetic analysis of the growth traits in Kermani sheep. Because TRM fits more appropriately than the FRM on the data, only the results obtained from fitting TRM were compared with SMM. Mokhtari et al. (2018) comparing the SMM and FRM for estimating the genetic parameters of early body weight traits in Raeini Cashmere goats, found smaller DIC for FRM than for SMM which shows the superiority of FRM over SMM. Amou Posht-e Masari et al. (2019) compared three multivariate animal models (SMM, FRM and TRM) for the genetic evaluation of the growth traits in Lori-Bakhtiari sheep. They concluded that TRM had more advantages than others in terms of the predictive ability of models. The ability of a model for predicting the data is crucial for animal breeders. The calculated MSE values for SMM, FRM and TRM for growth traits are shown in Table 4.

It can be concluded that TRM fitted the data more sufficiently than SMM. Under TRM, the MSE values for all traits were lower for TRM compared with the

SMM. The superiority of TRM over SMM was more evident for WW and 6MW. But for BW, MSE was similar under SMM, FRM and TRM; this was predictable because BW was chosen the parent trait in the present study. Mokhtari et al. (2018) reported lower MSE values for WW and 6MW in Raeini Cashmere goats for FRM compared to SMM. The superiority of SEM over SMM was also confirmed by Lopez de Maturana et al. (2010) by estimating the genetic parameters of calving-related traits in Holstein dairy cows.

Structural coefficients

By considering TRM, the posterior means of the structural coefficients related to the causal relationships among the early growth traits in Kermani sheep are presented in Table 5. These estimated values were statistically significant (99% highest posterior density interval did not include zero).

The corresponding structural coefficient related to the causal influence of BW on WW was 1.10 kg. Thus, it can be concluded that about 1.10 kg increase in WW will be expected following each one kg increase in BW. The magnitude of the causal influence of WW on 6MW was estimated as 0.70 kg. Therefore, one kg increase in WW will lead to 0.70 kg increase in 6MW. Considering TRM, the BW had an indirect causal effect on 6MW which is mediated via WW; 1 kg increase in BW, would increase the 6MW by 0.77 kg.

By taking the causal structure assumed under TRM (Fig. 2) into account, it can be concluded that the indirect causal influence of BW on 6MW in Kermani lambs is mediated via WW. Statistically significant direct causal influences of 1.94 kg (from BW on WW) and 2.48 kg (from BW on 6MW) in Raeini Cashmere goats were reported by Mokhtari et al. (2018). They also re-

Table 4. The MSE values for growth traits in Kermani lambs under the standard multivariate and temporal recursive models

Traits ¹	Model ²		
	SMM	FRM	TRM
BW	0.101	0.100	0.100
WW	2.834	2.485	2.187
6MW	5.489	4.451	4.172

¹BW: birth weight; WW: weaning weight; 6MW: weight at six months of age

²SMM: Standard multivariate model, FRM: Fully recursive multivariate model, TRM: Temporal recursive multivariate model

Table 5. Posterior means \pm posterior standard deviation (PSD) for the structural coefficients in Kermani lambs

Causal effect ¹	Mean \pm PSD	99% HPD ² interval
BW-WW	1.10 \pm 0.27	0.404-1.795
WW-6MW	0.70 \pm 0.04	0.597-0.803

¹BW: birth weight; WW: weaning weight; 6MW: weight at six months of age

²HPD: highest posterior density

Table 6. The Spearman's rank correlations of posterior means of the direct genetic effects for growth traits in Kermani sheep under SMM and TRM

Traits ¹		
BW	WW	6MW
1.00 **	0.96 **	0.88 **

¹BW: birth weight; WW: weaning weight; 6MW: weight at six months of age.

** : P-value <0.01

ported significant direct causal effect of 1.03 kg from WW on 6MW in Raeini goats.

The Spearman's rank correlations of posterior means of the direct genetic effects for growth traits in Kermani sheep under SMM and TRM are shown in Table 6.

Considering the causal relationships among the early growth traits, no influence on direct breeding values for BW was observed. The magnitude of the Spearman's rank correlation between the direct breeding values for WW and 6MW was lower than unity, implying re-ranking of animals for these traits under TRM, especially for 6MW. Amou Posht-e Masari et al. (2019) reported substantial changes in the estimated breeding values of Lori-Bakhtiari lambs for the growth traits under SMM and TRM.

Conclusions

The findings of the current investigation revealed the superiority of TRM over SMM in terms of DIC and the better predictive ability of model in terms of smaller MSE. Furthermore, significant and positive causal influences were detected from BW on WW and from WW on 6MW in Kermani lambs. Therefore, inclusion of the causal relationships among traits by using TRM instead of SMM is recommended for the genetic evaluation of early growth traits in Kermani lambs. Furthermore, accounting for the causal relationships among the studied traits may be advantageous for predicting the breeding values, and consequently the accuracy of ranking of lambs for the selective breeding purposes.

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