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Genetic analysis of growth curve traits in Iran-Black sheep breed: Comparison of standard multivariate and structural equation models

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Abstract In this study, a dataset comprising 20,328 body weight records from birth to 360 days of age was utilized to compare five growth curve models and genetic analysis of growth curve parameters in Iran-Black sheep. The data and genealogical information were collected between 1981 and 2007 from the Breeding Station of Abbasabad in the Khorasan Razavi province of northeast Iran. The performance of five statistical models including Brody, negative exponential, von Bertalanffy, Logistic, and Gompertz for describing the growth curve of the studied population was evaluated by applying the SAS software. The statistical measures used for model comparisons were Akaike's information criterion (AIC), root mean square error (RMSE), and adjusted coefficient of determination (R^2_{adj}). The Brody model, exhibiting the highest R^2_{adj} and the lowest values for both AIC and RMSE, was selected as the best model for characterizing the growth curve in this breed. Consequently, the parameters of the growth curve, including parameter A (considered as weight at maturity), B (considered as an integration constant), and K (maturation rate) were predicted by applying the Brody model. To investigate the effect of maternal components on the growth curve parameters, nine univariate animal models, including different combinations of the direct additive genetic, maternal additive genetic, maternal permanent environmental, and maternal temporary environmental effects, were fitted. Subsequently, two multivariate animal models, comprising the standard (SMM) and fully recursive (FRM) models were analyzed by using the Bayesian inference. The FRM outperformed SMM in terms of lower means square error (MSE) and higher Pearson's correlation coefficients between the actual and predicted records ($r(y, \hat{y})$) values, indicating better goodness of fit. The posterior means for heritability of A , B , and K parameters were low but statistically significant under SMM and FRM. It may be concluded that the growth trajectory traits of Iran-Black sheep are influenced mainly by non-additive genetic and environmental effects, emphasizing the importance of considering these effects for developing the corresponding breeding strategies. The Spearman's rank correlation coefficients between the estimated breeding values for growth curve traits under SMM and FRM indicated significant re-ranking of animals, favoring FRM for genetic evaluation in Iran-Black sheep.

Keywords: causal effect, genetic parameters, goodness of fit measures, growth trajectory, sheep

Introduction

Iran-Black sheep is the first composite breed in Iran, synthesized to improve characteristics such as the litter

size, weaning performance, wool quality, and adaptability to challenging environmental conditions in Baluchi sheep (Rashidi, 2012). The breeding program commenced in 1975,

and performance monitoring initiated in 1984. The genetic makeup of Iran-Black sheep comprises a 50% blend of gene pools of Baluchi and Chios sheep breeds. Bathaei and Leroy (1998) emphasized the importance of increased live body weight, commonly known as growth, as a crucial aspect of animal development. Growth is an important trait in livestock species and can be effectively characterized through statistical modeling (Eisen, 1976). This biological growth process can typically be divided into three distinct stages, as outlined by Waheed et al. (2011). In the initial stage, growth initiates from a defined point, with gradual increases in body weight observed. Subsequently, the second stage is described by a growth trajectory that exhibits a partially linear pattern until it reaches an inflection point. In the last stage, the growth curve reaches an asymptotic state. Monitoring the development of livestock species throughout their lifespan holds significance in formulating suitable feeding programs based on their body weight and identifying the most advantageous age for slaughter (Ghavi Hossein-Zadeh, 2017). Waheed et al. (2011) pointed out the magnitude of understanding the growth curve in developing farm management strategies. Conversely, a slow growth rate in animals may result in diminished market weight, subsequently influencing the profitability of breeding operations (Abegaz et al., 2010). Statistical models have garnered considerable attention as suitable means for addressing the growth trajectory of domestic species (Malhado et al., 2009). Teleken et al. (2017) emphasized the efficiency of these functions in quantifying biological parameters of growth, such as mature weight. Additionally, the methodologies employed for modeling the growth curve of farm animals serve as valuable instruments for enhancing production efficiency within livestock breeds (Vazquez et al., 2012). Several statistical models, including Logistic (Nelder, 1961), negative exponential (Brown et al., 1976), Richards (Richards, 1959), Gompertz (Laird, 1965), Brody (Brody, 1945), and von Bertalanffy (von Bertalanffy, 1957) have been utilized to describe the growth curve in various livestock species.

In biological systems, causal relationships might be present among traits, yet standard multivariate models (SMM) commonly employed for genetic assessment cannot cover such causal relationships. The SMM estimates correlations among traits without taking causal links into account. Structural equation models (SEM), introduced by Wright (1921), offer a more sophisticated statistical approach for investigating the causal relationships among phenotypes (Gianola and Sorensen, 2004). These models enable the exploration of causal relationships among traits within a multivariate context.

The growth curve in several sheep breeds in Iran has been studied by applying different statistical models. Zamani et al. (2016) studied the growth curve in Moghani sheep via random regression models by combining B-Spline and Legendre functions. They reported that B-Splines had high potential for genetic evaluation of body

weight in this breed. Other studies included model comparisons and genetic analysis of growth curve traits in various sheep breeds, such as Kermani sheep (Mokhtari et al., 2019), Kordi sheep (Mohammadi et al., 2019), and Moghani sheep (Ghavi Hossein-Zadeh, 2017) breeds, by applying SMM. However, Amou Posht-e Masari et al. (2021) investigated causal effects among growth curve traits in the Lori-Bakhtiari sheep breed by using the fully recursive model (FRM), a type of structural equation model (SEM). They pointed out that incorporating causal effects among growth curve traits within the FRM framework led to improved goodness of fit of the model compared to SMM. Moreover, neglecting these causal relationships resulted in significant changes in the ranking of estimated breeding values for growth curve traits in Lori-Bakhtiari lambs.

Hence, the main purpose of the present study was to infer the causal relationships among growth curve parameters in Iran-Black sheep using SEM. Furthermore, the performances of the standard multivariate and structural equation-based models were evaluated in terms of the goodness of fit measures, genetic parameter estimations, and the ranking of animals based on their breeding values.

Materials and methods

Flock management and data collection

In the breeding season, which lasts from late August to late October, estrous ewes were identified by teaser rams. Annually, approximately 10-12 rams were randomly assigned to mate with 20-25 ewes per ram, with individual sire identification recorded. Maiden ewes were introduced to fertile rams at approximately 18 months of age. Ewes remained within the flock for a maximum of 7 breeding cycles (up to 8 years of age), while rams were utilized for 2-3 mating seasons. Lambing typically took place from late January to late March. For this study, a dataset comprising 20,328 body weight records from birth to 360 days of age (10,220 records for male lambs and 10,108 records for female lambs) collected between 1981 and 2007 from the Sheep Breeding Station of Abbasabad in the Khorasan Razavi province, northeastern Iran, was utilized. These records pertained to 5,626 offspring descended from 114 sires and 1,359 dams. The dataset included measurements on body weight at birth, weaning, six months of age, nine months of age, and yearling age. The CFC program was employed to track pedigree information and facilitate subsequent analyses (Sargolzaei et al., 2006). Among the registered animals, those with both parents known, both parents unknown, and one parent known comprised 93.67%, 4.12%, and 2.21% of all individuals, respectively. Furthermore, 74.42% of animals had no progeny, while 25.58% had progeny.

Statistical analyses

In the present study, the statistical analyses performed at three stages, included fitting non-linear growth curve models on body weight and age data to determine the best model, investigating the importance of maternal effects on the growth curve parameters, and performing multivariate analyses.

The investigated statistical growth curve models

Five non-linear models were fitted to the live body weight-age records to determine the best growth curve model. These models included the von Bertalanffy, Brody, Logistic, Gompertz, and negative exponential. The mathematical formulations for growth curve models were as follows:

| | |
|-----------------------------|----------------------------|
| $y_t = A / (1 + B e^{-Kt})$ | Logistic model |
| $y_t = A e^{-Be^{-Kt}}$ | Gompertz model |
| $y_t = A (1 - B e^{-Kt})$ | Brody model |
| $y_t = A - (A e^{-Kt})$ | negative exponential model |
| $y_t = A (1 - B e^{-Kt})^3$ | von Bertalanffy model |

In these equations, y_t represents the body weight at age t (measured in days), where parameter A denotes the asymptotic weight, which is considered as the mature weight; parameter B denotes an integration constant associated with the initial body weight of the animals; parameter K represents the maturation rate, and e represents the base of the natural logarithm. The records were analyzed by using the NLIN procedure and the Gauss-Newton iterative method which implemented by SAS software (SAS, 2004). The performance of models for describing growth curves was assessed using three statistical metrics: Akaike's information criterion (AIC) (Akaike, 1974), root mean square error (RMSE), and adjusted coefficient of determination (R^2_{adj}). The AIC was computed as follows:

$$AIC = n \log \left(\frac{SS_e}{n} \right) + 2p$$

The RMSE was calculated as follows:

$$RMSE = \sqrt{\frac{SS_e}{n - p - 1}}$$

The R^2_{adj} was computed as follows:

$$R^2_{adj} = 1 - \left(\frac{n - 1}{n - p} \right) \times (1 - R^2)$$

where, n represents the number of observations, p denotes the number of model parameters, and SS_e is the residual sum of squares. The most suitable model among those tested was the one with the highest R^2_{adj} and the lowest AIC and RMSE.

The evaluation of maternal components of the growth curve traits

The impact of maternal components on the parameters of the growth curve was examined. Nine univariate animal models, incorporating different combinations of direct additive genetic, maternal additive genetic, maternal permanent environmental, and maternal

temporary environmental (or litter effect, representing the dam within a year) effects, were applied to analyze the growth curve traits under investigation. The investigated 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 parameters A , B and K ; b , a , m , pe , l , and e are the vectors of fixed, direct additive genetic, maternal additive genetic, maternal permanent environmental, maternal temporary environmental (litter), and the residual effects, respectively. The fixed effects taken into account for inclusion in the animal models consisted of the sex of lambs (males and females), dam age at lambing (2-7 years old), birth type (single, twin, and triplet), and birth year (1981-2007). The generalized linear model (GLM) procedure was utilized to identify the statistically significant fixed factors to be incorporated into the animal models (SAS, 2004).

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 $a \sim N(0, A\sigma_a^2)$, $m \sim N(0, A\sigma_m^2)$, $pe \sim N(0, I_{pe}\sigma_{pe}^2)$, $l \sim N(0, I_l\sigma_l^2)$ and $e \sim N(0, I_n\sigma_e^2)$. A and σ_{am} are the numerator relationship matrix and covariance between direct additive and maternal additive genetic effects, respectively. 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) proposed by Schwarz (1978) was utilized to ascertain the most suitable univariate animal model and computed as follows:

$$BIC = -2 \times \log L + p \times \log(n)$$

where, $\log L$ is the logarithm of likelihood, n is number of records, and p is number of parameters in the model. For each trait, the model exhibiting the lowest BIC was chosen as the best model.

Genetic analyses were conducted using the WOMBAT software developed by Meyer (2007). The best univariate animal model detected for each trait was used in the subsequent analyses. At the last stage of the study, two types of multiple-trait models comprising the standard mixed model (SMM) and fully recursive multivariate (FRM) were applied. 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:

$$\Delta y_i = X_i b_i + Z_{1i} a + Z_{2i} pe + Z_{3i} m + Z_{4i} l + e_i \quad \text{Cov (a,m) = } A\sigma_{am}$$

The Λ matrix represents the structural coefficients, where the diagonal elements are set to 1 and the off-diagonal elements are determined based on the cause-and-effect relationships among the traits. These structural coefficients are types of regression coefficients and estimated using SEM as described by Gianola and Sorensen (2004). Considering three traits, the matrix of structural coefficients under the FRM was formulated as follows:

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

In this context, the first trait causally affects the second and third traits, while the second trait causally influences the third trait. The causal structure, depicted in this study, is illustrated in Figure 1.

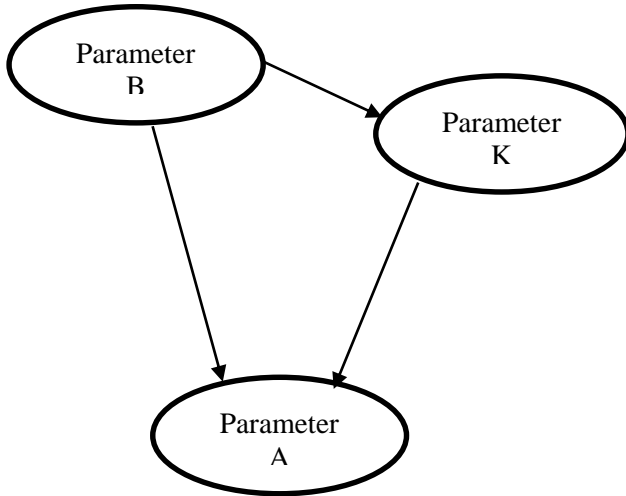


Figure 1. Multivariate fully recursive model considered among the studied growth curve traits in Iran-Black sheep (Parameter A: Asymptotic weight, which is considered as mature weight, Parameter B: An integration constant related to initial animal weight, Parameter K: Maturation rate). Each Arrow shows the direction of the causal effect.

At the likelihood level, SEM faces issues with identifiability because of additional parameters such as structural coefficients. To attain identification, it was assumed that residual correlations within the system were uncorrelated. In other words, the variance-covariance matrix of residuals (\mathbf{R}) in SEM was supposed to be a diagonal matrix. Moreover, a multivariate normal distribution with a null mean vector and (co)variance matrix $\mathbf{R} \otimes \mathbf{I}_n$ was supposed for residual effects, in which \mathbf{I}_n is an identity matrix and \mathbf{R} is the residual (co)variance matrix, \otimes representing the Kronecker product.

Multivariate analyses were done by applying the Bayesian approach via the GIBBS2F90 software (Misztal et al., 2002). The adequacy of the chain length and the burn-in period was assessed through visual examinations of trace plots generated from posterior samples of the parameters. In each multivariate model 200,000 iterations were executed, and the posterior

samples from each chain were thinned at intervals of 20 iterations. The initial 20,000 iteration samples were discarded as burn-in. Subsequently, the computation of posterior means and posterior standard deviations (PSD) of (co)variance components for each growth curve trait was done by using the POSTGIBBSF90 software developed by Misztal et al. (2002).

Lopez de Maturana et al. (2007) demonstrated 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. By considering two traits, parent trait is a trait which causally affect other trait. In the current investigation for fitting FRM, this method was used.

Statistical measures for model comparisons

The SMM and FRM were assessed via two statistical criteria: the mean square of error of prediction (MSE) and Pearson's correlation coefficient between the observed and predicted values of growth curve traits ($r(y, \hat{y})$), were computed through the PREDICTF90 software developed by Misztal et al. (2002). The model with lower MSE and higher $r(y, \hat{y})$ would be deemed the superior model.

System parameters

The parameters derived through SEM, termed system parameters, possess a distinct interpretation compared to their counterparts estimated under SMM, as outlined by Gianola and Sorensen (2004). Consequently, additional transformations are required to facilitate comparison between the parameters estimated under SEM and SMM, utilizing the following formulas provided by Gianola and Sorensen (2004):

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

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

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

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

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

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

The matrices \mathbf{G}^* , \mathbf{M}^* , \mathbf{PE}^* , \mathbf{L}^* , \mathbf{R}^* , and \mathbf{P}^* are the SMM-equivalent of (co)variance matrices for direct additive genetic, maternal additive genetic, maternal permanent environmental, maternal temporary environmental (litter), residual, and phenotypic effects which were estimated under FRM, respectively. \mathbf{R}^* is a matrix with non-zero off-diagonal elements.

The influence of causal effects on the ranking of animals based on EBVs

The impact of models (SMM and FRM) on the ranking of animals according to estimated additive breeding values was measured by employing the Spearman's rank

correlations between the posterior means of the estimated breeding values for all animals, as well as for subsets consisting of the top 50%, top 10%, and top 1% ranked animals. The estimated breeding values obtained under FRM, were adjusted to align with those of the SMM using the formula provided by Konig et al. (2008):

$$BV^* = \Lambda^{-1} BV$$

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

Results

Statistical comparisons of the growth curve models

The findings of model comparisons for the growth curve modeling in Iran-Black lambs using the applied statistical models are shown in Table 1. According to the AIC,

RMSE, and R^2_{adj} values, the Brody model was identified as the most suitable model for describing the growth curve in Iran-Black lambs. Conversely, the Gompertz model exhibited the highest AIC and RMSE values, along with the lowest R^2_{adj} compared to other models, indicating its lower efficacy in characterizing the growth curve of Iran-Black lambs compared with other models. Figure 2 displays the actual and predicted average body weights from birth to 360 days of age, achieved through fitting the Brody model. The trend indicates a steady increase in body weight with age. A Pearson's correlation coefficient of 0.99 ($P < 0.01$) was obtained between the actual and predicted body weights from birth to 360 days of age. Table 1 shows the estimates of the model parameters for the growth curve under the various models. In Brody model, the estimated values for growth trajectory parameters were 42.09 kg, 0.91, and 0.006 for *A*, *B*, and *K* parameters, respectively.

Table 1. Comparative statistics for goodness of fit measures and estimates of model parameters (\pm standard error) of the growth curve across the tested growth curves in Iran-Black sheep

| Model | Comparative measures [¥] | | | Model parameters ^{¥¥} | | |
|----------------------|-----------------------------------|---------|-------------|--------------------------------|-------------|--------------|
| | AIC | RMSE | R^2_{adj} | Parameter A | Parameter B | Parameter K |
| Brody | 124365.491 | 5.15741 | 0.8625 | 42.09±0.18 | 0.91±0.002 | 0.006±0.0001 |
| Negative exponential | 124709.301 | 5.20121 | 0.8601 | 40.23±0.14 | - | 0.007±0.0001 |
| von Bertalanffy | 125044.328 | 5.24426 | 0.8578 | 38.63±0.11 | 0.53±0.003 | 0.010±0.0001 |
| Gompertz | 140966.202 | 7.75871 | 0.6887 | NC | NC | NC |
| Logistic | 140772.123 | 7.72175 | 0.6917 | NC | NC | NC |

[¥]AIC: Akaike's information criterion, RMSE: Root mean square error, R^2_{adj} : Adjusted coefficient of determination

^{¥¥} Parameter A: Asymptotic weight, which is considered as mature weight, Parameter B: An integration constant related to initial animal weight, Parameter K: Maturation rate.

NC: Not converged

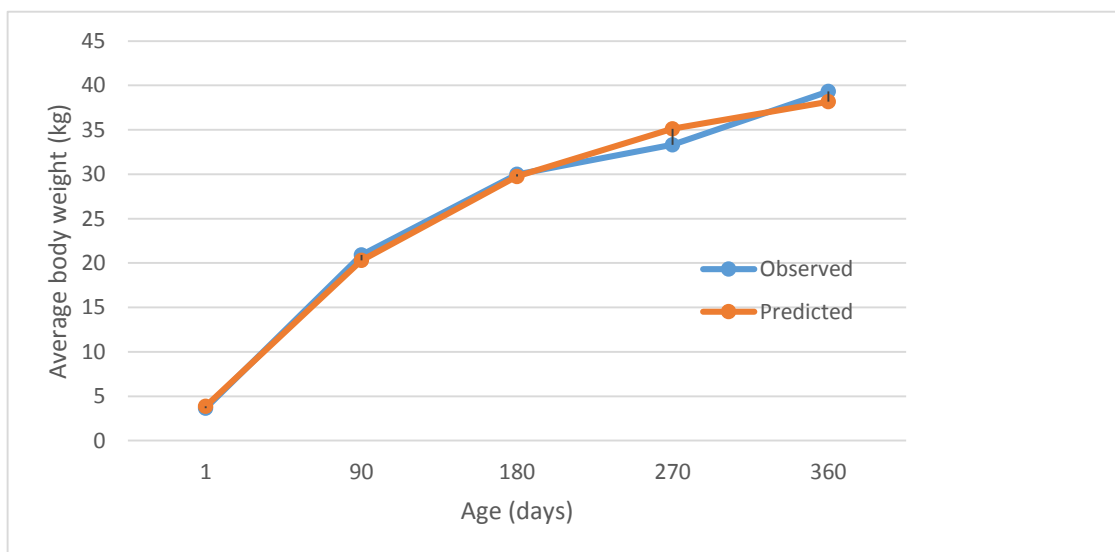


Figure 2. Real and predicted average body weights (kg) of the Iran-Black sheep at different ages by applying the Brody model.

The effects of fixed factors on the growth curve traits

Table 2 displays the descriptive statistics for the growth trajectory characteristics derived from fitting the Brody model. The coefficient of variation ranged from 29% (parameter *B*) to 70.15% (parameter *K*).

Additionally, Table 3 illustrates the least squares means of the growth curve traits across the various levels of the fixed effects under consideration. The birth year of lamb had significant influences on all the examined growth curve parameters ($P < 0.01$). The sex of lamb exerted a significant influence on all the analyzed

growth curve parameters ($P < 0.01$), with male lambs exhibiting superiority in parameters *A*, *B*, and *K* compared to female lambs. The birth type exhibited a significant influence on all the examined growth curve traits ($P < 0.01$). Single-born lambs displayed higher parameter *A* values compared to twins and triplets. In contrast, twins had higher parameter *A* values than triplet-born lambs ($P < 0.01$), with no statistically significant difference observed between twins and triplets ($P > 0.05$). Dam age significantly influenced parameters *A* and *B* ($P < 0.05$) but not parameter *K* ($P > 0.05$). Lambs born from ewes older than 2-year-old exhibited significantly higher estimated mature weights than those born from 2-year-old ewes.

Table 2. Descriptive statistics for the studied growth curve traits in Iran-Black sheep

| Item [‡] | Traits ^{‡‡} | | |
|-------------------|----------------------|--------------------|--------------------|
| | Parameter <i>A</i> | Parameter <i>B</i> | Parameter <i>K</i> |
| No. of records | 5096 | 5096 | 5096 |
| Mean | 41.53 | 0.91 | 0.0067 |
| S.D. | 13.04 | 0.03 | 0.0047 |
| C.V. (%) | 31.39 | 3.29 | 70.15 |
| Min. | 10.79 | 0.66 | 0.001 |
| Max. | 99.12 | 0.99 | 0.088 |

[‡] S.D.: standard deviation, C.V.: coefficient of variation, Min.: minimum value, Max.: maximum value

^{‡‡} Parameter *A*: Asymptotic weight, which is considered as mature weight, Parameter *B*: An integration constant related to initial animal weight, Parameter *K*: Maturation rate.

Table 3. Least squares means (\pm standard error) for the studied growth curve traits in Iran-Black sheep

| Effect | No. of lambs per sub-level | Traits [‡] | | |
|--------------|----------------------------|-------------------------------|----------------------------------|----------------------------------|
| | | Parameter <i>A</i> | Parameter <i>B</i> | Parameter <i>K</i> |
| Sex | - | ** | ** | ** |
| Male | 2573 | 43.78 \pm 0.59 ^a | 0.913 \pm 0.001 ^a | 0.0067 \pm 0.002 ^a |
| Female | 2523 | 38.96 \pm 0.58 ^b | 0.909 \pm 0.001 ^b | 0.0063 \pm 0.002 ^b |
| Birth type | - | ** | ** | ** |
| Single | 1600 | 43.46 \pm 0.61 ^a | 0.900 \pm 0.001 ^c | 0.0077 \pm 0.0002 ^a |
| Twin | 2925 | 41.77 \pm 0.57 ^b | 0.912 \pm 0.001 ^b | 0.0061 \pm 0.0002 ^b |
| Triplet | 571 | 38.84 \pm 0.73 ^c | 0.921 \pm 0.001 ^a | 0.0058 \pm 0.0003 ^b |
| Dam age (yr) | - | ** | ** | ns |
| 2 | 1586 | 39.75 \pm 0.60 ^b | 0.917 \pm 0.001 ^a | 0.0062 \pm 0.0002 ^a |
| 3 | 1319 | 41.54 \pm 0.62 ^a | 0.913 \pm 0.001 ^b | 0.0066 \pm 0.0002 ^a |
| 4 | 1002 | 42.06 \pm 0.64 ^a | 0.912 \pm 0.001 ^{b,c} | 0.0065 \pm 0.0002 ^a |
| 5 | 609 | 41.65 \pm 0.71 ^a | 0.910 \pm 0.001 ^c | 0.0067 \pm 0.0003 ^a |
| 6 | 372 | 41.99 \pm 0.81 ^a | 0.908 \pm 0.002 ^c | 0.0064 \pm 0.0003 ^a |
| 7 | 208 | 41.23 \pm 0.99 ^a | 0.908 \pm 0.002 ^c | 0.0068 \pm 0.0004 ^a |
| Birth year | - | ** | ** | ** |

[‡] Parameter *A*: Asymptotic weight, which is considered as mature weight, Parameter *B*: An integration constant related to initial animal weight, Parameter *K*: Maturation rate.

Within column in each subclass, means with common superscript(s) do not differ ($P > 0.05$, ns: not significant, ** $P < 0.01$).

The importance of maternal effects

Table 4 displays the BIC values obtained by fitting nine univariate animal models for each trait. The model including the direct additive genetic, maternal permanent environmental, and maternal temporary environmental (litter) effects (model 5) was detected as the best model for genetic analysis of parameters *A* and *B*. Conversely, the model featuring only the direct additive genetic effects (model 1) was determined as the best model for genetic analysis of parameter *K*.

The goodness of fit of the SMM and FRM

Table 5 shows the performance of SMM and FRM in terms of MSE and $r(y, \hat{y})$ for each trait. For all traits, FRM exhibited lower MSE and higher $r(y, \hat{y})$ values compared to SMM and therefore, was superior to SMM for genetic analysis of growth curve traits. Thus, the causal structure adopted in FRM (Fig. 1) appears suitable for depicting the causal relationships among the growth curve traits.

Structural coefficients

Table 6 presents the posterior means for the structural coefficients among growth curve traits, estimated

through the application of FRM, along with their corresponding 99% highest posterior density intervals (HPD). Notably, all estimated structural coefficients were statistically significant, with 99% of HPD intervals excluding zero. Specifically, the coefficients associated

with the causal effects of parameter *B* on parameters *K* and *A* were determined as -0.592 and 2.829, respectively. Additionally, the causal effect of parameter *K* on parameter *A* was estimated at -0.569.

Table 4. The BIC values for growth curve traits in Iran-Black sheep under different models

| Model | Traits [‡] | | |
|---------|---------------------|-----------------|-----------------|
| | Parameter A | Parameter B | Parameter K |
| Model 1 | 30378.32 | 14544.28 | 20333.76 |
| Model 2 | 30348.4 | 14501.95 | 20340.22 |
| Model 3 | 30356.02 | 14525.69 | 20341.73 |
| Model 4 | 30363.72 | 14532.16 | 20348.05 |
| Model 5 | 30318.85 | 14474.08 | 20348.11 |
| Model 6 | 30356.03 | 14509.6 | 20348.75 |
| Model 7 | 30362.01 | 14515.24 | 20355.87 |
| Model 8 | 30326.4 | 14481.91 | 20356.64 |
| Model 9 | 30332.98 | 14487.97 | 20363.76 |

[‡] Parameter A: Asymptotic weight, which is considered as mature weight, Parameter B: An integration constant related to initial animal weight, Parameter K: Maturation rate. The best model is shown in boldface.

Table 5. The goodness of fit measures for the studied traits under two multivariate models

| Traits [‡] | Model ^{‡‡} | | | |
|---------------------|---------------------|-----------------------|--------------------|-----------------------|
| | SMM | | FRM | |
| | ^{‡‡‡} MSE | ^{‡‡‡} r(y,ŷ) | ^{‡‡‡} MSE | ^{‡‡‡} r(y,ŷ) |
| Parameter A | 97.34 | 0.68 ** | 30.56 | 0.91 ** |
| Parameter B | 4.15 | 0.71 ** | 3.34 | 0.71 ** |
| Parameter K | 18.01 | 0.46 ** | 4.93 | 0.67 ** |

[‡] Parameter A: Asymptotic weight, which is considered as mature weight, Parameter B: An integration constant related to initial animal weight, Parameter K: Maturation rate.

^{‡‡} SMM: Standard multivariate model, FRM: Fully recursive multivariate model

^{‡‡‡} MSE: mean square error, r(y,ŷ)= Pearson's correlation between observed and predicted values

Table 6. Posterior means ± posterior standard deviation (PSD) for the structural coefficients under FRM

| Causal effect from | Mean ± PSD ^{‡‡} | 99% HPD interval ^{‡‡} |
|----------------------------|--------------------------|--------------------------------|
| Parameter B to Parameter K | -0.592±0.077 | -0.790 to -0.394 |
| Parameter B to Parameter A | 2.829±0.708 | 1.006 to 4.652 |
| Parameter K to Parameter A | -0.569±0.055 | -0.711 to -0.427 |

[‡] Parameter A: Asymptotic weight, which is considered as mature weight, Parameter B: An integration constant related to initial animal weight, Parameter K: Maturation rate.

^{‡‡} PSD: Posterior Standard Deviation, 99% HPD intervals did not include zero.

Posterior means of genetic parameters

Heritabilities

The posterior means ± standard deviations (PSD) of heritabilities for the growth curve parameters are shown in Table 7. When employing FRM, the posterior means for heritabilities were estimated at 0.17, 0.10, and 0.06 for parameters A, B, and K, respectively. Conversely, under SMM, the posterior means for heritabilities of parameters A, B, and K were 0.08, 0.06, and 0.07, respectively. It is noteworthy that the posterior means for heritabilities of the growth curve parameters under both SMM and FRM were statistically significant (95% of HPD intervals did not include zero). However, the differences between posterior means of the direct heritability estimates of the studied growth curve traits under both SMM and FRM were not statistically significant, with 95% of HPD intervals overlapping.

Posterior means for the ratio of the permanent maternal environmental variance to the phenotypic variance (pe^2) for parameters A and B were 0.04 and 0.06 (under SMM) and 0.13 and 0.06 (under FRM), respectively. Posterior means of pe^2 estimates for parameters A and B were statistically significant (95% of HPD intervals did not include zero). However, there were no statistically significant differences between pe^2 estimates for parameters A and B under SMM and FRM (95% of HPD intervals overlapped). Posterior means for the ratio of the maternal temporary environmental variance to the phenotypic variance (l^2) for parameters A and B were 0.09 and 0.10 (under SMM) and 0.15 and 0.15 (under FRM), respectively. Posterior means of l^2 estimates for parameters A and B were statistically significant (95% of HPD intervals did not include zero). However, there were no significant differences between l^2 estimates for parameters A and B under SMM and FRM (95% of HPD intervals overlapped).

Correlation estimates

The features of posterior means \pm PSD for genetic, phenotypic, and environmental correlations among the growth curve parameters are shown in Table 8. The posterior means of genetic correlations for growth curve parameters varied from -0.65 for *B-K* to 0.53 for *A-B* under SMM and from -0.30 for *A-K* to 0.43 for *A-B* under FRM. The phenotypic correlation estimates were statistically significant, with 95% of the highest posterior density (HPD) intervals not including zero. Under the SMM, these estimates ranged from -0.36 between parameters *A* and *K* to 0.65 between parameters *A* and *B*. Meanwhile, under the FRM, the estimates were from

-0.43 between parameters *A* and *K* to 0.26 between parameters *A* and *B*. In the context of the SMM, the posterior means of the residual correlations among the examined traits spanned from -0.41 (for *A-K*) to 0.74 (for *A-B*). Conversely, in the FRM, the corresponding estimates ranged from -0.68 (for *K-A*) to 0.43 (for *A-B*).

Influence of SMM and FRM on the ranking of animals based on EBVs

Generally, a descending pattern was evident in the Spearman's rank correlations between the breeding values under SMM and FRM for all selected categories, ranging from all animals to the top 1% ranked individuals (Table 9).

Table 7. Posterior means \pm 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 growth curve traits in Iran-Black sheep under SMM and FRM models

| Traits | SMM | | | FRM | | |
|--------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| | $h^2 \pm PSD$ | $pe^2 \pm PSD$ | $l^2 \pm PSD$ | $h^2 \pm PSD$ | $pe^2 \pm PSD$ | $l^2 \pm PSD$ |
| Parameter <i>A</i> | 0.08 \pm 0.03 | 0.04 \pm 0.01 | 0.09 \pm 0.02 | 0.17 \pm 0.07 | 0.13 \pm 0.04 | 0.15 \pm 0.02 |
| Parameter <i>B</i> | 0.06 \pm 0.02 | 0.06 \pm 0.01 | 0.10 \pm 0.02 | 0.10 \pm 0.02 | 0.06 \pm 0.01 | 0.15 \pm 0.02 |
| Parameter <i>K</i> | 0.07 \pm 0.02 | - | - | 0.06 \pm 0.03 | - | - |

* Parameter *A*: Asymptotic weight, which is considered as mature weight, Parameter *B*: An integration constant related to initial animal weight, Parameter *K*: Maturation rate.

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

Table 8. Posterior means \pm posterior standard deviation (PSD) for the genetic correlation (r_g), phenotypic correlation (r_p), and residual correlation (r_e) among the studied growth curve traits in Iran-Black sheep under SMM and FRM models

| Pair traits* | SMM | | | FRM | | |
|--|------------------|------------------|------------------|------------------|------------------|------------------|
| | $r_g \pm PSD$ | $r_p \pm PSD$ | $r_e \pm PSD$ | $r_g \pm PSD$ | $r_p \pm PSD$ | $r_e \pm PSD$ |
| Parameter <i>A</i> -Parameter <i>B</i> | 0.53 \pm 0.21 | 0.65 \pm 0.01 | 0.74 \pm 0.01 | 0.43 \pm 0.19 | 0.26 \pm 0.08 | 0.43 \pm 0.08 |
| Parameter <i>A</i> -Parameter <i>K</i> | -0.19 \pm 0.25 | -0.36 \pm 0.01 | -0.41 \pm 0.02 | -0.30 \pm 0.04 | -0.43 \pm 0.12 | -0.68 \pm 0.07 |
| Parameter <i>B</i> -Parameter <i>K</i> | -0.65 \pm 0.17 | -0.29 \pm 0.01 | -0.29 \pm 0.02 | -0.29 \pm 0.07 | -0.22 \pm 0.04 | -0.32 \pm 0.04 |

* Parameter *A*: Asymptotic weight, which is considered as mature weight, Parameter *B*: An integration constant related to initial animal weight, Parameter *K*: Maturation rate.

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

Table 9. Spearman's rank correlations of posterior means of direct genetic effects for studied growth traits in Iran-Black sheep under SMM and FRM models

| Traits * | All animals | 50% top-ranked | 10% top-ranked | 1% top-ranked |
|--------------------|-------------|----------------|----------------|---------------|
| Parameter <i>A</i> | 0.729 ** | 0.665 ** | 0.585 ** | 0.432 ** |
| Parameter <i>B</i> | 0.977 ** | 0.978 ** | 0.969 ** | 0.928 ** |
| Parameter <i>K</i> | 0.676 ** | 0.249 ** | 0.194 * | 0.122 * |

* Parameter *A*: Asymptotic weight, which is considered as mature weight, Parameter *B*: An integration constant related to initial animal weight, Parameter *K*: Maturation rate.

* P <0.05, ** P <0.01.

Discussion

Variability in the efficacy of different growth curve models in describing body weight changes over time is documented in the literature. Ahmadpanah et al. (2023) assessed five non-linear models including Brody, Gompertz, Logistic, von Bertalanffy, and Richards to characterize the growth curve in Kurdi sheep and concluded that the Brody model was the most suitable for delineating body weight changes. Similarly, Amou

Posht-e Masari et al. (2021) applied five statistical models, including Brody, Logistic, negative exponential, Gompertz, and von Bertalanffy to body weight-age records of Lori-Bakhtiari lambs with Brody model exhibiting the best performance among the tested models. Ghavi Hossein-Zadeh (2015b) compared six non-linear models, including Logistic, Brody, negative exponential, Gompertz, Richards, and von Bertalanffy on body weights of Shall sheep and determined that the Richards model was the most effective for characterizing

the growth curve in this breed. Parameter *A* is commonly interpreted as asymptotic mature weight. The asymptotic limit of each model, as age approaches infinity, does not approximate the heaviest weight attained by the animal. It is an asymptotic mean weight (Brown et al., 1976).

However, Malhado et al. (2009) highlighted the challenge of defining an optimal mature weight, as it varies depending on factors such as species, breed, and management practices. Using the Brody model, parameter *A* values were reported as 23.69, 43.37, and 64.84 in Kermani (Mokhtari et al., 2019), Kordi (Mohammadi et al., 2019), and Lori-Bakhtiari sheep breeds (Amou Posht-e Masari et al., 2021), respectively.

According to Malhado et al. (2009), parameter *B* lacks a specific biological interpretation and is considered an integration constant. The estimated value for parameter *B* in the current investigation (0.91) aligns with values obtained by previous studies. Mokhtari et al. (2019) reported a value of 0.877 in the Kermani breed under the Brody model, Mohammadi et al. (2019) found 0.905 in the Kordi sheep breed under the Brody model, and Amou Posht-e Masari et al. (2021) reported 0.93 in Lori-Bakhtiari sheep under the Brody model.

According to Lupi et al. (2016), animals with *K* values tend to reach maturity weight at a faster rate. The estimated *K* value in the current investigation (0.006) is consistent with values reported by Amou Posht-e Masari et al. (2021) in Lori-Bakhtiari sheep (0.005) and by Mohammadi et al. (2019) in Kordi sheep (0.007) breeds under the Brody model. However, higher estimates were obtained by Mokhtari et al. (2019) in the Kermani sheep breed under the Brody model (0.019).

The significant effects of birth year on the studied growth curve traits are potentially attributed to differences in climatic conditions and managerial practices across different years (Gbangboche et al., 2008). This observation aligns with previous findings indicating the significant impact of lamb birth year on growth curve traits in breeds such as Moghani (Rashedi Dehsahraei et al., 2023) and Kermani (Mokhtari et al., 2019) sheep. Consistent with our findings, Rashedi Dehsahraei et al. (2023) reported significant effects of lamb sex on Moghani growth curve parameters *A*, *B*, and *K*, with male lambs demonstrating superiority over females, as found in the the present study. Similarly, Mokhtari et al. (2019) observed the superiority of male Kermani lambs over females in parameters *A* and *K*, while no significant difference was found between male and female Kermani lambs for parameter *B*. In the present study, the highest and lowest values for parameter *B* were observed in triplet and single-born lambs, respectively. In contrast, Mokhtari et al. (2019) reported that birth type did not have a significant effect on the growth curve parameters in Kermani lambs.

The significant effects of dam age on the parameters *A* and *B* aligns with the notion highlighted by Gbongbache et al. (2008) that the maternal ability of ewes becomes more pronounced with age. London and Weniger (1995) also noted that first-parity ewes are still

in a growing phase, and there exists competition between dams and fetuses for nutrient consumption. Additionally, Mokhtari et al. (2019) reported that Kermani lambs born to 3-, 4-, and 5-year-old ewes had significantly higher estimated mature weights than those born to 2- and 6-year-old dams.

In the present study, maternal effects were important for genetic analysis of parameters *A* and *B*, which necessitate including these effects in models used for estimating (co)variance components for these parameters. This finding contrasts with previous reports indicating no significant influences of maternal effects on the growth curve traits of Shall (Ghavi Hossein-Zadeh, 2015a) and Lori-Bakhtiari (Amou Posht-e Masari et al., 2021) sheep breeds.

Model comparison by applying the MSE and $r(y, \hat{y})$ revealed the importance of considering causal relationships among the studied growth curve parameters into account for multivariate genetic analysis of these parameters in Iran-Black sheep. Superiority of FRM over SMM for genetic analysis of growth curve parameters in the Lori-Bakhtiari sheep breed was also pointed out by Amou Posht-e Masari et al. (2021).

The structural coefficient of parameter *B* on parameter *K* suggests that an increase in the parameter *B* value would correspond to a 0.592 unit decrease in the maturation rate (parameter *K*). While the positive structural coefficient of parameter *B* on parameter *A* shows that an increase in parameter *B* would correspond to a 2.829 kg increase in the estimated mature weight (parameter *A*). The negative causal effect of parameter *K* on parameter *A* indicates that each one-unit increase in parameter *K* would result in a decrease of parameter *A* in Iran-Black sheep by -0.569 kg. As shown in Figure 1, parameter *B* caused an indirect causal effect on parameter *A*, mediated via parameter *K*. Therefore, the overall causal effects of parameter *B* on parameter *A* are equal to the summation of direct (2.829) and indirect causal effects mediated via parameter *K* $[(-0.592) \times (-0.569) = 0.337]$ which is equal to 3.166; i.e., 3.166 kg increase in parameter *A* will be expected as a result of one kg increase in parameter *B*.

Consequently, lambs with a higher maturation rate would mature in a shorter period and consequently exhibit a lower estimated mature weight (Abegaz et al., 2010). In a similar vein, Amou Posht-e Masari et al. (2021) inferred causal relationships among the growth curve parameters of the Lori-Bakhtiari sheep breed using FRM, estimating causal effects of parameter *B* on parameter *K*, from parameter *B* on parameter *A*, and from parameter *K* on parameter *A* as -0.073, 10.319, and -0.601, respectively.

By comparing the direct heritability estimates of the growth curve parameters under SMM and FRM, it can be concluded that possible causal relationships among the investigated growth curve parameters did not significantly affect the posterior means of direct heritability estimates in Iran-Black sheep. Similar findings were reported by Amou Posht-e Masari et al. (2021) in Lori-Bakhtiari sheep. In addition, Mokhtari et al.

(2019) reported direct heritability estimates of 0.10, 0.03, and 0.04 for parameters *A*, *B*, and *K*, respectively, in Kermani sheep. Ghavi Hosseini-Zadeh (2017) reported heritability estimates of 0.2, 0.2, and 0.3 for *A*, *B*, and *K* parameters in Iranian Moghani sheep under a Bayesian approach, respectively, which were higher than the corresponding estimated values in the current investigation. Ghavi Hosseini-Zadeh (2015a) estimated heritability values of 0.13, 0.15, and 0.19 for parameters *A*, *B*, and *K* in Shall sheep, respectively.

The relatively low direct heritability estimates may be attributed to the substantial influence of non-additive genetic factors and/or environmental variations. Consequently, enhancing these parameters might require improvements in environmental conditions alongside direct genetic selection based on the estimated breeding values, not phenotypic values. It is widely recognized that factors such as breed characteristics, genetic diversity within the population, and the methodologies employed for parameter estimation can influence the heritability estimates for growth curve parameters (Ghavi Hosseini-Zadeh, 2017). In a study by Rashedi Dehsahraei et al. (2023) on growth curve parameters in Moghani sheep, differences were observed between REML and Bayesian genetic parameter estimates for the studied traits, highlighting the impact of methodological approaches on parameter estimation. In line with current findings, Ghavi Hosseini-Zadeh (2017) reported low estimates of 0.07 for both pe^2 of parameters *A* and *B* in Moghani sheep.

The estimated posterior means of the direct genetic correlations between parameters *A* and *B* were 0.53 under SMM and 0.43 under FRM. Consequently, an increase in the initial body weight may correspond to an increase in weight at maturity, which in turn entails additional feed particularly when the cost of supplementary feeding constitutes a significant portion of the total costs, as observed in Iranian sheep flocks (Bathaei and Leroy, 1998). In such scenarios, selection criteria may prioritize animals with more rapid growth rates at an early age and/or those that mature earlier. Bathaei and Leroy (1998) pointed out that a faster growth rate enhances the proportion of feed utilized for tissue synthesis and reduces the overall input per unit of body weight gain.

The primary biological genetic correlation among the growth curve parameters, as highlighted by Ghavi Hosseini-Zadeh (2015a), exists between Parameters *A* and *K*. In the current investigation, negative genetic correlations between these parameters were estimated under both SMM (-0.19) and FRM (-0.30). The estimated value under SMM was not statistically significant, with 95% of HPD intervals including zero. In contrast, the estimate under FRM was statistically significant (95% of HPD intervals did not include zero). This negative genetic correlation suggests that animals with higher adult weights generally exhibit lower growth rates compared to those with lower adult weights, as observed by da Silva et al. (2012). Notably, the direct genetic

correlation estimated between parameters *A* and *K* under SMM was not statistically significant, with 95% of HPD intervals including zero, whereas the corresponding estimate under FRM was statistically significant, with 95% of HPD intervals not including zero.

In this study, the posterior means for genetic correlations between parameters *B* and *K* were -0.65 (under SMM) and -0.29 (under FRM), both of which were statistically significant (95% of HPD intervals did not include zero). However, there was no significant difference between correlations, as evidenced by the 95% HPD intervals overlapping. Amou Posht-e Masari et al. (2021) reported a negative value of -0.97 for the direct genetic correlation between parameters *B* and *K* in the Lori-Bakhtiari sheep breed under a FRM.

The positive phenotypic correlation estimates between parameters *A* and *B* suggest that an increase in the initial body weight of lambs may lead to an increase in the mature live weight. Amou Posht-e Masari et al. (2021) documented positive and substantial estimates of 0.79 and 0.99 between the phenotypic parameters *A* and *B* in the Lori-Bakhtiari sheep breed under SMM and FRM, respectively. They also observed negative and statistically significant (95% HPD intervals not including zero) phenotypic correlation estimates for parameters *A-K* (-0.36 and -0.43) and *B-K* (-0.29 and -0.22) under both SMM and FRM, with no statistically significant difference between the two models (95% HPD intervals overlapped). Additionally, Amou Posht-e Masari et al. (2021) reported higher negative estimates of -0.72 (under SMM) and -0.97 (under FRM) for phenotypic correlations between parameters *A* and *K* in Lori-Bakhtiari sheep compared to the corresponding estimates in the present study. They also found high negative values of -0.62 (under SMM) and -0.94 (under FRM) for phenotypic correlation between parameters *B* and *K* in Lori-Bakhtiari sheep. The negative residual correlation observed between parameters *A* and *K* suggests that enhancing the environmental conditions for early maturity may not positively impact on the mature weight of the Iran-Black sheep breed.

Investigating the outcomes of SMM and FRM on the ranking of EBVs of animals revealed that it is essential to account for causal relationships among growth curve parameters in the genetic evaluation of Iran-Black sheep. Failure to consider these relationships may result in inaccuracies in ranking the animals, particularly those of superior quality. Notably, in the current study, as depicted in Figure 1, parameter *B* is regarded as a parent trait, leading to the least alteration in animal rankings when utilizing both SMM and FRM. Conversely, significant changes in animal rankings were observed for parameters *A* and *K*, underscoring the crucial role of employing appropriate models for selecting superior animals to maximize genetic progress in the genetic evaluation of growth curve parameters in the Iran-Black sheep breed. This observation aligns with the findings by Amou Posht-e Masari et al. (2021) in the Lori-Bakhtiari sheep breed.

Conclusion

It was concluded that the Brody model can be a suitable statistical tool for predicting the live weight of Iran-Black sheep breed from birth up to 360 days of age. Studying the causal links between growth curve parameters in the genetic evaluation of growth curve parameters in Iran-Black sheep by using the FRM led to a higher level of goodness of fit compared to the SMM. Substantial reductions in the levels of additive genetic variation were observed across all growth curve parameters analyzed, likely stemming from heightened phenotypic variance due to significant non-additive genetic influences and environmental factors. For achieving a desirable growth curve shape and developing an effective breeding plan for this breed, emphasis should be placed on improving the environmental conditions that impact growth curve parameters. Analyses of Spearman's rank correlations between the posterior means of estimated breeding values for growth curve parameters demonstrated that integrating the causal relationships among these parameters in the model could significantly alter the rankings of these animals.

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