Effect of Different Residual Variances on Genetic Parameters of Test Day Milk Yields

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Abstract

Heterogeneous residual variance effects on genetic parameters were examined for test day milk yields of Turkish Holsteins. A third order random regression models including the fixed, random additive genetic and permanent environmental effects were used. One of these models, RV10, residual variances is assumed to be different for each test day milk yields. The RV1 model has constant residual variance for each test day. Sequential (RV2 to RV9) and non-sequential (NRV2 to NRV9) groups of residual variances were also described in the models in order to compare estimates of variance components. The univariate analysis of milk yields for each test days was performed to define variance groups. The predicted residual variances ranged from 5.62 to 11.75 and from 5.61 to 11.71 for RV and NRV models, respectively. Estimates of additive genetic variances changed between 0.55-6.76 for RV and 0.08-2.46 for NRV models. Permanent environmental variances were found between 2.36 and 18.60 for RV and 6.92 to 18.85 for NRV models. Heritability estimates varied from 0.02 to 0.43 for RV and 0.01 to 0.13 for NRV models. As a result, more accurate genetic parameter estimates are achieved by controlling the residual variances. RV10 model should be preferred to define details of the milk yield residual variances for each test day. However, RV5 model has been determined that an alternative model as compared with RV10.

Keywords: Residual variance, Random regression model, Genetic parameter, Holstein Friesian

Denetim Günü Süt Veriminin Genetik Parametre Tahminine Farklı Hata Varyanslarının Etkisi

Özet

Bu çalışmada Siyah Alaca'ların denetim günü süt verimine ait genetik parametre tahminine heterojen hata varyanslarının etkisi incelenmiştir. Bu amaçla sabit etkileri, şansa bağlı genetik ve kalıcı çevre etkilerini içeren üçüncü dereceden şansa bağlı regresyon modelleri kullanılmıştır. Bu modellerden RV10 modelinde hata varyansları her bir denetim gününde farklı kabul edilmiştir. RV1 modelinde ise hata varyansları tüm denetim günlerinde sabit kabul edilmiştir. Varyans bileşenleri tahminlerinin karşılaştırılmasında ardışık (RV2-RV9) ve ardışık olmayan (NRV2-NRV9) hata varyansı gruplarını içeren modeller kullanılmıştır. Söz konusu grupların belirlenmesinde denetim günü süt verimlerinin her biri için tek değişkenli analiz uygulanmıştır. Ardışık hata varyansı tanımlanan modellerde hata varyansı tahmini 5.62 ile 11.75 arasında ve ardışık olmayan hata varyansı tanımlanan modellerde ise 5.61 ile 11.71 arasında değişmiştir. Ardışık ve ardışık olmayan hata varyanslı modellerde eklemeli genetik varyanslar sırasıyla 0.55 ile 6.76 ve 0.08 ile 2.46 arasında tahminlenmiştir. Kalıcı çevre varyansları ise ardışık modellerde 2.36 ile 18.60 ve ardışık olmayanlarda 6.92 ile 18.85 arasında tahminlenmiştir. Kalıtım derecesi tahminleri de ardışık modeller için 0.02 ile 0.43 arasında ve ardışık olmayan modeller için 0.01 ile 0.13 arasında elde edilmiştir. Sonuç olarak, hata varyanslarının kontrol altına alınmasıyla daha güvenilir genetik parametre tahminlerine ulaşılmıştır. Her bir denetim günündeki hata varyansının tanımlamasında RV10 modelinin kullanımı tavsiye edilmiştir. Bunun yanı sıra, RV5 modelinin RV10 modeline göre alternatif bir model olduğu belirlenmiştir.

Anahtar sözcükler: Hata varyansı, Şansa bağlı regresyon modeli, Genetik parametre, Siyah Alaca

INTRODUCTION

In animal science, repeated measures such as milk yield, body weight and food intake have been analyzed with different models [1]. Genetic evaluation of milk production traits in dairy cattle can be improved by using test day models instead of aggregated 305 day production records [2-4]. In recent years, many countries have commonly used random regression models for production traits to improve the efficiency of the selection programs.

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Assuming homogeneous residual variance is a common approach in these models. However, this assumption may lead to lower or higher impact on the evaluation for different parts of the lactation. Several studies have shown that the residual variance changes over time because of herd management, weather conditions, lactation number, age at calving, month of calving, days in milk, pregnancy status, medical treatments and milking times etc. [5-9]. Generally, these mentioned environmental factors make the residual variances larger and more variable at the beginning and at the end of the lactation in comparison with those at the middle part. Therefore, information coming from each part of the lactation where the residual variance is actually larger than the assumed homogeneous value will has lower weight than it really has [10]. In addition, Olori et al.[6] conveyed that constant residual variance assumption causes residual variances to be underestimated and heritabilities to be overestimated in early stages of lactation. Instead of constant residual assumption, heterogeneous of residual variance can be included in the models. Different approaches have been proposed based on heterogeneous residual variance during lactation. In some previous studies, lactation divided into different periods with assuming homogeneity of residual variance within the period and heterogeneity between them [6,11,12]. This approach is easy to implement and can be useful in the sense that it provides more useful information on the expected pattern of residual variance which changes over lactation. However, defining the different arbitrary classes of heterogeneous of residual variance is more important for a good model. If the identification of the classes in terms of residual variance is not accurate, the proposed model will not be correct [10]. Olori et al.[6,7] reported that a correct estimation of residual variance in each class depends on which lactation stages are assumed to have the same residual variance.

Few earlier studies have been proposed heterogeneity of residual variance in random regression model for the estimation of genetic parameters for test day milk records. Olori et al.[6] investigated constant and varied residual variances in the scope of random regression models. They found that constant residual variance structure in random regression models alters estimates of residual variance in early lactation but has no significant effect on the additive genetic and permanent environmental variances. Olori et al.[7] also modeled third, fourth and fifth order random regression models with varying residual variance groups (constant, 4, 10 and 37 measurement error classes) for estimates of variance components. They obtained declined estimates of residual variances as the order of fit of the additive genetic, phenotypic and permanent environmental variances increased. Moreover, Rekaya et al.[11] compared alternative models to analyze test day yields in the Spanish Holstein Friesian population. They adopted two random regression models with have constant residual variance and allowed 30 residual variance classes. They estimated smaller residual variances under heterogeneous residual variance model. In their study larger residual variances showed lower heritability estimates at the beginning and end of the lactation. Lo'pez-Romero et al.[10] considered homogeneous and heterogeneous of residual variance with three and 30 arbitrary measurement error classes of different length in random regression models with third and fifth order additive genetic and permanent environmental effects. Residual variances obtained from 30 arbitrary intervals were constant between 70 and 300 days of lactation and tended to increase towards beginning and end of the lactation. The assumptions on the residual variance pattern did not affect the estimates of the daily additive genetic variance and only affect the estimates of daily permanent environmental variance in the first part of the lactation. Fujii and Suzuki [13] estimated genetic parameters for milk yield by using random regression models under heterogeneous residual variances and tested residual variances in three models with linear and quadratic exponential functions of calving year and also divided residual variances into five groups according to calving year. They estimated permanent environmental variances larger than additive genetic variances and the pattern of the permanent and additive genetic variances were very similar in different models. But estimates of residual variances were increased along lactation.

Heterogeneous residual variance assumptions have not been adequately highlighted in the literature. In this study, therefore, several random regression models under homogeneous and heterogeneous residual variance assumptions with sequential residual variance classes of test days were employed for analyses of variance components. Unlike previous studies, random regression models under non-sequential residual variance classes of test days for analyses of variance components were also investigated with this study. All models were compared based on their fitting performance and estimates of genetic parameters for milk yields of Turkish Holstein Friesians.

MATERIAL and METHODS

Data

Holstein milk records from different farms who are the members of Isparta province Cattle Breeders Association in Turkey were the material of this study. Milk yields were collected at monthly periods (TD1-TD10) from 2001 through 2011. Test day milk records less than 5 kg were excluded from the analyses. Only records collected between DIM 5 and DIM 307 were included. Age at first calving was also limited between 20 and 51 month. In the final, data set total of 43206 test day milk records from 6085 Turkish Holstein Friesian cows in 248 herds were analyzed. The descriptive statistics of final data set were given in *Table 1*.

Table 1. *Descriptive statistics of the final data*

Tablo 1. *Veri setine ilişkin tanımlayıcı istatistikler*

Item	No.
Records	43206
Mean TD records per cow	18.78
Herds	248
Herd-year-season level	3809
Animals with records	6085
Sires with progeny records	667
Dams with progeny records	4241

Method

The random regression models under different residual variance structure were applied to first lactation test day milk yield records of Turkish Holsteins. Third order Legendre polynomial model was preferred to obtain the best fit [7,14-19]. The used random regression model is as follows:

$$y_{ijk} = HYS_i + \sum_{m=1}^{5} \beta_m X_m(t_{jk}) + \sum_{m=1}^{3} \alpha_{jm} \phi_m(t_{jk})$$
$$+ \sum_{m=1}^{3} p_{jm} \phi_m(t_{jk}) + e_{ijk}$$

where y_{ijk} is the kth test day milk yield of the cow j at i^{th} herd-year-season, HYS_i is the ith herd-year-season effect, β_m is the mth fixed regression coefficients associated with the mth covariate, t_{jk} is the kth test day of the cow j, $X_m(t_{jk})$ is the mth covariates (X_1: Age at first calving, c=305, X_2=DIM/c, X_3=$(X_2)^2$, X_4=ln(c/DIM), X_5==$(X_4)^2$ depending on DIM=t, of the Ali and Schaeffer [20] function evaluated at t_{jk}), α_{jm} is the mth additive genetic random regression coefficients for cow j, p_{jm} is the mth permanent environmental random regression coefficients for cow j, ϕ_m is the mth polynomial and e_{ijk} is the random residual effect with $e_{ijk} \sim N(0,\sigma^2 e_{ijk})$.

In this random regression model several residual variance groups were designed. Residual variance was firstly assumed constant (RV1 model) through lactation. On the contrary to RV1, residual variance was assumed different for each test day with RV10 model. Then univariate analysis of milk yields for each test days was performed with the univariate models as given below:

$$y_{ijk} = HYS_i + \alpha_j + e_{ijk}$$

where y_{ijk} is the kth test day milk yield of the cow j at i^{th} herd-year-season, HYS_i is the ith herd-year-season effect, α_j is the additive genetic effect for cow j and e_{ijk} is the random residual effect.

Sequential (RV) and non-sequential (NRV) groups for residual variance were described according to results of this preliminary analysis *(Fig. 1)*. Residual variance patterns for RV and NRV groups were shown in *Fig. 1*. For example, in RV2, two residual variance groups were described with 1 (for the first five test days) and 2 (for the last five test

days). However, in NRV2 the two groups were not described sequentially as RV2 *(Fig. 1)*.

Analyses were performed using DFREML statistical package [21]. The goodness of fit of the model was investigated by Akaike's information criterion, AIC [22]. This likelihood based criterion has been calculated as: AIC= -2 × LogL + 2 × p where p denotes the number of parameters estimated. The model which gives the lowest AIC values was chosen as the better approximating model [10,23]. Furthermore, residual variance structures were compared Likelihood ratio test-LRT [24] within sequential and non-sequential residual variance groups. LRT for model i and j was LRT_{ij}= -2 × ($LogL_i - LogL_j$). In the LRT, the Log Likelihood (LogL) differences were tested using Chi-square (χ^2) test with the degree of freedom determined as the number of the parameter differences between the models [25].

RESULTS

Fitting Performance of Models

The fitting performance of the RV and NRV models were presented in *Table 2*. However, only the comparisons of the models with previous one were given in the last column of *Table 2*. Fitting performance of all RV and NRV models

Table 2. *LogL and AIC values of the RV and NRV models*

Tablo 2. *RV ve NRV modellerinde LogL ve AIC değerleri*

RV Group	Parameter No.	AIC	LogL Values	LRT
Constant RV	13	111088	-55525	-
RV2	14	140279	-70119	-29188*
RV3	15	140286	-70122	-6*
RV4	16	140191	-70074	96*
RV5	17	140154	-70054	40*
RV6	18	140218	-70085	-62*
RV7	19	140550	-70250	-330*
RV8	20	140546	-70247	6*
RV9	21	140210	-70078	338*
RV10	22	140143	-70043	70*
Constant RV	13	111088	-55525	-
NRV2	14	140209	-70084	-29118*
NRV3	15	140194	-70076	16*
NRV4	16	140699	-70327	-502*
NRV5	17	140147	-70050	554*
NRV6	18	140590	-70271	-442*
NRV7	19	140164	-70057	428*
NRV8	20	140148	-70048	18*
NRV9	21	140232	-70089	-82*
RV10	22	140143	-70043	92*

* Values within a column differ significantly at P<0.05

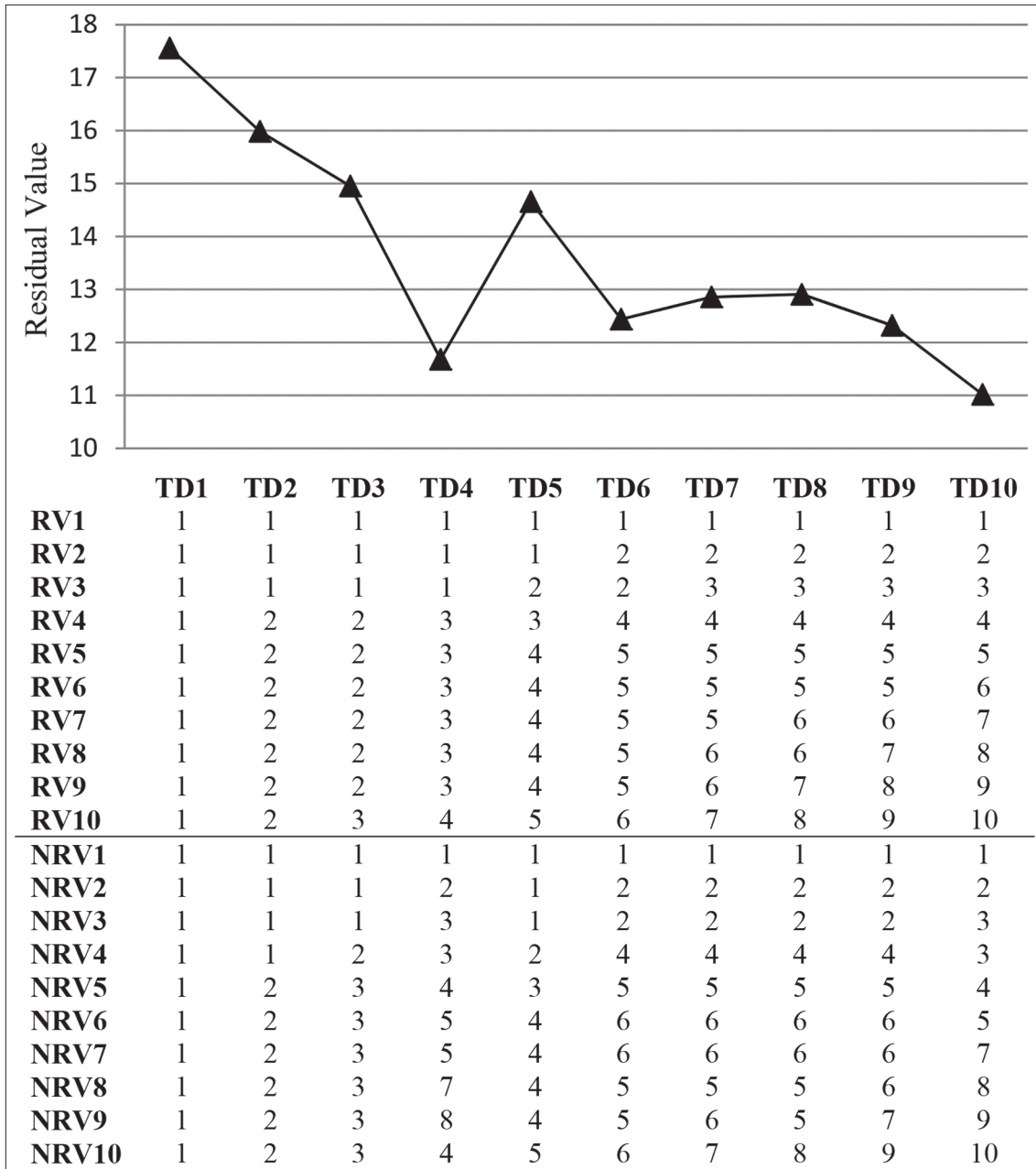|	TD1	TD2	TD3	TD4	TD5	TD6	TD7	TD8	TD9	TD10
RV1	1	1	1	1	1	1	1	1	1	1
RV2	1	1	1	1	1	2	2	2	2	2
RV3	1	1	1	1	2	2	3	3	3	3
RV4	1	2	2	3	3	4	4	4	4	4
RV5	1	2	2	3	4	5	5	5	5	5
RV6	1	2	2	3	4	5	5	5	5	6
RV7	1	2	2	3	4	5	5	6	6	7
RV8	1	2	2	3	4	5	6	6	7	8
RV9	1	2	2	3	4	5	6	7	8	9
RV10	1	2	3	4	5	6	7	8	9	10
NRV1	1	1	1	1	1	1	1	1	1	1
NRV2	1	1	1	2	1	2	2	2	2	2
NRV3	1	1	1	3	1	2	2	2	2	3
NRV4	1	1	2	3	2	4	4	4	4	3
NRV5	1	2	3	4	3	5	5	5	5	4
NRV6	1	2	3	5	4	6	6	6	6	5
NRV7	1	2	3	5	4	6	6	6	6	7
NRV8	1	2	3	7	4	5	5	5	6	8
NRV9	1	2	3	8	4	5	6	5	7	9
NRV10	1	2	3	4	5	6	7	8	9	10

Fig 1. Patterns of RV and NRV groups according to univariate analysis of residual variances of each test day

Şekil 1. Denetim günü hata varyanslarının tek değişkenli analizine göre RV ve NRV grupları
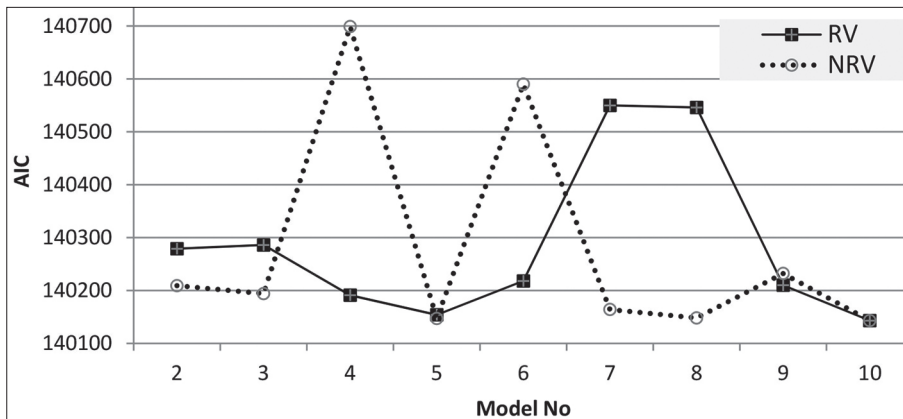

Fig 2. Changes of AIC values for all RV models

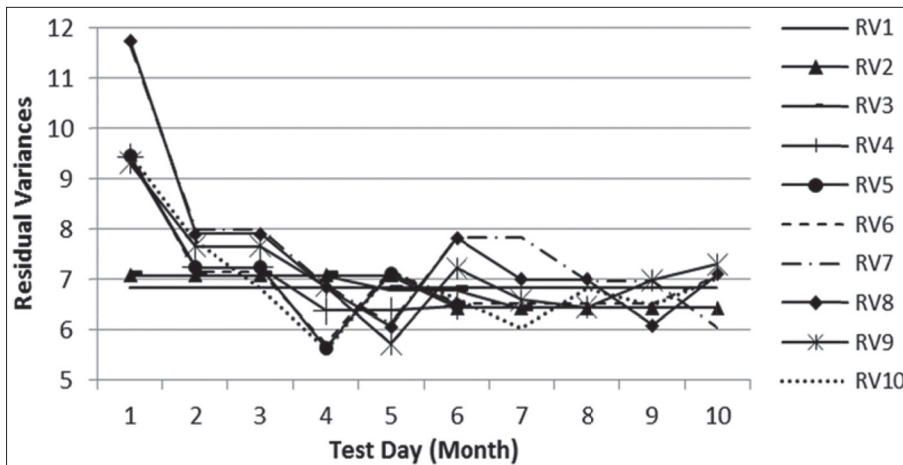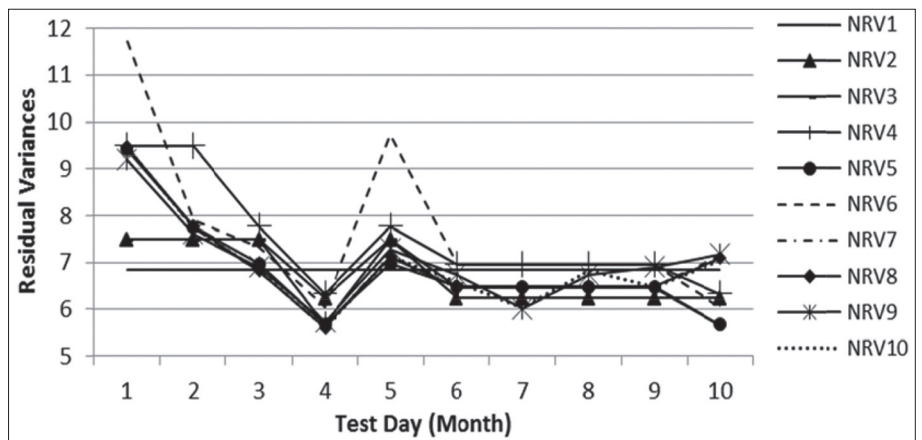**Şekil 2.** RV modellerinde AIC değerlerinin değişimi

Fig 3. Change of residual variances of the test day milk yields under RV models

Şekil 3. RV modellerinde denetim günü süt verimi hata varyansının değişimi

Fig 4. Change of residual variances of the test day milk yields under NRV models

Şekil 4. NRV modellerinde denetim günü süt verimi hata varyansının değişimi

were found significantly different due to LRT results. On the other hand, the RV1 model which has the least number of parameter and constant residual variance, showed a better performance with the lowest AIC value. AIC values of other models were closer each other compared with RV1. But nevertheless, there are still some differences among models for AIC values *(Table 2)*. Especially RV5, RV10 and NRV5 had a better performance. Among them the RV5 model defines residual variance structure in detail at the beginning and peak of lactation while RV10 model separately evaluates residual variances of each test day milk yields *(Fig. 2)*. Similar fitting structure is also valid for the LogL values.

Residual Variances

The variability of the residual variances was explored by plotting the estimated residuals from the random regression RV and NRV models in *Fig. 3* and *Fig. 4*, respectively. Residual variances changed from 5.62 to 11.75 for RV models and from 5.61 to 11.71 for NRV models. The higher residual variance was obtained at the first test day and then decreased to 5-8 test days for the next test days *(Fig. 3, Fig. 4)*. When compared all RV and NRV models, NRV4 and NRV6 models gave higher residual variance estimates *(Fig. 4)*. In fact, these are the models that have the worst results in model fitting *(Table 2)*.

Estimates of Other Variance Components and Genetic Parameters

Estimates of additive genetic variances varied from 0.55 to 6.76 for RV and 0.08 to 2.46 for NRV models. Changes of the permanent environmental variances were found between 2.36 to 18.60 for RV and 6.92 to 18.85 for NRV models. The heritability estimates for test day milk yields from RV and NRV models were summarized in *Table 3*. The estimates ranged from 0.02 to 0.48 for RV and 0.01 to 0.17 for NRV models. In terms of heritabilities, there is a similarity among models except the RV1, RV6 and RV9 models.

The RV1 model gave higher estimates of heritability at beginning and end of lactation compared with the models specified for the study *(Table 3, Fig. 5-a)*. However, it has similar heritability estimates ($h^2 \sim 0.10$) with other models in the middle of lactation. On the other hand, permanent environmental effect did not change during lactation for the RV1 model. Variability of heritability estimates during lactation can be explained by variability in the genetic variances.

When compared all models, in the middle of the lactation heritability estimates from the RV9 model is two times ($h^2 \sim 0.20$) and RV6 model is four times

Table 3. *Heritability estimates and sum of absolute differences for RV and NRV models*
Tablo 3. *RV ve NRV modellerinde kalıtım derecesi tahminleri ve mutlak sapmalar toplamı*

Model	TD										SAD[1]
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	
Constant RV	0.32	0.22	0.14	0.11	0.10	0.12	0.17	0.26	0.37	0.48	1.37
RV2	0.10	0.12	0.13	0.13	0.12	0.12	0.11	0.10	0.08	0.05	0.06
RV3	0.10	0.12	0.13	0.13	0.12	0.12	0.11	0.10	0.08	0.05	0.06
RV4	0.09	0.12	0.12	0.13	0.13	0.12	0.11	0.10	0.07	0.05	0.06
RV5	0.09	0.11	0.12	0.13	0.12	0.12	0.11	0.09	0.07	0.04	0.02
RV6	0.02	0.11	0.23	0.38	0.41	0.43	0.36	0.23	0.10	0.02	1.45
RV7	0.10	0.11	0.10	0.11	0.11	0.10	0.10	0.11	0.11	0.12	0.25
RV8	0.07	0.09	0.10	0.11	0.12	0.11	0.11	0.10	0.10	0.08	0.19
RV9	0.04	0.09	0.14	0.19	0.19	0.19	0.17	0.14	0.09	0.04	0.4
RV10	0.09	0.11	0.13	0.14	0.12	0.12	0.11	0.09	0.07	0.04	0
NRV2	0.09	0.10	0.11	0.12	0.11	0.12	0.12	0.11	0.10	0.07	0.15
NRV3	0.10	0.11	0.12	0.13	0.11	0.12	0.11	0.09	0.07	0.05	0.05
NRV4	0.07	0.08	0.10	0.12	0.11	0.12	0.11	0.10	0.09	0.08	0.18
NRV5	0.09	0.11	0.12	0.13	0.12	0.11	0.11	0.10	0.09	0.08	0.1
NRV6	0.07	0.09	0.10	0.12	0.10	0.12	0.11	0.11	0.09	0.09	0.2
NRV7	0.05	0.10	0.15	0.17	0.13	0.10	0.04	0.01	0.01	0.06	0.36
NRV8	0.09	0.11	0.12	0.13	0.12	0.12	0.11	0.09	0.07	0.05	0.03
NRV9	0.07	0.10	0.12	0.13	0.12	0.12	0.12	0.11	0.09	0.07	0.13

[1] *SAD: Sum of absolute differences of heritability estimates for test day milk yields of the model from estimates of RV10 model*
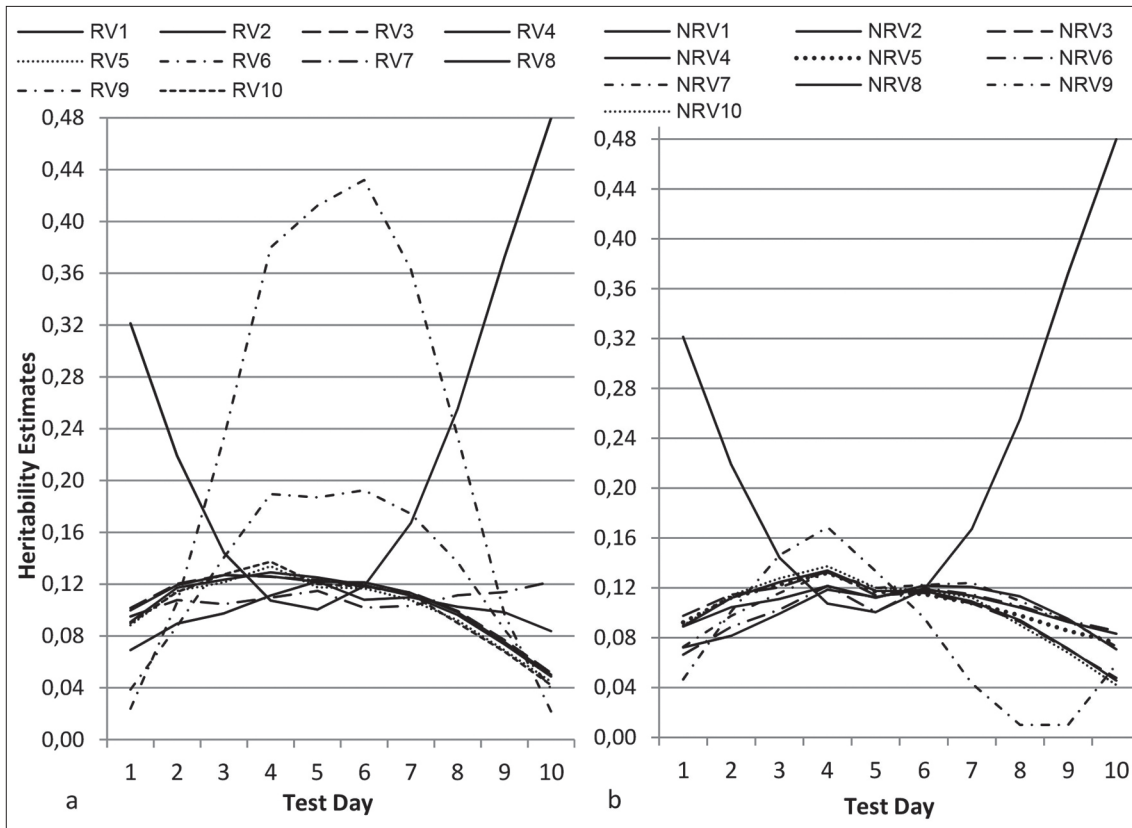

Fig 5. Changes of heritability estimates over lactation from RV models *(left)* and NRV models *(right)*

Şekil 5. RV *(sol)* ve NRV modellerinde *(sağ)* kalıtım derecesi tahminlerinin değişimi

(h² ~ 0.40) greater than the estimates from other models *(Fig. 5-a)*. Considering sum of absolute differences of heritability estimates of each test days in the model from the estimates obtained in RV10 model, RV5 model has the least deviation. Heritability estimates from NRV models were found closer each other than estimates of RV models *(Fig. 5-b)*. Only NRV7 model had different and fluctuating pattern. This model had lower heritability estimates at the beginning of the lactation and then the estimate increased up to fourth test day, then it fell rapidly approaching to zero at the eight test day and then increased again at the end of lactation *(Fig. 5-b)*. The models evaluated in the present study exhibited similar results for estimates of genetic and permanent environmental effects.

DISCUSSION

Regarding to fitting performance, RV and NRV models have not been found similar in majority. The LRT results were almost different among models. The RV1 model was the best model which was commonly used in literature [6,7,17,26]. However, the RV5, RV10 and NRV5 models recommended because of their detail descriptions on residual variances. The estimated residual variances were found higher at the beginning of the lactation and decreased along the lactation as expected. These estimates ranged from 5.62 to 11.75 for the RV models and ranged from 5.61 to 11.71 for the NRV models. Similar patterns and closer results of the residual variances have been reported by Olori et al.[6]. On the other hand, these estimates were higher than those estimated by Rekaya et al.[11] and Fujii and Suzuki [13].

We found that the estimates of additive genetic variances varied from 0.55 to 6.76 for the RV models. The estimates of additive genetic variances illustrated fluctuating values according to sequential RV models. In the model RV1 that error variance assumed constant, the additive genetic variances were higher at the beginning and end of the lactation, but lower at middle of the lactation. However genetic variances were estimated higher at middle of the lactation for the RV6 and RV9 models. Moreover, estimates of additive genetic variances were 0.08 to 2.46 for the NRV models. The estimates of additive genetic variances for both RV and NRV models were lower when compared with the findings of previous studies [6,7,10,11,13].

Permanent environmental variances were between 2.36 to 18.60 for RV and 6.92 to 18.85 for NRV models. In previous studies [7,12] higher permanent environmental variances were obtained but Rekaya et al.[11] reported lower estimates in their studies when compared with the present study. In addition, all models had same tendency with higher permanent environmental variances at the start and end of lactation, but lower at the middle of the lactation. This result has been obtained by other authors [6,12,13] under different RV models.

In this study, heritability estimates ranged from 0.02 to 0.43 and from 0.01 to 0.13 for RV and NRV models, respectively. For all models specified under the study, heritability estimates were lower at beginning and late part of lactation as estimates of additive genetic variances. Particularly, the RV6 and RV9 models overestimated heritabilities during middle lactation. This was probably the cause of the high additive genetic variances and low estimates of residual variances. Although the pattern of heritabilities was the same but our estimates were lower than those estimated by Olori et al.[6,7]; Rekaya et al.[11] and Lo'pez-Romero et al.[12].

The model under constant residual variance assumption gave opposite estimates for additive genetic variances and heritability values when compared to other models considered. Thus it can be seen that more accurate parameter estimates are achieved by controlling the residual variance with heterogeneous residual variance assumption. However, defining the classes of heterogeneous residual variances is more important for the accurate parameter estimates. Besides sequential pattern, the heterogeneous residual variance groups can be classified as non-sequential pattern. When it is asked to define details of the milk yield residual variances for each test day, RV10 model should be preferred. However, if there are problems due to model complexity for residual variances the model which defines residual variances in detail at beginning, peak of the lactation, and evaluates together other parts of the lactation, should be used. In this study RV5 is the alternative model especially for parameter estimates and its simplicity as compared to RV10.

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