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Longitudinal analysis of growth traits in Rayeni goats via random regression

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ABSTRACT

This study analyzed 13198 test-day body weight records of 4817 Rayeni goats, aged from birth to 365 days, collected over 20 years (1990-2010) at Baft Breeding Station, Iran. Growth trajectories were investigated using random regression (RR) models with varying degrees of Legendre polynomial (LP) functions to estimate genetic and phenotypic parameters. Genetic analyses were conducted using WOMBAT software, considering fixed effects (birth year, dam age, birth type, and sex) and random effects (direct additive genetic effects, maternal genetic effects, and animals' permanent environmental effects). RR models were compared using Akaike's Information Criterion (AIC) and Schwarz's Bayesian Information Criterion (BIC) to determine the best fit. The optimal model (Leg723) included a seventh-order LP for direct additive genetic effects, a second-order for maternal genetic effects, a third-order for individual permanent environmental effects, and a step function with five heterogeneous classes for residual variances. Direct heritability fluctuated, increasing from birth (0.23) to weaning (0.63), then declining to nine months (0.36), and rising again at twelve months (0.47), whereas maternal heritability exhibited a decreasing trend with age. Direct genetic and phenotypic correlations between kid weights ranged from -0.27 to 0.76 and -0.02 to 0.79, respectively, and increased as the time interval between weighings decreased. This study demonstrates that RR models are effective tools for evaluating growth trajectories in Rayeni goats. Additionally, medium to high direct genetic heritability estimates from birth to one year indicate potential for genetic improvement by selecting for body weight traits in Rayeni goats reared in harsh tropical conditions.

Keywords: body weight, genetic parameters, Legendre polynomial, Rayeni goat

INTRODUCTION

Animals and plants constitute an essential component of national wealth across all countries, and their conservation and proliferation are of considerable importance. McKenzie-Jakes (2007) estimates the global goat population to be approximately 450 million, spanning at least 210 distinct breeds worldwide. In tropical regions, small ruminants, particularly goats and sheep, are vital to the livelihoods of a substantial portion of the population, thriving in low-input production systems and exhibiting remarkable adaptability to arid and harsh climates (Kosgey and Okeyo, 2007). Goats, in particular, play a crucial economic role in developing regions, serving as an essential resource for impoverished rural communities (Abdel Aziz, 2010). In Iran, the goat population exceeds 26 million, with these animals primarily maintained in rural and nomadic systems for the production of meat, cashmere, and milk, providing a significant source of income for farmers. The Rayeni breed is the most prominent native breed, primarily distributed across the southern and southeastern regions of Iran. It is a dual-purpose breed traditionally managed under rural systems and tropical climatic conditions (Maghsoudi et al., 2009). The population of Rayeni goats is estimated to be around two and a half million, predominantly concentrated in Kerman Province. This breed demonstrates notable genetic diversity and holds substantial potential for breeding and biotechnological applications (Baghizadeh et al., 2009).

To understand the genetic potential of animals and establish an efficient genetic improvement program, precise prediction of genetic parameters of economically important traits using appropriate statistical models is necessary. Heritability and genetic correlations are essential for designing breeding programs (Bilal and Khan, 2009). Genetic evaluation methods that incorporate comprehensive animal information, estimate precise environmental factors, and increase selection accuracy are crucial for a robust breeding strategy (Sarmento et al., 2016). The random regression (RR) method can be used for these genetic predictions, as it effectively utilizes multiple records per animal. The application of RR in animal breeding was established by researchers focused on improving genetic evaluation predictions for dairy cattle (Schaeffer and Dekkers, 1994; Jamrozik and Schaeffer, 1997). The use of RR models in genetic evaluations of animals has grown in recent decades due to benefits such as the feasibility of incorporating specific environmental effects for each record, increased accuracy of breeding values, and the ability to calculate variance at every age and covariance between different ages (Schaeffer, 2004; Meyer, 2005).

RR models are used for the genetic evaluation of traits that are measured at different times during the lifetime or physiological cycle of an animal because it allows studying the variation of a trait as a function of age. The application of RR Models in animal breeding research has seen a significant surge in recent years, establishing itself as the preferred approach for the genetic evaluation of longitudinal traits across diverse livestock species. This methodology has been widely adopted for assessing genetic variations in dairy cattle (Bahreini Behzadi and Mehrpoor, 2017; Padilha et al., 2019), beef cattle (Boligon et al., 2011), sheep (Paneru et al., 2024), and goats (Brito et al., 2018), demonstrating its versatility and effectiveness in facilitating advancements in livestock genetics. Body weight is a trait that can be assessed at multiple time points throughout an animal's life, yet its underlying genetic mechanisms may change over time (Albuquerque and Meyer, 2001; Schaeffer, 2004). Understanding the functional relationship describing weight variation across different developmental stages is essential for animal breeders, as it provides critical insights into genetic changes affecting this trait. Such knowledge enhances selection predictions and facilitates the refinement of growth trajectories. RR models, specifically designed to analyze repeated measurements, have demonstrated superiority over multiple-trait models for the genetic evaluation of weight-related traits (Lewis and Brotherstone, 2002; Fischer et al., 2004; Paneru et al., 2024).

Despite the benefits of RR models, there is limited research on their application in evaluating the genetic growth parameters of Iranian sheep and goat breeds. Given the advantages of RR models in predicting genetic parameters, the present study aims to estimate genetic covariance functions for growth trajectories in Rayeni goats by applying RR models with both identical and non-identical degrees of Legendre polynomial functions.

MATERIALS AND METHODS

This study did not require approval from the Animal Care and Use Committee, as the analyses were conducted using existing field data obtained under standard farm management practices. The dataset, collected at the Rayeni Goat Breeding Station in Kerman Province, Iran, spans from 1990 to 2010. Located near Baft City in southeastern Kerman, the station recorded 13198 body weight records from birth to one year of age for 4817 Rayeni goats, after editing. These goats were born to 1315 dams and 228 sires. The completeness of a pedigree enhances its ability to illustrate population changes over time and structural shifts within the population. A deeper pedigree provides more detailed insights into genetic relationships within a population, forming the foundation of genetic evaluation models in animal studies. In the studied population, the average number of equivalent complete generations was calculated to be 3.9. While there is no definitive minimum "pedigree depth" required to ensure the accuracy of genetic evaluations, a pedigree containing at least three to five generations of known ancestors is generally considered a suitable starting point. This criterion is met in the studied population. Additionally, assessing the number of animals with known parentage is one of the simplest methods for evaluating pedigree completeness. In this study, approximately 55% of the animals had both parents identified.

The Rayeni Goat Breeding Station was established in 1965 with 180 goats, including 8 bucks, 120 does, and 52 kids, to improve economically important traits such as body weight and cashmere weight through data recording and genetic and phenotypic evaluation (Mokhtari et al., 2017). In general, the animals were managed under conventional management conditions, with natural pastures being the most important source of feed. The annual rainfall in Kerman Province is less than 250 mm. The climate is hot and relatively dry, with temperatures reaching up to 35 °C in summer and moderate temperatures in winter. The mating period began between August and October, with kids born from January to February. The kids were weighed and ear-tagged as soon as possible after birth (Mohammadi et al., 2012).

CFC software (Sargolzaei et al., 2006) was used to check pedigrees and recode animal data. Genetic parameters were estimated using the method of restricted maximum likelihood and the average information algorithm, implemented in WOMBAT software (Meyer, 2007). SAS software (SAS 9.2, 2009) and the GLM procedure were used to test the significance of fixed effects, including birth year (20 levels), sex (female and male), birth type (single, twin, and triplet), and dam age (2 to 8 years and 9 years or older). The same fixed effects were applied across all models, ensuring that restricted maximum likelihood estimates and information criteria for the random regression model were of a different order of fit for random effects, allowing direct comparison. Outliers were detected using the standard deviation (SD) method, and observations outside the mean ± 3SD interval were considered outliers and excluded from the dataset. All animals were typically weighed at birth, weaning (three months), six months, nine months, and 12 months of age. Body weights recorded after 360 days of age were disregarded. Animals with three or more records within the indicated age range were included in the analysis. The GLM procedure of SAS was used for preliminary least squares analyses to determine the order of polynomial regression required to model the population mean of the growth trajectory. (Co)variance components and genetic parameters of growth traits were estimated using random regression models. RR models account for both genetic and environmental effects at the individual animal level, aligning them with animal models. In this study, the following general RR model was used:

$$y_{ijklm} = \mu + BY_i + DA_j + BT_k + S_l +$$

$$+ \sum_{m=0}^{2} \beta_m \emptyset_m(t^*) + \sum_{m=0}^{k_A-1} \alpha_{im} \emptyset_m(t^*) +$$

$$+ \sum_{m=0}^{k_M-1} \gamma_{im} \emptyset_m(t^*) + \sum_{m=0}^{k_C-1} \delta_{im} \emptyset_m(t^*) + \varepsilon_{ijklm}$$

where y_{ijklm} represents the observed phenotypic value; μ is the overall mean; BY_i is the fixed effect of birth year; DA_j is the fixed effect of dam age; BT_k is the fixed effect of birth type; S_l is the fixed effect of sex; β_m is the fixed quadratic regression on orthogonal polynomials of age, modeling the mean age trend of the growth trajectory; t^* denotes the standardized age at recording, ranging from -1 to +1; $\emptyset_m$ (t^*) represents the m^{th} Legendre polynomial of standardized age. The variables α_{im}, γ_{im} and δ_{im} correspond to the random regression coefficients for additive direct genetic effects, maternal additive genetic effects, and animal permanent environmental effects, respectively; k_A, k_M, and k_C represent the corresponding orders of fit. Lastly, ε_{ijklm} accounts for random measurement error, denoting the temporary environmental effect. The standardized age at recording t^* is defined by the following equation:

$$t^* = -1 + \frac{2(t - t_{min})}{(t_{max} - t_{min})}$$

where t is age at the time of data collection, t_{min} and t_{max} are the minimum and maximum ages represented in the dataset, respectively (Schaeffer, 2004). The second to seventh orders of LP were fitted for all random effects to identify the most appropriate model that describes the growth trajectory. Residual variances were assumed to be heterogeneous over time and were modelled using a step function with five classes of variance.

Analyzed models were compared using two information criteria: Akaike's Information Criterion (AIC) and Schwarz's Bayesian Information Criterion (BIC). These criteria enforce penalties according to the number of estimated parameters (Wolfinger, 1993). The general equations of the information criteria are as follows:

$$AIC = -2logL + 2p,\ BIC = -2logL + plog(N - r),$$

where p is the number of estimated parameters, N is the number of data points, r is the rank of the incidence matrix of fixed effects, and $logL$ is the logarithm of the likelihood function. The calculation of eigenfunctions for RR coefficients of the best model was carried out using the IML procedure in SAS software.

RESULTS AND DISCUSSION

To model the relationship between weight and age, orthogonal polynomial functions of second, third, and fourth orders were applied. The findings indicate that the mean growth trajectory was best represented using a fixed second-order regression, which effectively captured the trends based on orthogonal polynomial functions of age. The second-order model demonstrated a strong fit to the observed growth pattern, indicating that quadratic trends sufficiently describe the main variations in body weight as animals age. Higher-order polynomials, while providing flexibility in capturing subtle fluctuations, introduced additional complexity without substantial improvements in model accuracy. Given these results, the second-order regression model serves as an optimal balance between precision and interpretability, making it particularly suitable for practical applications in genetic and growth modelling. Table 1 presents the characteristics of body weights at five important selected ages of Rayeni goats.

The mean values for various growth traits at selected ages were consistent with those reported by Mohammadi et al. (2012). However, birth and weaning weights were lower than those reported by Gholizadeh et al. (2010). This discrepancy is more likely due to differences in methodological approaches to data collection rather than variations in sample size, assuming both studies employed representative sampling techniques. Additionally, differences in data preprocessing, such as the removal of outliers, may have influenced the reported mean values, particularly if extreme observations were excluded. Furthermore, modifications in dataset size or structure, including variations in the distribution of age groups or selection criteria, could have affected the final reported averages. The coefficient of variation and standard deviation showed an increasing trend from birth to one year of age, indicating a smaller environmental effect on body weights near birth. Over 60% of kids were lost from birth to yearling due to mortality and insufficient or low-quality pasture resulting from extensive conditions, which led to some kids being sold. The relatively low rainfall in Kerman province significantly impacts the quantity of available forage.

Fitted random regression (RR) models with the logarithm of the likelihood function (logL), AIC, and BIC values are shown in Table 2. Comparing different models showed that increasing the order of fit for the direct genetic effect from 2 to 7 improved logL, AIC, and BIC values, evidenced by an increase in logL and a reduction in AIC and BIC. Unequal orders of fit for the three random effects provided a better fit. Increasing the order of fit for maternal genetic and animal permanent environmental effects higher than the fourth order (not shown in Table 2) significantly increased both information cri-

Table 1. Characteristics of the data structure for five selected body weight traits

Character[a]	BW	WW	W6	W9	YW
Mean (kg)	2.32	10.39	14.38	16.99	17.48
Standard deviation (kg)	0.42	2.94	3.68	4.23	3.83
Coefficient of variation (%)	18.17	23.04	25.57	24.87	21.91
Number of records	4817	3280	2855	1439	807

[a] BW, birth weight; WW, weaning weight at three month; W6, six month weight; W9, nine month weight; YW, yearling weight.

teria, AIC and BIC, and was therefore not considered. In conclusion, an evaluation of all criteria indicated that the model incorporating a seventh-order Legendre polynomial (LP) for the additive genetic effect, a second-order LP for the maternal genetic effect, and a third-order LP for the animal permanent environmental effect, comprising 42 parameters and denoted as Leg723, was the most appropriate for fitting the growth data of Rayeni goats. The next best-performing model in terms of efficiency was Leg633; however, it also contained a relatively high number of parameters (38), making it unsuitable for classification as a more parsimonious model. Based on these considerations, the Leg723 model was selected as the final model. Other studies on goat and sheep growth data have generally shown that a lower order of LP could be sufficient to fit the data (Fischer et al., 2004, 2006; Ghafouri Kesbi et al., 2008; Kariuki et al., 2010; Kheirabadi and Rashidi, 2016). In the majority of RR studies, the second to fifth orders of LP were fitted for all random effects. Improving data fit by increasing the order of random effects has been found in several studies (Meyer, 2000; Lewis and Brotherstone, 2002). Meyer (2000) reported that increasing the order of fit from 2 to 4 improved the data fit, but the change in fit degree from 4 to 6 did not create any significant difference in logL.

Table 2. Models, number of parameters (NP), maximum log-likelihood (logL), Akaike's information criterion (AIC) and Bayesian information criterion (BIC) for different analyses

Model[a]	NP	BIC	AIC	logL
Leg222	14	23334.69	23229.90	-11600.95
Leg223	17	22763.13	22635.89	-11300.94
Leg224	21	22756.53	22599.35	-11278.67
Leg322	17	22560.19	22432.95	-11199.47
Leg323	20	22324.11	21974.42	-10967.21
Leg333	23	22591.40	22419.25	-11186.62
Leg422	21	22253.55	22094.37	-11026.18
Leg423	24	22265.06	22055.49	-10999.74
Leg434	31	22293.90	22061.87	-10999.93
Leg522	26	22280.04	21985.43	-10966.71
Leg533	32	22282.63	21943.12	-10939.56
Leg544	40	22256.51	21957.12	-10938.55
Leg622	32	22258.58	21989.07	-10962.53
Leg633	38	22259.09	21944.67	-10934.33
Leg644	46	22304.29	21959.99	-10933.99
Leg722	39	22281.98	21990.07	-10956.03
Leg723	**42**	**22251.84**	**21937.48**	**-10926.73**
Leg724	46	22285.99	21941.70	-10929.84
Leg733	45	22280.72	21943.90	-10931.95

[a] Leg$K^a K^m K^{pe}$; K^a, K^m and K^{pe} denote the number of regression coefficients fitted for direct genetic, maternal genetic and permanent environmental effects.

Lewis and Brotherstone (2002) reported that increasing the degree of fit from 3 to 5 improved the fitted RR model. The result of the current study in finding a linear polynomial RR model (order of fit, k = 2) for the maternal genetic effect was in agreement with Fischer et al. (2004, 2006). In general, increasing the number of parameters slightly increased the log-likelihood (logL) value. The number of parameters in the studied models ranged from 14 to 46.

Variance-covariance components and correlations between the random regression (RR) coefficients and eigenvalues, as well as their proportions, for additive genetic, maternal genetic, and permanent environmental coefficient matrices, are presented in Table 3. The first eigenvalue for the three random effects was medium to large (49-98%), indicating that the majority of the total variance proportion can be explained by the first eigenfunction of each covariance function. The first four eigenvalues of the additive genetic effect accounted for approximately 98.06% of genetic variation in growth traits, while the other eigenvalues explained very small variations and could be considered less significant. For the maternal genetic effect, the first eigenvalue, and for the permanent environmental effect, the first two eigenvalues, accounted for 98.40% and 99.8% of total variations, respectively, which was comparable to the amount of additive genetic variation. There were positive correlations between the linear and intercept coefficients for additive genetic and permanent environmental effects. Additionally, correlations between the intercept and quadratic to sextic coefficients were negative for the direct genetic effect, except for the cubic coefficient.

Eigenvalues indicate the amount of variation explained by the corresponding eigenfunction (Kirkpatrick et al., 1990). If the first eigenvalue is large, the selection process can create rapid changes in the attribute under selection (Kirkpatrick et al., 1990; Olori et al., 1999).

Table 3. Estimates of variances (diagonal, boldface type), covariances (below diagonal), and correlations (above diagonal) between RR coefficients and eigenvalues (λ) of the coefficient matrices achieved by model leg723

0	1	2	3	4	5	6	λ	λ%
Additive genetic effect								
6.07	0.29	-0.32	0.37	-0.25	-0.56	-0.28	7.58	49.10
1.22	**2.80**	-0.38	-0.66	-0.16	-0.40	0.13	3.64	23.60
-1.09	-0.88	**1.84**	-0.16	-0.68	-0.14	-0.51	3.16	20.40
0.88	-1.07	-0.22	**0.92**	0.17	0.07	0.05	0.76	4.96
-0.67	-0.29	-0.99	0.18	**1.13**	0.61	0.48	0.27	1.77
-1.68	-0.81	-0.23	0.81	0.78	**1.46**	0.74	0.00	0.03
-0.76	0.24	-0.75	-0.54	0.55	0.97	**1.16**	0.00	0.00
Maternal genetic effect								
0.03	-0.34						0.03	98.40
-0.001	**0.01**						0.00	1.53
Permanent environmental effect								
4.77	0.28	-0.60					5.37	70.40
0.76	**1.55**	0.60					2.25	29.40
-1.49	0.85	**1.30**					0.00	0.06

In the present study, for maternal genetic effects, the first eigenvalue and its corresponding eigenfunction account for more than 98% of genetic variation, indicating that maternal genetic factors play a significant role in shaping growth trait expression in offspring. Regarding permanent environmental effects, the first and second eigenvalues and their corresponding eigenfunctions explain more than 98% of phenotypic variation influenced by environmental conditions, suggesting that while environmental factors contribute to phenotypic expression, they have a relatively smaller impact compared to genetic components. Comparison of eigenvalues for the three random effects suggests that a random regression (RR) model with an unequal order of Legendre Polynomial (LP) would likely be the most appropriate fitting model. As shown in Table 2, using equal order of fit for the three random effects confirmed that the results were not appropriate. According to Meyer (2005), the first three eigenfunctions typically explain the majority of genetic variation, regardless of the polynomial function used. Kheirabadi and Rashidi (2016) showed that the first two eigenvalues and related eigenfunctions accounted for 96.8% of additive genetic variance. According to Kirkpatrick et al. (1990), eigenfunctions corresponding to the genetic covariance matrix provide insight into the effects of selection across the growth trajectory.

The first two main eigenfunctions related to the direct genetic effect are shown in Figure 1. The first eigenfunction for the entire growth trajectory was positive. The second eigenfunction was negative from birth to day 126 of the growth period, positive until the age of 306 days, and then negative from age 306 to 360 days.

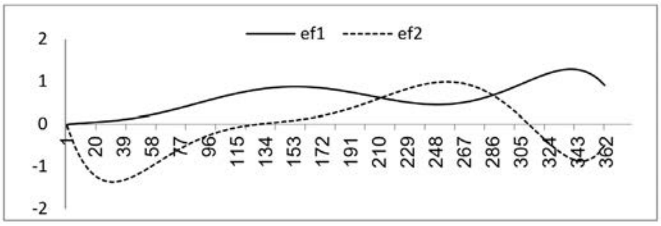

Figure 1. Eigenfunctions related to the first (ef1) and second (ef2) eigenvalues for the additive genetic effect obtained with the Leg723 model

In the present study, the first eigenfunction illustrates that growth is mainly controlled by genes with similar effects between early and late ages. Consequently, selection for increased body weight at any age will increase weight at all ages. This means that the majority of variance for the direct genetic effect is explained by a factor that is constant across all ages. The second eigenfunction explained 23.6% of genetic variation and exhibited a fluctuating trend. However, the change in sign of the second eigenfunction values suggests contrasting effects on body weight between different phases of the growth trajectory. It is expected that the rate of genetic change through selection based on the second eigenfunction will be low because this part is responsible for a small amount of additive genetic variance compared to the first eigenfunction.

Table 4 illustrates different variance components estimated from birth to 12 months of age. The additive genetic and permanent environmental variances showed a steady increase over the growth trajectory, while phenotypic variance increased remarkably from birth to yearling. Conversely, maternal additive genetic variance declined steadily, with the maximum amount at birth and the lowest amount at 12 months of age. The residual variances exhibited a fluctuating trend throughout the growth trajectory. As shown in Table 4, between the two traits, nine-month weight and yearling weight, which are close to the marketable weight, the highest estimated direct genetic variance was 8.61 kg^2 at 12 months of age. This indicates that genetic variability in this trait is most prominent at this stage. An increasing pattern of variation for direct additive genetic and phenotypic variances has been reported by Lewis and Brotherstone (2002), Fisher et al. (2004), Ghafouri Kesbi et al. (2008), Abegaaz et al. (2010), Kariuki et al. (2010), Safaei et al. (2010), Jannoune et al. (2015), and Kheirabadi and Rashidi (2016). The greatest maternal genetic variance was observed for birth weight, whereas its estimated values for other traits were minimal and exhibited a decreasing trend. Several studies have reported differing patterns in maternal genetic variance changes with aging.

Table 4. Estimates of direct additive genetic (σ_a^2), maternal additive genetic (σ_m^2), permanent environmental (σ_{pe}^2), residual (σ_e^2) and phenotypic (σ_e^2) variances at selected ages obtained with Leg723 model

Variance components	BW	WW	W6	W9	YW
σ_a^2	0.03	5.59	7.22	6.14	8.61
σ_m^2	0.02	0.02	0.02	0.02	0.01
σ_{pe}^2	0.02	2.75	4.86	4.00	6.65
σ_e^2	0.06	0.50	1.17	6.85	3.19
σ_e^2	0.14	8.85	13.27	17.00	18.47

BW, birth weight; WW, weaning weight at three months; W6, six-month weight; W9, nine-month weight; YW, yearling weight

The declining trend identified in the present study aligns with the findings of Bahreini Behzadi et al. (2007) and Rashidi et al. (2008). In contrast, Fischer et al. (2004) found that maternal genetic variance remained relatively stable throughout the growth trajectory. Some studies have indicated that maternal genetic variance increases postnatally, reaching its peak between 120 and 180 days before subsequently declining (Ghafouri Kesbi et al., 2008; Safaei et al., 2010). The individual permanent environmental variance showed an increasing trend, indicating more environmental changes with ageing and greater influence of the environment on animals (Molina et al., 2007; Ghafouri Kesbi et al., 2008; Kariuki et al., 2010).

Trends in direct and maternal heritabilities are presented in Figure 2, illustrating the variation in these genetic parameters across different developmental stages. The highest direct heritability for body weight was observed at three months, showing a sharp increase from birth (0.23) to weaning (0.63). However, heritability subsequently declined to 0.36 at nine months before rising again to 0.47 at twelve months. These fluctuations in direct heritability suggest that genetic and environmental variance components interact differently across growth stages. If genetic variance increased consistently at a higher rate than environmental variance, a steady upward trend in heritability would be expected. However, the observed variations imply that additional factors, such as environmental influences or selection effects, may contribute to these changes over time. The fluctuating trend in direct heritability also underscores the importance of having sufficient data at both the beginning and end of the growth trajectory. A similar pattern in the covariance function, where data were most limited at the trajectory's endpoint, was also observed by Meyer (2001) and Fischer et al. (2004). Meyer (2004) suggested that the "end range" issue in the covariance function could be mitigated if most animals had a minimum number of records equivalent to the polynomial order used to model direct and permanent environmental effects. Ensuring uniform data distribution across the entire growth curve was identified as a crucial factor. Meyer (2002) and Molina et al. (2007) attributed irregular changes in heritability at older ages to the limited number of observations available. A gradual increase in direct heritability with age has been documented in several studies, including those by Lewis and Brotherstone (2002), Fischer et al. (2004), Molina et al. (2007), Ghafouri Kesbi et al. (2008), and Kheirabadi and Rashidi (2016). This trend is likely due to the progressive expression of genes with additive genetic effects on body weight traits as animals mature.

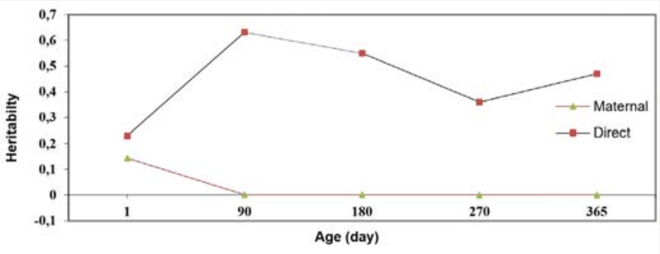

Figure 2. Trends in direct and maternal heritabilities of body weight from birth to later ages

The highest maternal heritability is observed at birth (0.14), followed by a decline at weaning (three months, 0.002). At later ages, it remains very low, approaching zero (0.001). These findings suggest that maternal genetic effects play a significant role during early growth phases but diminish as the animal matures. This general downward trend has been reported in multiple studies, including those by Bahreini Behzadi et al. (2007) and Rashidi et al. (2008). The observed decline in maternal heritability from birth to later ages suggests a diminishing maternal genetic influence on body weight as the offspring matures, likely due to the increasing impact of direct genetic and environmental factors on growth. Robison (1981) reported that maternal effects in mammals are significant in young animals but tend to decrease with age.

Similarly, Albuquerque and Meyer (2001) found that maternal genetic effects begin to decline before and around weaning. This reduction occurs because maternal influences, such as milk production and care, play a crucial role during early life but diminish as direct genetic effects become more dominant in later stages of growth. Since maternal heritability is higher at younger ages, selecting animals based on early-age body weights may favor stronger maternal genetic effects. However, this does not necessarily lead to an overall improvement in maternal ability unless direct selection for maternal traits is implemented. Effective selection for maternal ability requires a focus on traits such as reproductive performance, milk yield, and offspring survival, rather than solely considering early body weight.

Table 5 presents estimates of direct genetic correlations and phenotypic correlations for body weights at selected ages. Direct genetic correlations ranged from -0.27 to 0.76, while phenotypic correlations varied between -0.02 and 0.79 across different age stages. Phenotypic correlations were positive for all body weight traits except for birth weight correlations with weights at three, six, and nine months, which were negative and relatively low. In general, genetic and phenotypic correlation estimates decline as the interval between weight measurements increases, as closely observations exhibit greater similarity, while those taken further apart show weaker associations. The RR model treats all weight records as the same, correlated trait measured at different time points, allowing for the analysis of trait variation across different developmental stages.

The decreasing pattern of genetic and phenotypic correlations with increasing age between weights is consistent with those reported in the literature (Fischer et al., 2004; Ghafouri Kesbi et al., 2008; Abegaz et al., 2010; Kariuki et al., 2010; Kheirabadi and Rashidi, 2016; Naderi, 2018). The direct genetic correlations were positive between all body weight traits, indicating that selection for body weight at any age should result in positive genetic changes for body weight at other ages. Positive genetic correlation estimates have been reported in several studies (Ghafouri Kesbi et al., 2008; Abegaz et al., 2010; Kheirabadi and Rashidi, 2016).

Table 5. Estimates of direct genetic correlations (above the diagonal) and phenotypic correlations (below the diagonal) among weights at selected ages, obtained using the Leg723 model

Character[a]	BW	WW	W6	W9	YW
BW	-	0.27	0.26	0.19	0.11
WW	-0.004	-	0.76	0.58	0.49
W6	-0.02	0.79	-	0.53	0.50
W9	-0.001	0.35	0.50	-	0.48
YW	0.04	0.24	0.30	0.39	-

[a] BW, birth weight; WW, weaning weight; W6, six month weight; W9, nine month weight; YW, yearling weight

The low genetic correlation between birth weight and weights at 9 and 12 months of age indicated that early body weights near birth are not necessarily under the same genetic control as weights at older ages. Therefore, various body weights throughout a kid's growth trajectory should be considered as different but correlated traits (Lewis and Brotherstone, 2002; Fischer et al., 2004; Kariuki et al., 2010; Kheirabadi and Rashidi, 2016). The genetic correlations between weaning weight and later weights were high, indicating that selection for increased body weight at weaning will also result in genetic changes for body weights at older ages. Phenotypic correlations were generally lower than the corresponding direct genetic correlations. Kariuki et al. (2010), Kheirabadi and Rashidi (2016), and Fischer et al. (2004) also reported lower phenotypic correlation estimates compared to genetic correlations.

Generally, the RR model requires more computational time compared to simple and multi-trait animal models. However, this computational demand can be alleviated by utilizing a high-performance computing system or selecting a lower-order RR model. Previous research has demonstrated that reducing the order of RR models can significantly decrease computation time while preserving predictive accuracy (Li et al., 2020; Paneru et al., 2022). In the current study, computational efficiency was not a primary consideration; therefore, the results of the optimal model were reported without accounting for processing time. Given the increasing use of multiple weight trait recordings by sheep and goat breeders, the RR model presents itself as a viable alternative for genetic evaluation of weight traits. One of its key advantages is its ability to generate a smooth variance-covariance function along the developmental trajectory, thereby minimizing sensitivity to measurements that deviate from the mean age of a specific growth stage. In contrast, multi-trait models may introduce bias for animal groups positioned at the boundaries of a weight stage—a limitation that the RR model effectively mitigates (Paneru et al., 2024).

CONCLUSIONS

This study confirms that body weight heritability in Rayeni goats ranges from moderate to high, enabling effective selective breeding even in challenging environments. Weaning weight at three months shows the highest heritability and strong genetic correlation with later growth, making it a key selection criterion. Incorporating performance-based and pedigree-driven selection enhances genetic progress and adaptability. Additionally, fluctuating residual variance across growth stages necessitates heterogeneous variance structures for accurate genetic evaluation. RR models enhance genetic evaluation accuracy for longitudinal traits but require large datasets and complex computations, posing challenges for resource-limited breeding programs. However, this computational demand can be alleviated by utilizing a high-performance computing system or selecting a lower-order RR model. Traditional genetic models may be more practical when data is scarce. The observed heritability estimates and genetic correlations suggest selection can shape growth trajectories in Rayeni goats, though large-scale application of RR models remains difficult. A two-tiered strategy is recommended: prioritizing weaning weight in commercial herds for productivity while refining genetic evaluations in nucleus herds to support long-term genetic improvement, ensuring both economic viability and genetic sustainability.

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