

ESTIMATION OF (CO)VARIANCE COMPONENTS AND BREEDING VALUES FOR TEST-DAY MILK PRODUCTION TRAITS OF HOLSTEIN DAIRY CATTLE VIA BAYESIAN APPROACH

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Abstract: Genetic parameters of milk, fat, and protein yields were estimated in the first lactation of Holstein dairy cattle. The records were collected during the period 2006 to 2011 and analyzed fitting the random regression model. The data included 41178, 25397 and 18716 test-day records of milk, fat and protein yields, respectively that produced by 4746, 3437 and 2525 cows respectively. Fixed effects in model included herd-year-month of test day and age-season of calving. The fixed and random regressions were modeled with normalized Legendre polynomials and (co)variance components were estimated by Bayesian method and Gibbs sampling was used to obtain posterior distributions. Estimates of heritability for milk, fat and protein yields ranged from 0.18 to 0.26; 0.06 to 0.11 and 0.09 to 0.22, respectively. Heritabilities for 305-d milk, fat and protein yields were 0.36, 0.23 and 0.29, respectively. For milk and protein yields, heritabilities were lower at the early of lactation due to the trends of lower additive genetic variance, higher permanent environmental variance. Genetic correlations for milk, fat and protein yields ranged from 0.14 to 1.00; 0.39 to 1.00 and 0.27 to 1.00, respectively. Ranges of estimated breeding values for 305-d yield of milk, fat and protein yields were from -1194.48 to 1412.44; -210.57 to 271.22 and -194.08 to 203.25, respectively. According to the results of this study, random regression model seems to be a flexible and reliable procedure for the genetic evaluation of milk production traits and it can be useful in the breeding programs for Iranian dairy cattle.

Key words: Bayesian method, genetic correlation, heritability, test day record

Introduction

The topic of genetic evaluation of dairy cattle using random regression model (RRM) has been investigated by several researches, and some countries have already implemented routine genetic evaluation of large commercial dairy populations using a RRM. Random regression model were introduced by *Henderson (1982)*. *Schaeffer and Dekkers (1994)* suggested their use in dairy cattle breeding for the analysis of test day production records. There are several advantages of using RRM compared with 305-d of lactation. The 305-d yields are predicted from few observations may give rise to bias (*Jakobsen et al., 2002*). Furthermore, short lactations on culled cows or records in progress must be extended, which also may lead to bias. In a RRM, extension procedures are not needed, and temporal environmental effects of individual test days can be taken into account (*Ptak and Schaeffer, 1993; VanRaden, 1997*). Areas of dairy cattle breeding that have already utilized RRM include milk production, persistency, body weight, fertility, disease, feed intake.

In milk production traits, the RRM analysis provides many solutions for each animal, and from these solutions, estimated breeding value (EBV) of each animal can be calculated for each part of lactation. Variance and covariance components for the RRM were estimated by *Jamrozik and Schaeffer (1997)* from a data file of records for 6516 Canadian Holstein cows and 50,412 test-days (TD). A total of 45 parameters were estimated for a single-trait RRM for milk, fat, and protein yields during first lactation. In recent years, there has been increased emphasis on estimating genetic parameters of milk production traits using RRM that have been reported for several cow populations by fitting various functions to model (*Jakobsen et al., 2002; Hammami et al., 2008; Bohlouli et al., 2013*). Nevertheless, national genetic evaluation for production traits is carried out using 305 days records by Animal Breeding Center of Iran.

The main purpose of present study was to estimate the genetic parameters of milk production traits of Holstein dairy cattle via RRM. This paper describes how the RRM solutions can be utilized for selection.

Material and Methods

Data:

Data consisted of TD records milk, fat and protein yields of Holstein dairy cows and were collected by Animal Breeding Center of Esfahan, Iran. Records of the first lactation of cows calving between 2006 and 2011 were considered in the analyses. Daily records for milk, fat, and protein yields were in the ranges 2.0 to 64 kg, 0.07 to 3.62 kg and 0.09 to 2.20 kg respectively. Cows were required to have a

minimum of five TD records between 5 and 305 DIM with the first test day at 075 DIM. Herd-year of calving subclasses was required to have a minimum of 10 cows. Finally, data set consisted of 41178, 25397 and 18716 records for milk, fat and protein yields respectively that produced by 4746, 3437 and 2525 cows respectively. Pedigree was traced as far back as possible. The data are summarized in Table 1. Figure 1 shows trajectories of milk, fat, and protein yield by month of lactation. Peaks of milk, fat and protein yields occurred on about third month of lactation.

Table 1. Description of the database for each trait

	Milk yield	Fat yield	Protein yield
Number of records	41178	25397	18716
Number of animals with record	4746	3437	2525
Number of sire	454	386	342
Total number of animals in pedigree	12650	10522	8688
Number of HTD	487	393	214
Number of dam	3485	2788	2090
Average daily yield (kg)	32.66	1.10	0.99
Mean age of cow at first calving	25.64	25.54	25.46
Average TD records per cow	8.91	7.68	7.67

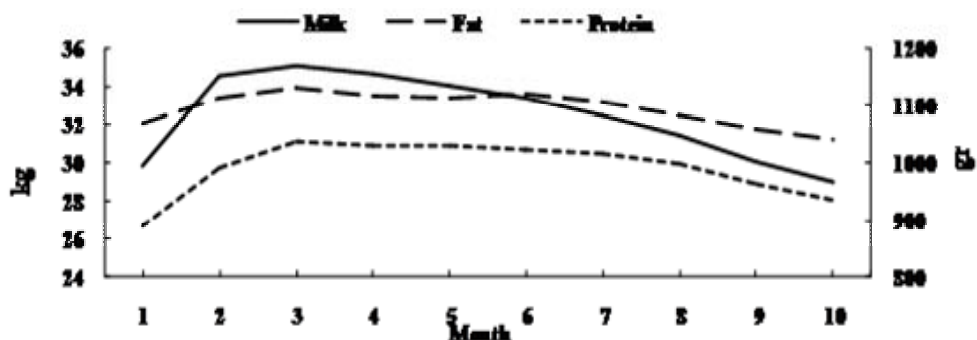


Figure 1. Average milk yield (kg), fat yield (gr) and protein yield (gr) based on month of lactation

Statistical model:

The choice of fixed effects to be considered was statistically significant with GLM procedure of SAS (*Statistical Analysis System, 2003*). The following RRM was used to estimate variance components for test-day milk production traits of first lactation:

$$y_{ijkl} = HTD_l + \sum_{n=0}^4 \beta_{jn} z_n(d) + \sum_{n=0}^4 \alpha_{kn} z_n(d) + \sum_{n=0}^4 \gamma_{kn} z_n(d) + e_{ijkl}$$

where y_{ijkl} was the l th test-day record of the k th cow; HTD_l was a fixed effect of the i th herd-year-month of test day; β_{jn} was the j th fixed regression coefficient specific to the j th age-season class by DIM ($j=24$); α_{kn} was the n th random regression coefficient for the additive genetic effect of k th cow by DIM; γ_{kn} was the n th random regression coefficient for the permanent environmental effect of k th cow by DIM; $z_n(d)$ was a vector of covariates of size n describing the shape of the lactation curve of fixed and random regressions evaluated at d th DIM; and e_{ijkl} was the random residual effect that residual variances were considered homogeneous along the lactation. The (co)variance structure follows:

$$\text{Var} \begin{bmatrix} \alpha \\ \gamma \\ e \end{bmatrix} = \begin{bmatrix} A \otimes G_\alpha & 0 & 0 \\ 0 & I_k \otimes P_\gamma & 0 \\ 0 & 0 & I_l \sigma_e^2 \end{bmatrix}$$

where G_α is covariance matrices of random regression coefficients of dimension for direct genetic effects by DIM; A is the additive genetic relationship matrix; P_γ is (co)variance matrix of random regression coefficients for permanent environmental effects by DIM; and σ_e^2 is residual variance. G_α and P_γ were 5×5 (co)variance matrices; I_k is an identity matrix of size $k \times k$ for the permanent environmental effect (k is the number of cows with records) and I_l is an identity matrix of size $l \times l$ for the residual (l is the number of test-day records). The fixed and random regressions were modeled with normalized Legendre polynomials (Kirkpatrick et al., 1990). The first five polynomials were calculated by the following formula:

$$\begin{aligned} \Phi_0 &= 0.7071w^0; \\ \Phi_1 &= 1.2247w^1; \\ \Phi_2 &= (-0.7906w^0) + 2.3717w^2; \\ \Phi_3 &= (-2.8062w^1) + 4.6771w^3 \text{ and} \\ \Phi_4 &= 0.7955w^0 - 7.9550w^2 + 9.2808w^4 \end{aligned}$$

Where, w is a standardized unit of the DIM and ranged from -1 to +1 and is derived as:

$$w = 2(t_i - t_{\min}) / (t_{\max} - t_{\min}) - 1$$

Where, t_{\min} and t_{\max} are equal to 5 and 305 DIM, respectively.

The additive genetic and permanent environmental (co)variances matrices as a function of DIM were calculated as $\Phi G \Phi'$ and $\Phi P \Phi'$ respectively; Where, Φ is a 301×5 matrix of Legendre polynomial function of DIM; and diagonal of these (co)variances matrices were additive genetic variances (σ_a^2) and permanent environmental variances (σ_{pe}^2). Therefore, heritability for i th DIM ($h_{(i)}^2$) was calculated as:

$$h_{(i)}^2 = \frac{\sigma_{a(i)}^2}{\sigma_{a(i)}^2 + \sigma_{pe(i)}^2 + \sigma_e^2}$$

where, $\sigma_{a(i)}^2$ is additive genetic variances of i th DIM; $\sigma_{pe(i)}^2$ is permanent variances of i th DIM; and σ_e^2 is residual variance. Vector of 305-d polynomials (q_{305d}) were obtained by summing up the coefficients of Legendre polynomials from day 5 to day 305 and the additive genetic variance and permanent environmental variance of 305-d yield were calculated as $q_{305d} G q_{305d}'$ and $q_{305d} P q_{305d}'$ respectively. Then heritability for 305-d yield (h_{305d}^2) was calculated as:

$$h_{305d}^2 = \frac{\sigma_{a(305d)}^2}{\sigma_{a(305d)}^2 + \sigma_{pe(305d)}^2 + 301 \times \sigma_e^2}$$

Solutions for the random regression coefficients for each animal can be used to EBVs for any point in the lactation curve between 5 and 305 DIM. For example, EBV for the animal l at 150 DIM will be:

$$EBV_{l,150} = q_{150} \times a_l'$$

where a_l represents solution for animal l , and q_{150} is the vector of coefficients of the Legendre polynomial corresponding to 150 DIM and therefore EBV of 305 day yield for the animal l ($EBV_{l,305-d}$) was derived as follows via summation of the EBV for each day in the period from 5 to 305 DIM:

$$EBV_{l,305-d} = \sum_{c=5}^{305} BV_{l,c}$$

Analyses were performed by using the GIBBS2F90 software (Misztal *et al.*, 2002), which is a Fortran 90 program using a Bayesian approach via the Gibbs sampling algorithm. A single chain of 200,000 samples was run, with the first

20,000 samples discarded as burn-in and posterior means and standard deviations of parameters were calculated from every 100th sample of 180,000 samples.

Results and Discussion

Posterior means of additive genetic and permanent environment variances of random regression coefficients estimated based on animal model for milk production traits given in Table 2. The correlations between additive genetic random regression coefficients of milk, fat and protein yields ranged from -0.57 to 0.74, -0.76 to 0.45 and -0.53 to 0.56, respectively; and for permanent environment random regression coefficients ranged from -0.39 to 0.15, -0.72 to 0.52 and -0.80 to 0.27, respectively. Posterior standard deviations for additive genetic curve parameters were in the range from 2.39 to 0.06, 0.004 to 0.002 and 0.002 to 0.00007 for milk, fat and protein yields, respectively and for permanent environment curve parameters were in the range from 1.92 to 0.08, 0.003 to 0.0001 and 0.002 to 0.0001 for milk, fat and protein yields, respectively. Residual variances were considered homogeneous over the lactation period and were equal to 10.72, 0.04 and 0.01 for milk, fat and protein yields, respectively.

Table 2. Posterior means of additive genetic (G_n) and permanent environment (P_n) variances of random regression coefficients estimated with forth-order of Legendre polynomials ($n= 0$ to 4) for each trait. Genetic correlations between curve parameters are in bold. (Values for fat and protein yields are multiplied by 10^{+3})

Trait		G_0	G_1	G_2	G_3	G_4		P_0	P_1	P_2	P_3	P_4
Milk yield	G_0	18.20	1.91	-	0.61	-	P_0	32.17	2.09	-	0.13	-
	G_1	0.42	1.15	-	0.43	-	P_1	0.15	5.80	-	-	0.02
	G_2	-0.53	-	0.44	-	0.05	P_2	-0.18	-	2.02	-	-
	G_3	0.26	0.74	-	0.30	-	P_3	0.03	-	-	0.89	-
	G_4	-0.31	-	0.17	-	0.18	P_4	-0.12	0.01	-	-	0.61
Fat yield	G_0	11.32	1.53	-	-	-	P_0	39.01	3.58	-	0.21	-
	G_1	0.37	1.48	-	-	0.03	P_1	0.25	5.41	-	-	0.78
	G_2	-0.07	-	0.53	-	0.09	P_2	-0.14	-	3.00	-	-
	G_3	-0.02	-	-	0.16	-	P_3	0.03	-	-	1.11	-
	G_4	-0.18	0.09	0.45	-	0.07	P_4	-0.42	0.52	-	-	0.42

					0.75					0.07	0.20	
Protein yield	G_0	8.64	1.99	-	0.14	-	P_0	21.01	2.53	-	0.10	0.02
	G_1	0.56	1.48	-	-	0.08	P_1	0.27	4.05	-	-	-
	G_2	-0.42	-	0.28	-	0.04	P_2	-0.11	-	1.55	-	0.02
	G_3	0.17	-	-	0.08	0.00	P_3	0.03	-	-	0.44	-
	G_4	-0.16	0.35	0.42	0.00	0.04	P_4	0.01	0.01	0.03	-	0.37

Additive genetic, permanent environment and residual variances by DIM for milk, fat, and protein yields are shown in Figure 2. Generally, permanent environment variances had more irregular trends over the lactation when compared with genetic variances.

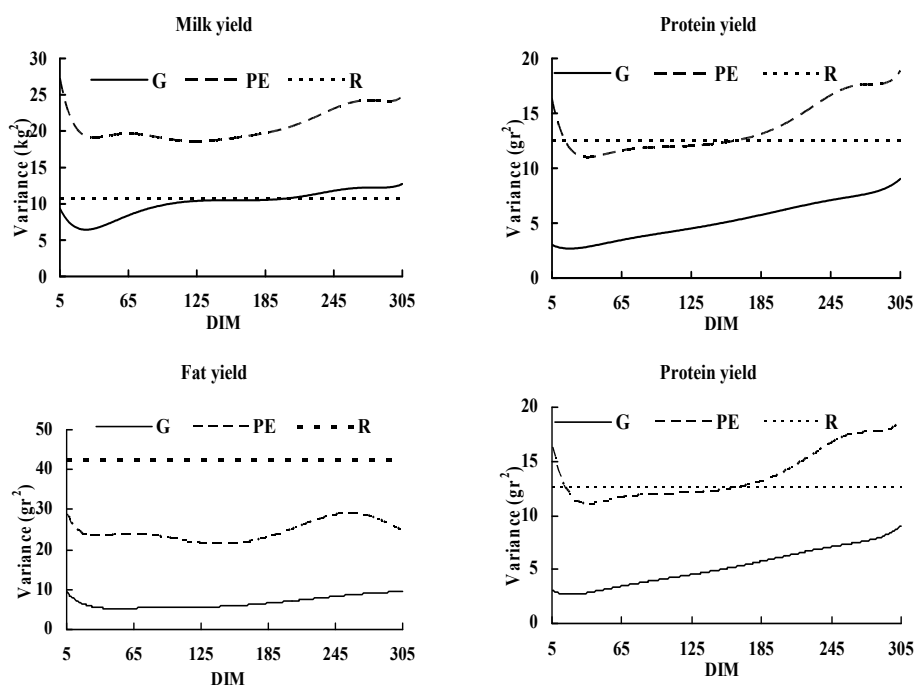


Figure 2. Additive genetic (G), permanent environmental (PE) and residual (R) variances of milk, fat and protein yields as a function of days in milk (DIM)

Heritabilities as a function of DIM, calculated from the (co)variance estimates in animal models for milk, fat, and protein test-day yields are shown in

Figure 3. Estimates of heritability for milk, fat and protein yields ranged from 0.18 to 0.26; 0.06 to 0.11 and 0.09 to 0.22, respectively; and heritabilities for 305-d milk, fat and protein yields were 0.36, 0.23 and 0.29, respectively.

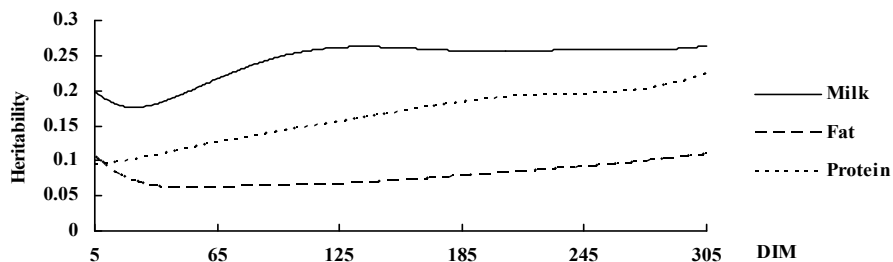


Figure 3. Heritability for milk, fat and protein yields as a function of days in milk (DIM)

Genetic and permanent environmental correlations between test-day milk yields, test-day fat yields, and test-day protein yields at different stages of lactation are shown in Figure 4. Estimates of genetic correlation for milk, fat and protein yields ranged from 0.14 to 1.00, 0.39 to 1.00 and 0.27 to 1.00, respectively. The genetic correlations between DIM close together are close to unity, and the correlations gradually decline as the distance between DIM increases and the low genetic correlations observed between early period of lactation and other days.

Permanent environmental correlations were always positive and for milk, fat and protein yields ranged from 0.33 to 1.00, 0.20 to 1.00 and 0.36 to 1.00, respectively.

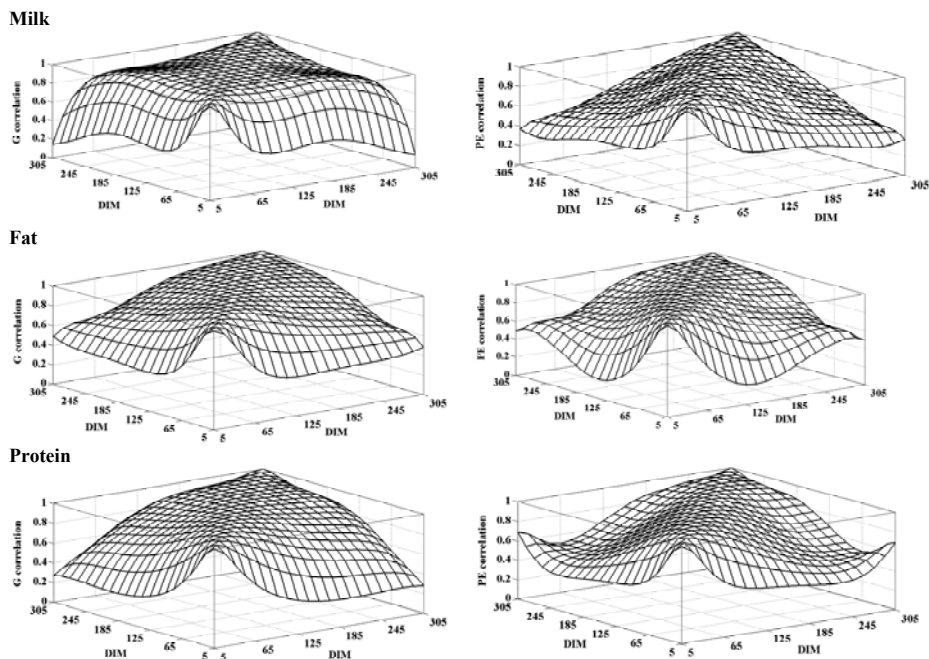


Figure 4. Additive genetic (G) and permanent environmental (PE) correlations between test-day milk yields, test-day fat yields, and test-day protein yields at different days in milks (DIM)

Ranges of EBV for 305-d yield of milk, fat and protein yields were from -1194.48 to 1412.44, from -210.57 to 271.22 and from -194.08 to 203.25, respectively; and standard deviations were 282.97, 148.23 and 136.64, respectively. The random regression solutions and EBV for 305-d milk, fat and protein yields of best bulls are given in Table 3.

Table 3. Additive genetic random regression solutions (\tilde{a}_i) and estimated breeding values of 305-d yield (EBV_{305d}) of 5 best sires for each trait.

Trait	Sire	No. of daughters	\tilde{a}_0	\tilde{a}_1	\tilde{a}_2	\tilde{a}_3	\tilde{a}_4	EBV _{305d}
Milk yield	1	29	6.11	-0.14	0.44	0.64	0.29	1301.44
	2	102	5.08	-0.11	-0.88	0.09	-0.58	1079.21
	3	68	4.80	-0.58	0.38	-0.51	0.55	1023.62
	4	59	4.78	0.49	-0.06	-0.71	-0.37	1016.64
	5	151	4.72	0.88	1.22	0.06	0.58	1008.75
Fat yield	1	92	0.88	1.79	-0.28	1.42	1.15	189.60
	2	175	0.82	-0.49	-0.86	-0.23	0.06	172.37
	3	109	0.77	0.55	0.96	-0.87	0.57	166.09
	4	23	0.76	-0.06	0.27	0.71	-0.68	160.52
	5	45	0.72	-0.49	-0.12	-1.29	-0.18	152.89
Protein yield	1	37	0.76	-0.47	-0.46	0.06	-1.14	158.44
	2	125	0.70	-0.50	-0.77	0.07	0.35	149.16
	3	103	0.65	0.20	1.47	-1.14	0.83	143.35
	4	81	0.65	-0.02	-0.69	0.38	-0.47	135.91
	5	70	0.60	-0.81	-0.45	-0.34	0.35	127.99

Clearly the estimates of heritability were not constant throughout the lactation. For all traits, permanent environment variances were higher at the beginning of lactation. These trends shown that non-genetic factors tend to influence the production traits in the beginning of lactation (*Ludwick and Petersen, 1943*); therefore, heritabilities are lower in the beginning of lactation (Figure 3). These results are similar to those observed by *Cobuci et al. (2011)* and *Bohlouli and Alijani (2012)*. The ratio of residual variance to phenotypic variance of traits might indicate that the model of analysis was more suitable for milk yield than for fat and protein yields, which had higher proportion of residual variances. It could be that there are other critical factors influencing fat and protein yields which the model did not account for (*Abdullahpour et al., 2013*).

Heritabilities for fat yield were lower than for milk and protein yields. This is in accordance with other studies (*Gengler et al., 1999; Jakobsen et al., 2002; Bohlouli and Alijani, 2012*). For milk and protein yields, heritabilities were lower at the early of lactation due to the trends of lower additive genetic variance, higher permanent environmental variance and similar residual variance in comparison with other stages of lactation. For milk there was a tendency towards higher heritability estimates in the middle of lactation, which is in accordance with many other similar investigations (*Jakobsen et al., 2002; Bohlouli et al., 2013*). For protein yield, daily heritabilities increased during the lactation. Daily heritabilities for fat yield were decreasing from beginning of the lactation until around DIM 50 and then slowly increased afterward. Results reported by *Biassus et al. (2011), Hammami (2009)* are similar to these estimations. Nevertheless, current study found higher heritabilities for milk production records that collected from one province. Heritabilities obtained from the data of one herd (*Ahrabi et al., 2005*) or

providing a new source of information into the model of analysis such as temperature-humidity index (*Bohlouli et al., 2013*) were significantly higher compared to estimated heritabilities of great number of herds within several provinces (*Razmkabir et al., 2009*). For this reason, in circumstances of high diversity of climates, environmental changes, management and feeding systems like Iran, about traits like milk yield, for which an animal is highly sensitive to these factors, a test day model might result in much greater residual variance and hence lower heritability (*Abdollahpour et al., 2013*).

The low genetic correlations that observed between early period of lactation and other days means that the phenotypic expressions in the different DIM should be considered as separate traits, determined by partly different sets of genes. The figures of Genetic and permanent environmental correlations are typical of several studies that modeled the lactation curve using random regression model (*e.g. Biassus et al., 2011; Bohlouli et al., 2013; Abdollahpour et al., 2013*). Generally, different heritability and genetic parameters among population are related to variation in data structure, genetic potential of milk production traits, climate changes, herd management, statistical models and estimation methods of (co)variances.

RRM assumes heterogeneous additive genetic effects throughout the lactation. Therefore, RRM allows for different between cows in the shape and level of the distribution of the additive genetic effect throughout lactation. This is done by regression of the additive genetic effect on individual DIM via a lactation curve function. Thus, a 305 days estimate of a cow's breeding value corresponds to the area under lactation curve.

Conclusion

Currently, genetic evaluations for dairy cattle are performed in most countries using TD models rather than traditional lactation models. Advantages of the RRM are that the environmental effects peculiar to each TD can be analyzed, the shape of the lactation curve is allowed to differ for each animal and the solutions allow calculation of EBV for partial lactation yields. A disadvantage of RRM is an increased computational requirement because more TD records need to be processed compared with 305-d yields. Currently research should be focused on defining the RRM to be implemented, investigating the environmental effects to be included in the model and estimating the covariance structure among observations and genetic parameters for traits to be included in the breeding programs for dairy cattle in Iran.

According to the results of this study, random regression model seems to be a flexible and reliable procedure for the genetic evaluation of milk production traits of used data. Then, when computationally feasible, RRM is recommended for the

routine genetic evaluation of national dairy cattle. In addition, current random regression model assume homogeneous residual variance throughout lactation. In the future, models may account for heterogeneous residual variance and this could increase accuracy of genetic evaluation.

Acknowledgements

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Procena komponenti (ko) varijanse i priplodne vrednosti za test-dan proizvodne osobine mleka holštajn muznih krava korišćenjem bajesovski pristupa

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Rezime

Procenjivani su genetski parametri prinosa mleka, masti i proteina u prvoj laktaciji holštajn muznih krava. Podaci su prikupljeni u periodu od 2006 do 2011 godine i analizirani korišćenjem *random regression model-a*. Podaci uključuju 41.178, 25.397 i 18.716 test – dnevnih podataka o prinosu mleka, mlečne masti i proteina, poreklom od 4.746, 3.437 i 2.525 krava. Kao fiksni efekti u modelu uključeni su zapat, godina i mesec testiranja, starost i sezona teljenja. Fiksne i slučajne regresije su modelirane putem normalizovanih *Legendre-ovih* polinoma dok su komponente kovarijanse utvrđene korišćenjem *Bayes-ove* metode, a *Gibbs-ovo* uzorkovanje je korišćeno za dobijanje posteriornih distribucija. Procene heritabiliteta za prinos mleka, masti i proteina kretale su se rasponu od 0,18 do 0,26; 0,06 do 0,11 i 0,09 do 0,22, respektivno. Heritabiliteti za prinos mleka u laktaciji od 305 dana, prinos masti i proteina iznosili su 0,36, 0,23 i 0,29, respektivno. Heritabiliteti za prinos mleka i proteina bili su niži u ranoj laktaciji, zbog trenda niže aditivne genetičke varijanse odnosno permanentno više varijanse životne sredine. Genetske korelacije za prinos mleka, masti i proteina kretale su se od 0,14 do 1,00; 0,39 do 1,00 i 0,27 do 1,00, respektivno. Opsezi procenjene priplodne vrednosti za prinos mleka, masti i proteina u laktaciji od 305 dana kretali su se od -1194,48 do 1412,44; -210,57 do 271,22 i -194,08 do 203,25, respektivno. Prema rezultatima ove studije, *random regression model* je fleksibilan i pouzdan postupak za genetsko vrednovanje proizvodnih osobina mleka i kao takav može biti od koristi u programima oplemenjivanja iranskih mlečnih goveda.

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