

Determination of the genetic and non-genetic variations in growth curve of Zandi lambs by random regression models

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Abstract The aim of this study was to model the variances and covariances of body weight in Zandi sheep from 60 to 365 days of age using random regression models (RRM). Legendre polynomials of different orders were used to model the direct and maternal covariances. Mean trends were also modeled through a quadratic regression on orthogonal polynomials of age. Homogeneity and heterogeneity of the residual variance were considered along the growth trajectory. Different models were compared by log-likelihood ratio test (LRT) and Akaike's information criterion (AIC). Results showed that simple repeatability model in which orders of 1 were used for all random effects could not adequately model variations in growth curve of Zandi lambs. A RRM with Legendre polynomials of orders 3, 3, 3, and 3 for direct additive genetic, individual permanent environment, maternal additive genetic and maternal permanent environmental effects was selected as the most parsimonious model. The power of the parsimonious model decreased when maternal effects were excluded from the analysis, indicating the necessity of including maternal effects in the model for genetic evaluation of Zandi lambs. Considering the heterogeneity of residual variance along with the growth trajectory improved the overall properties of the model. Direct heritability (h^2) decreased from 0.3 at 60 days of age to 0.15 at about 120 days and then increased with age gradually and reached 0.39 at 365 days of age. The individual permanent environmental effect (p^2) decreased from 0.43 at 60 days of age to 0.23 at 180 days of age and fixed between 0.25 and 0.30 thereafter. Maternal heritability (m^2) was 0.03 at 60 days of age, increased to a peak around 240 days of age (0.22) and decreased with age thereafter. The ratio of maternal permanent environmental variance to phenotypic variance (c^2) was below 0.03 throughout the trajectory. Estimates of coefficients of variation (CV) revealed the presence of considerable genetic and environmental variability in growth curve of Zandi sheep which can be exploited for breeding purposes. Both direct and maternal correlations were positively high between adjacent weights but decreased as the distance between ages increased.

Keywords: sheep, body weight, random regression models, heritability, genetic correlation

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Introduction

Small ruminants, especially native breed types, play an important role in the livelihoods of a considerable part of human population in the tropics from socio-economic aspects (Zamani et al., 2015). Therefore, integrated attempt in terms of management and genetic improvement to enhance production is of crucial importance (Mohammadabadi and Sattayimokhtari, 2013). There are approximately 25 million heads of sheep in Iran (Ghafouri-Kesbi and Gholizadeh, 2017) consisting of 27 breeds and ecotypes which are mainly raised for meat production (Khodabakhshzadeh et al., 2016).

Recently in Iran demand for meat and mutton has increased at a significant rate mainly because of population growth and improved living standards. This means that the meat production should be increased either by

increasing the number of animals or increasing the productivity per animal. Statistics show that in the last three decades, the sheep population has experienced a sharp decrease by roughly 30% (Sefidbakht, 2011). Therefore, the only way to increase meat production would be increasing the productivity per animal. This is possible by applying efficient selection programs. This strategy has been followed in recent years and some results have been published (Mokhtari and Rashidi, 2010; Mohammadi et al., 2012; Gholizadeh and Ghafouri-Kesbi, 2015). In some cases, the results are somewhat lower than expected. One approach to increase the efficiency of selection programs is to increase the accuracy of genetic evaluation. This can be achieved by replacing traditional evaluation methods with random regression

models (RRM; Henderson Jr., 1984). Originally, the RRM was suggested to model the biological human data but its advantages encouraged the animal breeders to apply it in the genetic evaluation of livestock when repeated measurements or longitudinal data (measurements obtained sequentially from the same animal over time) are available. Milk yield records and body weights measured along the time are typical examples of repeated measurements. Dealing with repeated measurements, the RRM can model covariances through regression, a feature that has been used in studying body weight in sheep (Lewis and Brotherstone, 2002; Ghafouri-Kesbi et al., 2008; Safaei et al., 2010), beef cattle (Albuquerque and Meyer, 2001; Arango et al., 2004) and poultry (Rafat et al., 2011). In contrast to the traditional multi-trait models (MTM) that provide point predictions, RRM allows the prediction of breeding values for the growth curve as a whole, for any point or interval within the growth trajectory (Lewis and Brotherstone, 2002). Meyer (2004) stated that using RRM instead of traditional MTM increase the accuracy of genetic evaluation. Any increase in the accuracy of genetic evaluation is desired as it increases the genetic gain.

The Zandi sheep is a fat-tailed small-size breed. The coat-color of the new-born lamb is black, but gradually changes with age, in such a way that black, light-brown and gray adult animals are found. Historically, Zandi breed had its origin in the southern province of Iran known as Fars (Ghafouri-Kesbi et al., 2011). Today, they are reared in central areas of Iran, in Tehran and Qom provinces (Ghafouri-Kesbi et al., 2011). Due to its large population (about 2 million heads), there is considerable interest in genetically improving Zandi sheep in order to enhance their growth performance. Although, genetic information for growth-related traits has been reported for some of Iranian sheep breeds (Eskandarinasab et al., 2010; Rashidi et al., 2013; Gholizadeh and Ghafouri-Kesbi, 2015; Ghafouri-Kesbi and Gholizadeh, 2017), RRM has hardly been applied to growth data. Since increase in accuracy of breeding values is the direct consequence of applying RRM, use of RRM seems to be necessary. Therefore, the aim of this study was to analysis the growth curve of Zandi sheep by RRM. The findings might provide new insights regarding the genetic and non-genetic variations in growth curve and can be exploited by the breeders of Zandi sheep.

Materials and methods

Data and flock management

Data and pedigree information on Zandi lambs were obtained from the Breeding Station of Zandi sheep. This

station was established in 1981 in the Khojir National Park between Tehran and Abali at 35°45'E and 51°40'N, 1547 m above mean sea-level, with temperate summers and cool winters, and an average rainfall of approximately 300 mm/yr. The founder animals of unknown pedigree were purchased from various sheep producers in the region. The first lambs were born in 1982 and the flock has been maintained as a close flock. In general, the flock is reared according to the conventional husbandry procedures. The mating season commences in August. Ewes on heat undergo artificial insemination (AI) and mating between very closely related animals is avoided. Usually, 20-25 ewes are inseminated with semen of one ram. Animals that do not conceive by AI are allowed to mate naturally at a ratio of 10-15 ewes per ram. Lambing commences in December. At birth, lambs are weighed, ear tagged, sexed, and their pedigree information recorded. Birth date is also recorded. The mean suckling period is 90 days. Animals are grazed on natural pasture during the spring, summer and autumn seasons and hand-fed indoors during winter.

No live weight records were available from birth to 60 days of age, thus only 60–365 day BW records were included in the data set. As recommended by Fischer et al. (2004), birth weight was excluded from the analysis because of the low genetic correlation of the birth weight with body weights measured later in life and seems to be a different trait (Fischer et al., 2004; Ghafouri-Kesbi et al. 2008). In addition, there is evidence that inclusion of birth weight may cause some problems such as increased order of polynomial fit, occurrence of “end effects of polynomials” and difficult fitting of data (Fischer et al., 2004). There were few records after 365 days that were omitted to prevent computational problems due to small number of records. Furthermore, records with doubtful dates or weights were also removed from the data file. This yielded a total of 9699 records on 4187 animals that were the progeny of 170 sires and 1450 dams.

Statistical analysis

The least squares analysis, using the GLM procedure of SAS (2004), was used to determine the significance of the fixed effects. The model included the effects of birth year, sex, type of birth and age of dam at lambing. All fixed effects were significant ($P < 0.05$) and therefore included in the final analyses.

Four sets of RR coefficients were fitted to the data. Direct and maternal genetic effects were assumed to be proportionate to the numerator relationship matrix. Further analyses considering different orders of fit for the

four random effects were carried out subsequently to determine the most parsimonious model describing the data. The general model is represented as:

$$y_{ij} = F_{ij} + \sum_{m=0}^3 \beta_m \phi_m(t_{ij}^*) + \sum_{m=0}^{k_{A-1}} \alpha_{im} \phi_m(t_{ij}^*) + \sum_{m=0}^{k_{M-1}} \gamma_{im} \phi_m(t_{ij}^*) + \sum_{m=0}^{k_{C-1}} \delta_{im} \phi_m(t_{ij}^*) + \sum_{m=0}^{k_{Q-1}} \rho_{im} \phi_m(t_{ij}^*) + \varepsilon_{ij} \quad (1)$$

where, y_{ij} is the j th record from i th animal; t_{ij}^* is the standardized ($-1 < t < 1$) age at recording; $\phi_m(t_{ij}^*)$ is the m th legendre polynomials of age; F_{ij} is a set of fixed effects; β_m are the fixed regression coefficients for modeling the population mean; α_{im} , γ_{im} , δ_{im} and ρ_{im} are the random regression coefficients for direct genetic, maternal genetic, and direct and maternal permanent environmental effects, respectively; k_{A-1} , k_{M-1} , k_{P-1} and k_{C-1} are the corresponding order of (polynomial) fit for each effect and ε_{ij} denotes the residual (measurement error) effect. Log-likelihood ratio test (LRT) and Akaike's Information Criterion (Akaike, 1973) were used to compare models with different orders of fit and random effects. The WOMBAT program of Meyer (2007) which uses the average information (AI) algorithm was used to analyze the data.

After determining the most parsimonious model including the direct and maternal effects, the maternal genetic and maternal permanent environmental effects were excluded from the model and differences in likelihoods were monitored to determine whether including the maternal effects in genetic evaluation procedure is necessary or not.

It has been argued that heritabilities do not provide a good means of comparing variation at different ages, when different levels of environmental variation exist (Houle, 1992; Kruuk et al., 2000). Therefore, the estimates of variance components were used to calculate the coefficients of variation. The additive coefficient of variation (CV_A) was calculated as:

$$CV_A = 100 \times \sqrt{V_A} / \bar{x} \quad (2)$$

where, V_A is the additive genetic variance and \bar{x} is the sample mean. The " $\sqrt{V_A} / \bar{x}$ " ratio measures "variability", while the ratio " V_A / V_P " measures "heritability" of the trait. Coefficients for other random effects can be expressed in a similar fashion. Compared to the raw variances, coefficients of variation are expected to be less sensitive to the scale effects arising from an increasing

mean weight with age (Houle, 1992).

Two strategies were considered for modeling the residual variance (ε). In the first strategy, homogeneity of the residual variance for the whole period was considered. In the second strategy, heterogeneity of residual variance was considered along growth trajectory by dividing the growth trajectory to 5 growth phases, namely 60 to 120, 121 to 180, 181 to 240, 241 to 300, and 301 to 365 days of age and allocating a residual variance to each phase.

Results and discussion

Figure 1 shows the number of records and mean weights at different points of growth trajectory. Two growth phases with different growth rates are detectable, one from 60 to 180 days of age with approximately linear increase in body weight, and another one from 180 to 365 days of age with decreased growth rate. The mean weight and standard deviation for the whole period were 27.46 kg and 7.72 kg, respectively. Data characteristics and pedigree structures are shown in Table 1. The pedigree consisted of 5930 animals distributed in 9 generations; the pedigree was deep enough to allow accurate estimation of the genetic parameters.

Several models with different orders of fit were fitted to the data to find a parsimonious model that described the data adequately. Of all models fitted, the description of five models is listed in Table 2. According to LogL and AIC values, the simple repeatability model (the intercept model; 1-1-1-1) was not statistically suitable to model direct and maternal random effects. Arango et al. (2004), analyzing the growth data of beef cattle, reported that a simple repeatability model could not describe the longitudinal data adequately. In addition, greater estimates of error variances for 5 growth phases obtained with simple repeatability model compared to other models indicated that those variances tended to

Table 1. Summary of pedigree and data structure of the Zandi sheep

	N
No. of Generations (including base generation)	9
No. of Animals in the pedigree file	5930
No. of Animals with progeny	1620
No. of Animals without progeny	4370
No. of Sires with progeny	170
No. of Sires with progeny and record	168
No. of Dams with progeny	1450
No. of Dams with progeny and record	965
No. of Grand sire	133
No. of Grand dam	752
No. of Animals with record	4187

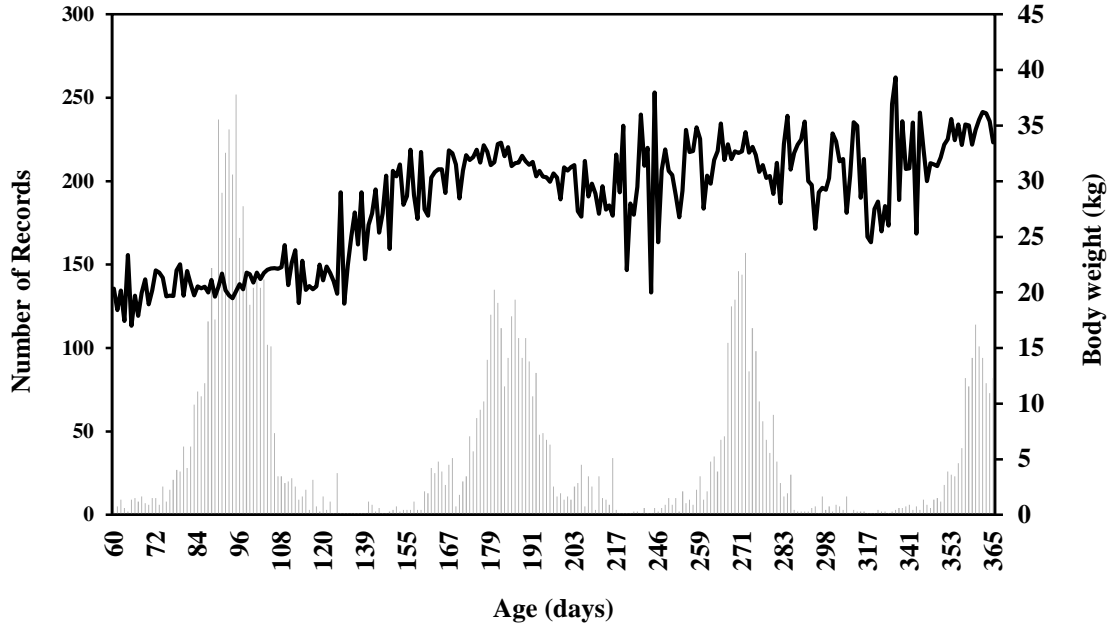


Figure 1. Number of records (gray columns) and mean weights (black line) at different ages

Table 2. Order of fit for direct (K_A) and maternal (K_M) genetic, individual permanent (K_P) and maternal permanent (K_C) environmental effects (best model in bold)

Model	K_A	K_P	K_M	K_C	N_p^b	LogL ^c	AIC ^d	E1	E2	E3	E4	E5
1	1	1	1	1	9	-18588.13	36194.26	10.38	14.20	10.99	16.54	26.27
2	2	2	2	2	17	-18207.40	36448.81	8.48	13.07	10.00	8.48	12.36
3	3	3	3	3	29	-18104.76	36267.52	7.67	14.40	12.25	13.68	16.79
4	3	3	3	3	25	-18323.43	36696.86	9.54	9.54	9.54	9.54	9.54
5	3	3	-	-	17	-18369.75	36773.50	7.94	14.01	11.86	17.00	17.96

^b N_p : Number of parameters, ^cLogL: Log likelihood function, ^dAIC: Akaike’s information criterion; E1-E5: estimates for residual variances for 5 growth phases (60 to 120, 121 to 180, 181 to 240, 241 to 300, and 301 to 365 days of age).

pick up variation due to insufficient order of fit (Meyer, 1999). The simple repeatability model is limited with its assumptions. It assumes that all genetic variances and covariances are of the same magnitude, all phenotypic variances are considered identical and phenotypic correlations and covariances among all measurements are equal (Meyer and Hill, 1997). These assumptions contradict most of the published reports (Albuquerque and Meyer, 2001; Lewis and Brotherstone, 2002). Increasing the order of fit from 1-1-1-1 to 3-3-3-3 improved the LRT and AIC values, a finding which has been previously reported by Lewis and Brotherstone, (2002), Arango et al. (2004) and Ghafouri-Kesbi et al. (2008). Therefore, model 3 which had 25 parameters was chosen as the most parsimonious model. Higher-order polynomials are more flexible and consequently are able to follow the changes in covariances more closely. However, the performance of higher-order polynomials is limited by the problem of “oscillation” or Runge’s phenomenon (Kirkpatrick et al., 1994; Meyer, 1998b).

Therefore, we did not increase the orders of fit beyond 3 to prevent computational problems related to high order polynomials (Meyer, 2005). In analyzing sheep growth data with RRM, usually orders equal or lower than 3 have been used (Fischer et al. 2004, Safaei et al. 2010).

The assumption that the residual term is constant over time (Model 4) had undesirable effects on the overall properties of the model, as also reported in other studies (Albuquerque and Meyer, 2001; Meyer, 2001; Huisman et al., 2005). To accommodate the fluctuation in residual variance with the age, considering heterogeneity of the residual variance over time is necessary (Albuquerque and Meyer, 2001).

By excluding the maternal effects from the most parsimonious model (Model 3) a significant decrease in Log L was observed (Model 5). Similar results were reported for growth data in sheep using traditional univariate models (Ghafouri-kesbi and Eskandarinasab, 2008; Ghavi Hossein-Zadeh, 2012; Gholizadeh and

Ghafouri- Kesbi, 2015) and Random Regression Models (Ghafouri-Kesbi et al., 2008), indicating the necessity of including the maternal effects where lambs are genetically evaluated for growth traits.

Table 3 presents the estimates of covariances and correlations between RR coefficients for model 3 with $K=3, 3, 3, 3$. As observed, the most variable coefficient was the intercept. Correlations between the intercept and linear coefficient ranged from -0.173 (maternal permanent environmental effect) to 0.626 (maternal genetic effect). Correlations between the intercept and quadratic regression coefficient ranged from -0.985 (maternal permanent environmental effect) to almost unity (individual permanent environmental effect). Some of the eigenvalues were zero which is due to the strong correlations between regression coefficients (Albuquerque and Meyer, 2001). Large eigenvalues indicate considerable genetic variation in growth curve and the potential for changing growth curve genetically. The first eigenvalue of the K matrix for A, M, P and C shows that 80-84% of the total variance can be explained by the first eigenfunction of each covariance function. Fischer et al. (2004) reported that 89-94% of total variation in Poll Dorset sheep was explained by the first eigenfunction of each covariance function, which is close to our findings; this was 95-98% in Mehraban sheep (Ghafouri-Kesbi et al., 2008).

Estimates of variance components, genetic parameters and coefficients of variation for weights from 60 to 365 days of age, extracted from the most parsimonious

Table 3. Estimated coefficient matrices of the covariance functions and the corresponding eigenvalues of the covariance matrices and the correlation (above diagonal) between random regression coefficients for direct genetic (A), maternal genetic (M), individual permanent environmental (P) and maternal permanent environmental (C) effects

	0	1	2	Eigenvalue
A				19.64 (83%)
	17.941	0.516	-0.268	3.39 (14%)
	4.906	5.036	-0.099	0.66 (3%)
	-0.963	-0.190	0.71	
M				
	1.5327	0.627	-0.616	3.16 (82%)
	1.1788	2.302	0.225	0.71 (18%)
	-0.14770	0.066	0.037	0.00 (0.0%)
P				
	3.3739	0.556	0.985	3.87 (84%)
	1.1405	1.247	0.404	0.75 (16%)
	0.095	0.024	0.002	0.00 (0.0%)
C				
	1.435	-0.171	-0.985	1.49 (80%)
	-0.126	0.376	0.003	0.36 (20%)
	-0.254	0.004	0.046	0.00 (0.0%)

model (Model 3) are shown in Figures 2, 3, and 4, respectively. The patterns for direct genetic and permanent environmental variances was similar in a way that they decreased after birth to a smallest value around 120 days of age, increased with age thereafter and reached the maximum value at 365 days of age, which is in agreement with Ghafouri-Kesbi et al. (2008). Maternal genetic variance increased after 60 days of age to a peak around 180 days of age and decreased gradually thereafter. The maternal permanent environmental variance decreased from 60 to around 120 days of age and then increased until 365 days of age.

Direct heritability estimates decreased after 60 days of age (0.30) until animals were about 120 days old (0.15) and increased sharply until 365 days of age (0.39). In particular, the direct heritability increased faster at ages at which maternal heritability tended to be the lowest. The increased pattern for heritability is in agreement with most studies (Albuquerque and Meyer, 2001; Ghafouri-Kesbi et al., 2008), and may be due to increase in the expression of genes with additive effects on body development and decrease in variances due to maternal effects at later ages. Likewise, CV_A which measures the additive genetic variability in body weight of Zandi lambs had a similar pattern with h^2 in general; with a minimum value found between 150 and 160 days of age. The CV_{AS} can be high in traits with low heritabilities if there is high residual error variance in the trait (Houle 1992; Wilson et al., 2005). The CV_A scales the components of the additive genetic variance by the trait mean instead of total variance and therefore is not confounded by the magnitude of other variance components. Under selection, the levels of CV_A directly determine the magnitude of response to selection. Regarding CV_A , two peaks were detectable: one between 220 to 250 days and another between 320 to 340 days at which body weights can be the target of selection. The individual permanent environmental effect (p^2) decreased rapidly from 0.43 at 60 days to a value of 0.35 at about 120 days of age, slowly decreased until 180 days of age (0.23) and then fluctuated between 0.25 and 0.30 until the end of the trajectory. The pattern for CV_P differed from p^2 in such a way that it decreased slowly until 180 days of age and gradually increased thereafter. Maternal heritability estimates (m^2) increased from 60 days of age (0.03) to 240 days of age (0.22) and decreased with age thereafter. At weaning (≈ 90 -100 days), the estimates of m^2 were between 0.11 and 0.14. Persistency of m^2 after weaning may be due to carry-over of maternal effects from weaning weight. Such carry-over of maternal effects beyond weaning are biologically sensible; particularly when lamb growth to weaning is restricted by low ewe milk

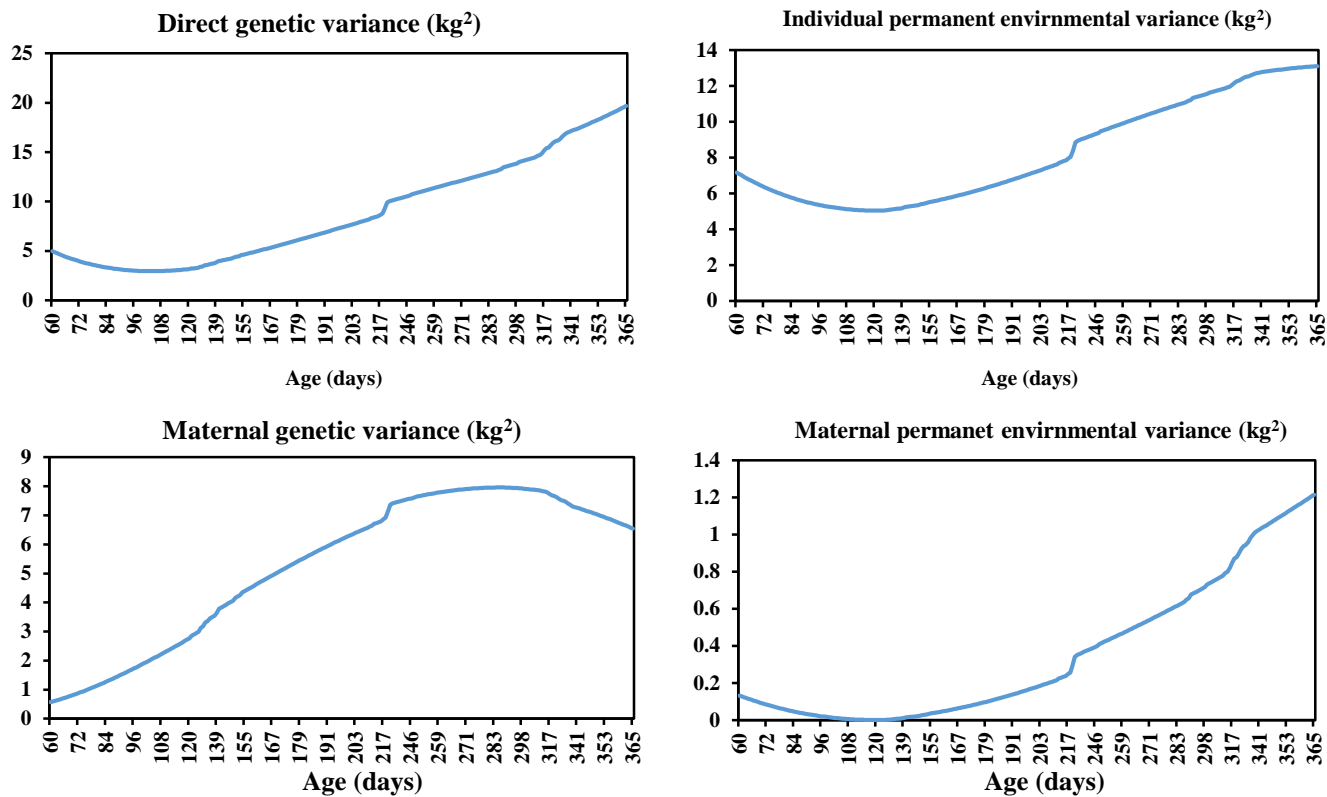


Figure 2. Estimates of variance components

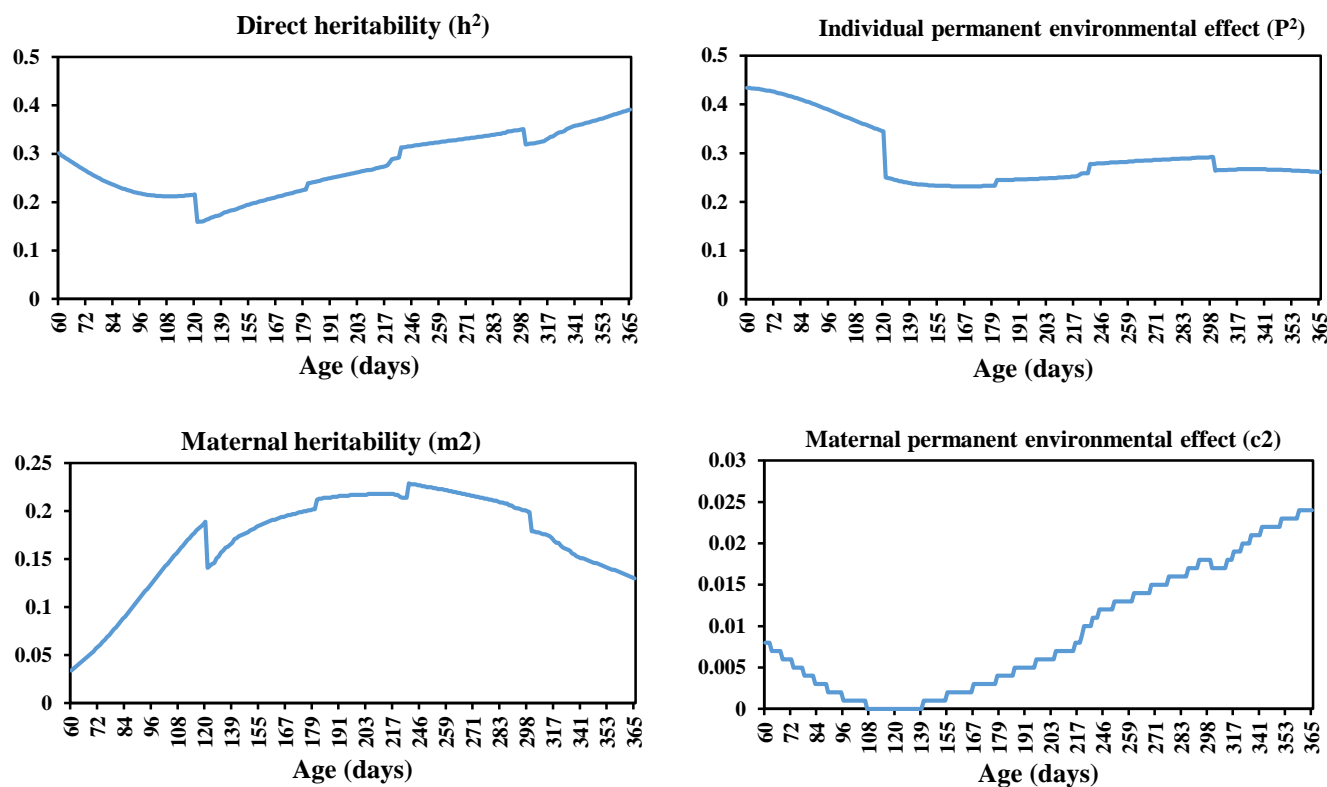


Figure 3. Estimates of direct and maternal heritability and individual and maternal permanent environmental effects

Genetic and non-genetic variations of growth curve in Zandi lambs

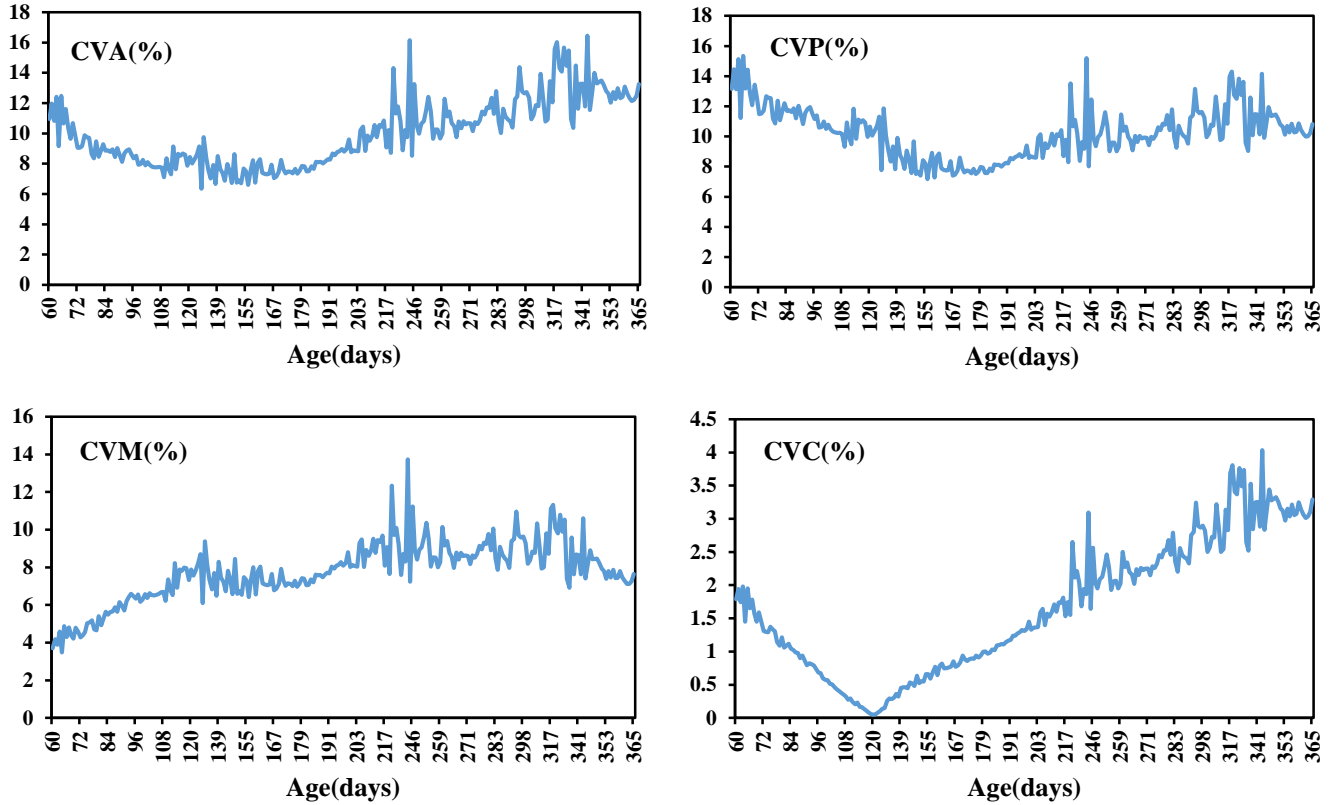


Figure 4. Estimates of direct genetic (CV_A), individual permanent (CV_P), maternal genetic (CV_M) and maternal permanent environmental coefficient of variation (CV_C)

production either due to large litter size or seasonal constraints on feed (Bradford, 1972; Snyman et al., 1995). It is more evidenced by estimates of CV_M with a peak between 220 and 240 days of age as well as estimates of c^2 and CV_C with sharp increases after weaning. However, estimates of c^2 and CV_C were below 0.03 and 5%

throughout the trajectory, which indicated that maternal permanent environmental effect has little contribution in phenotypic variation of body weight in Zandi lambs; therefore this effect can be excluded from the model of genetic evaluation. By including only one of the maternal effects (additive genetic or permanent environment-

Table 4. Correlations between body weights at different ages

Age1	Age2	r_a	r_p	r_m	r_c
60	60	1	1	1	1
60	123	0.641	0.553	0.72	0.285
60	196	0.231	0.335	-0.14	-0.163
60	279	0.083	0.190	-0.499	-0.475
60	365	0.087	0.157	-0.507	-0.699
123	123	1	1	1	1
123	196	0.885	0.996	0.555	0.718
123	279	0.737	0.499	0.063	0.894
123	365	0.501	-0.468	-0.202	0.248
196	196	1	1	1	1
196	279	0.945	0.422	0.826	0.954
196	365	0.705	-0.543	0.537	-0.496
279	279	1	1	1	1
279	365	0.886	0.532	0.908	-0.212
365	365	1	1	1	1

r_a : Direct genetic correlation, r_p : individual permanent environmental correlation, r_m : Maternal genetic correlation, r_c : Maternal permanent environmental correlation.

tal) in the model, most of the maternal variation would be accounted for (Meyer, 1992).

Correlations between selected body weights are listed in Table 4. The pattern of direct and maternal genetic and individual and maternal permanent environmental correlations is the same; in that correlations decreased as the distance between the tests increased. The genetic correlations between body weight at 60 days and around 9 and 12 months of age were smaller than 0.1, indicating that genes controlling 60-day body weight has little contribution to development of body weight at higher ages and *vice versa*. Therefore, small correlated response in body weight at higher ages is expected following selection for 60-day body weight. This is in agreement with previous reports (Lewis and Brotherstone, 2002; Arango et al., 2004; Ghafouri-Kesbi et al., 2008). The direct genetic correlations between body weights taken at higher ages were highly positive; suggesting that they may be under the same genetic control. Maternal genetic correlations between 60-day body weight and body weights at higher ages were negative which indicates that the genes of dams which contribute in milk production have some unfavorable effects on post-weaning body weights.

In general, results showed the inadequacy of simple repeatability model to deal with repeated body weight records as evidenced by LRT and AIC values. An RRM with orders of fit of 3, 3, 3 and 3 for direct genetic, maternal genetic, individual permanent and maternal permanent environmental effects was selected as the most parsimonious model for analysis. Results from this model revealed presence of genetic variation in the growthcurve of Zandi lambs and that this genetic variation was not constant throughout the growth trajectory and fluctuated with advancing age. Body weights beyond 200 days of age had greater genetic variability and heritability and therefore greater genetic response would be expected through genetic selection. While maternal genetic effects had a considerable contribution to the phenotypic variation in body weight of Zandi lambs, the contribution of maternal permanent environmental effect was negligible and therefore can be excluded in genetic evaluation models. Genetic and permanent environmental correlations between body weights decreased as the distance between the pairs of ages increased.

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References

- Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. *Proceedings of the 2nd International Symposium of Information Theory*. Budapest, Hungary.
- Albuquerque, L.G., Meyer, K., 2001. Estimates of covariance function for growth to 630 days of age in Nelore cattle. *Journal of Animal Science* 79, 277-275.
- Arango, J.R., Cundiff, L.V., Van Vleck, L.D., 2004. Covariance function and random regression models for cow weight in beef cattle. *Journal of Animal Science* 82, 54-67.
- Bradford, G.E., 1972. The role of maternal effects in animal breeding: VII. Maternal effects in sheep. *Journal of Animal Science* 35, 1324-1334.
- Eskandarinasab, M.P., Ghafouri-Kesbi, F., Abbasi, M.A., 2010. Different models for evaluation of growth traits and Kleiber ratio in an experimental flock of Iranian fat-tailed Afshari sheep. *Journal of Animal Breeding and Genetics* 127, 26-33.
- Fischer, T.M., van der Werf, J.H.J., Banks, R.G., Ball, A.J., 2004. Description of lamb growth using random regression on field data. *Livestock Production Science* 89,175-185.
- Ghafouri-Kesbi, F., Abbasi, M.A., Afraz, F., Babaei, M., Baneh, H., Abdollahi Arpanahi,R., 2011. Genetic analysis of growth rate and Kleiber ratio in Zandi sheep. *Tropical Animal Health and Production* 43, 1153-1159.
- Ghafouri-Kesbi, F., Eskandarinasab M.P., Shahir, M.H., 2008 Estimation of direct and maternal effects on body weight in Mehraban sheep using random regression models. *Archiv Tierzucht* 51, 235-246.
- Ghafouri-Kesbi, F., Gholizadeh, M. 2017. Genetic and phenotypic aspects of growth rate and efficiency-related traits in sheep. *Small Ruminant Research* 149, 181-187.
- Gholizadeh, M., Ghafouri-Kesbi, F., 2015. Quantifying direct and maternal effects for growth-related traits and evaluating the response of Baluchi sheep to a 27-year selection program. *Small Ruminant Research* 130, 8-14.
- Henderson, Jr., C.R., 1982. Analysis of covariance in the mixed model: higher level, nonhomogeneous, and random regressions. *Biometrics* 38, 623-640.
- Houle, D., 1992. Comparing evolvability and variability of quantitative traits. *Genetics* 130, 195-204.
- Huisman, A.E., Veerkamp, R.F., van Arendonk, J.A.M., 2002. Genetic parameters for various random regression models to describe the weight data of pig. *Journal of Animal Science* 80, 575-582.
- Khodabakhshzadeh, R., Mohammadabadi, M.R., Esmailizadeh, A., Moradi Shahrehabak, H., Bordbar, F., Ansari Namin, S. 2016. Identification of point mutations in exon 2 of GDF9 gene in Kermani sheep. *Poland Journal of Veterinary Science* 19, 281-289.

- Kirkpatrick, M., Hill, W.G., Thompson, R., 1994. Estimating the covariance structure of traits during growth and aging, illustrated with lactation in dairy cattle. *Genetic Research* 64, 57-69.
- Kruuk, L.E.B., Clutton-Brock, T.H., Slate, J., Pemberton, J.M., Brotherstone, S., Guinness, F.E., 2000. Heritability of fitness in a wild mammal population. *Proceedings of the National Academy of Sciences* 97, 698-703.
- Lewis, R.M., Brotherston, S., 2002. A genetic evaluation of growth in sheep using random regression techniques. *Journal of Animal Science* 74, 63-70.
- Meyer, K. 2007. WOMBAT – a program for mixed model analyses by restricted maximum likelihood. User's Guide. Animal Genetics and Breeding Unit, University of New England, Armidale, Australia.
- Meyer, K., 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. *Livestock Production Science* 31, 179-204.
- Meyer, K., 1998. Estimating covariance functions for longitudinal data using a random regression model. *Genetic Selection Evolution* 30, 221-240.
- Meyer, K., 1999. Estimates of genetic and phenotypic covariance functions for post-weaning growth and mature weight of beef cows. *Journal of Animal Breeding and Genetics* 116, 181-205.
- Meyer, K., 2001. Estimates of direct and maternal covariance function for growth of Australian beef calve from birth to weaning. *Genetic Selection Evolution* 33, 487-514.
- Meyer, K., 2004. Scope of random regression model in genetic evaluation of beef cattle for growth. *Livestock Production Science* 86, 68-83.
- Meyer, K., 2005. Advance in methodology for random regression analyses. Animal Genetics and Breeding Unit, University of New England, Armidale, Australia, NSW 2351.
- Meyer, K., Hill, W.G., 1997. Estimation of genetic and phenotypic covariance functions for longitudinal or 'repeated' records by restricted maximum likelihood. *Livestock Production Science* 47, 185-200.
- Mohammadabadi, M.R., Sattayimokhtari, R., 2013. Estimation of (co) variance components of ewe productivity traits in Kermani sheep. *Slovak Journal of Animal Science* 46, 45-51.
- Mohammadi, M., Moradi Shahrehabak, M., Vatankhah, M., Moradi Shahrehabak, H., 2012. Direct and maternal (co)variance components, genetic parameters, and annual trends for growth traits of Makooei sheep in Iran. *Tropical Animal Health and Production* 7, 233-243.
- Mokhtari, M.S., Rashidi, A., 2010. Genetic trends estimation for body weights of Kermani sheep at different ages using multivariate animal models. *Small Ruminant Research* 88, 23-26.
- Rafat S.A., Namavar, P., Shodja, D.J., Janmohammadi, H., Khosroshahi, H.Z., David, I., 2011. Estimates of the genetic parameters of turkey body weight using random regression analysis. *Animal* 5, 1699-1704
- Rashidi, A., 2013. Genetic parameter estimates of body weight traits in Iran-Black sheep. *Journal of Livestock Science and Technologies* 1, 50-56.
- Safaei, M., Fallah-Khair, A., Seyed-Sharifi, R., Haghbin Nazarpak, H., Sobhabi, A., Yalchi, T., 2010. Estimation of covariance functions for growth trait from birth to 180 days of age in Iranian Baluchi sheep. *Journal of Food, Agriculture and Environment* 8, 659-663.
- SAS, 2004. Users Guide version 9.1: Statistics. SAS Institute, Cary, NC.
- Sefidbakht, N., 2011. Future aspect of sustainable animal production in Iran, focusing on the sheep and goat. *The First Seminar on Animal Production in the Tropical Environment*. Shahid Bahonar University of Kerman, Iran, 1-9 (In Farsi).
- Snyman, M.A., Erusmus, G.J., Van Wyke, J.B., Olivier, J.J., 1995. Direct and maternal (co) variance component and heritability estimates for body weight at different ages and fleece traits in Afrino sheep. *Livestock Production Science* 44, 229-235.
- Soufy, B., Mohammadabadi, M. R., Shojaeyan, K., Baghizadeh, A., Ferasaty, S., Askari, N., Dayani, O. 2009. Evaluation of myostatin gene polymorphism in Sanjabi sheep by PCR-RFLP method. *Animal Science Research* 19, 81-89.
- Wilson A.J., Coltman, D.W., Pemberton, J.M., Overall, A.D.J., Byrne, K.A., Kruuk, L.E.B., 2005. Maternal genetic effects set the potential for evolution in a free-living vertebrate population. *Journal of Evolutionary Biology* 18, 405-414.
- Zamani, P., Akhondi, M., Mohammadabadi, M.R. 2015. Associations of Inter-Simple Sequence Repeat loci with predicted breeding values of body weight in sheep. *Small Ruminant Research* 132, 123-127.

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بررسی نوع ژنتیکی و غیر ژنتیکی در منحنی رشد گوسفندان زندی با استفاده از مدل‌های رگرسیون تصادفی

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چکیده هدف این پژوهش، مدل‌سازی واریانس‌ها و کوواریانس‌های وزن بدن گوسفند‌های زندی بین سن‌های ۶۰ تا ۳۶۵ روزگی با به کارگیری مدل‌های رگرسیون تصادفی بود. چندجمله‌ای‌های لجن‌در با درجه‌های متفاوت برای مدل‌سازی اثرهای مستقیم و مادری استفاده شدند. میانگین منحنی رشد جمعیت نیز با روش رگرسیون درجه ۲ از سن رکوردگیری برازش شد. در ضمن، یکنواختی و عدم یکنواختی واریانس باقیمانده در طول منحنی رشد در نظر گرفته شد. مدل‌های مختلف با استفاده از آزمون لگاریتم نسبت درست‌نمایی (LRT) و شاخص اطلاعات آکائیک (AIC) مورد مقایسه قرار گرفتند. نتایج نشان داد که مدل تکرارپذیری ساده که در آن از درجه برازش ۱ برای مدل‌سازی اثرات مستقیم و مادری مورد استفاده قرار گرفته بود نمی‌تواند به خوبی تغییرات در منحنی رشد گوسفندان زندی را مدل‌سازی نماید. یک مدل رگرسیون تصادفی با درجات برازش ۳، ۳، ۳ و ۳ به ترتیب برای اثرات ژنتیکی افزایشی مستقیم، محیطی دائمی حیوان، ژنتیکی افزایشی مادری و محیطی دائمی مادری به عنوان بهترین مدل انتخاب شد. توانایی برازش بهترین مدل با خروج اثرات مادری از مدل کاهش یافت که نشان‌دهنده ضرورت در نظر گرفتن اثرات مادری در مدل ارزیابی ژنتیکی بره‌های زندی است. در نظر گرفتن غیریکنواختی واریانس باقیمانده در طول دوره رشد منجر به بهبود خصوصیات کلی مدل گردید. وراثت‌پذیری مستقیم (h^2) از مقدار ۰/۳ در سن ۶۰ روزگی به ۰/۱۵ در سن ۱۲۰ روزگی کاهش یافت و سپس به صورت تدریجی افزایش یافته و در سن ۳۶۵ روزگی به مقدار ۰/۳۹ رسید. اثر محیطی دائمی حیوان (p^2) از مقدار ۰/۴۳ در سن ۶۰ روزگی به ۰/۲۳ در سن ۱۸۰ روزگی کاهش یافت و پس از آن بین ۰/۲۵ و ۰/۳ ثابت شد. وراثت‌پذیری مادری (m^2) در سن ۶۰ روزگی ۰/۰۳ بود و تا سن ۲۴۰ روزگی افزایش یافته و به حداکثر میزان ۰/۲۲ رسید و پس از آن روند کاهشی به خود گرفت. اثر محیطی دائمی مادری (c^2) در کل دوره مورد بررسی در حدود ۰/۰۳ قرار داشت. برآوردهای ضریب تغییرات (CV) مقادیر قابل توجه از تغییرپذیری ژنتیکی و محیطی در منحنی رشد گوسفندان زندی را نشان داد که می‌تواند جهت اهداف اصلاحی مورد بهره‌برداری قرار گیرد. همبستگی‌های مستقیم و مادری بین وزن بدن در سنین مجاور به طور قابل ملاحظه‌ای مثبت و بالا بود، اما با افزایش فاصله بین روزهای رکوردگیری کاهش یافت.