Random Regression Test-Day Model for Milk Yield in Sahiwal Cattle, Kenya

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Abstract

A total of 19,313 test-day milk yield records for 1,892 Sahiwal cattle from first three lactations were used to describe variation in milk yield using Random Regression Model (RRM) with Legendre Polynomials (LP). Data were recorded between 1978 and 2002. Variance components were estimated by Restricted Maximum Likelihood method. Thirty models from first to fourth order Legendre Polynomials were used to describe additive genetic and permanent environmental effects in each parity. Both heterogeneous and homogeneous models were considered. Heterogeneous residual variances were modeled by considering eight classes. Most suitable LP order was selected based on Logarithm of likelihood function (-2logL), Akaike Information (AIC) and Schwarz's Bayesian Information (BIC) criterion. Different error covariance structures were compared using Likelihood ratio test with significance of differences between models obtained using a chi-square test. Model LP (5,5RV8) with 5 additive genetic and 5 permanent environmental random regression coefficients was sufficient to model variability in milk yield across the three parities. The first three Eigen values and first four Eigen values, respectively, explained over 98% of total variation of random regression coefficients for additive genetic and permanent environmental effects. Heritability estimates for daily milk yield in parities one, two and three ranged from 0.15 to 0.27, 0.05 to 0.17 and 0.16 to 0.38, respectively. Genetic correlations between daily milk yields in parities one, two and three ranged from 0.332 to 0.995, 0.13 to 0.996197 and 0.092 to 0.988, respectively. Average heritability estimates for lactation milk yield for parities one two and three, respectively, were 0.309, 0.144 and 0.422. Sire Rank correlations between model LP(5,5RV8) and the lower models in parities one, two and three ranged from -0.089 to 0.222, -0.132 to 0.295 and -0.100 to 0.177, respectively. Product moment correlations between model LP(5,5RV8) and lower models ranged from 0.773 to 0.984, 0.805 to 0.958 and 0.919 to 0.989 in parities one, two and three, respectively.

Key Words: Sahiwal, Test-day, Milk yield, Random Regression Model, Legendre Polynomial

Introduction

Sahiwal is dual-purpose cattle indigenous to Pakistan and India, and were imported to Kenya in the 1930s and 1940s. The breed has been utilized in smallholder farming systems, beef and dairy ranching in marginal areas of Kenya which form 80% of the country (Muhuyi **et al.,** 1999). Selection for milk yield in Sahiwal cattle in Kenya has been mainly made on the basis of lactation milk yield which does not account for effects that are specific to individual daily yields (Ilatsia *et al.,* 2007). Fixed Regression test-day Model was previously used by Ilatsia *et al.*, (2007) to estimate genetic and phenotypic parameters in Sahiwal cattle where variance components were estimated using various univariate and multi-trait fixed regression test-day models which defined contemporary groups either based on year-season of calving or year season of test-day. The model, however, assumed a standard lactation curve for cows in similar contemporary groups and homogeneity of residual variances throughout lactation. The model also ignored lactation persistency. Random regression test-day models are being utilised in dairy cattle genetic evalautions of both bulls and cows (Kaygisiz, 2013) because of their ability to account for environmental effects of each test-day and to model a trajectory of lactation for individual genotypes or groups of animals, and possibilty of genetic evaluations for persistecy of production. The Model also increases accuracy of genetic evaluation due to increasing volume of data per animal (Ghaderi-Zefrehei *et al.,* 2014) and possibilty of genetic evaluation for any part of lactation curve (Mohammadi *et al.,* 2014). Incomplete lactations are projected from available test-day records with requirement that cow had been milked for a minimum number of days or had at least two test-day records (Kaygisiz, 2013).

Legendre polynomials have been applied in RRM to describe variations in longitudinal data of dairy cattle (Laureano *et al.,* 2014). Kirkpatrick & Heckman (1989) proposed use of covariance functions with LP, to model variance structure of longitudinal data, and to estimate additive genetic and permanent environmental variances (Peixoto *et al.,* 2014). Objective of this study was to identify appropriate order of LP to describe daily variations in milk yield for Sahiwal cattle in Kenya.

Materials and Methods

Materials

Test-day milk yield records were obtained from National Sahiwal Stud, which is maintained by Kenya Agricultural and Livestock Research Organizations (KALRO) at National Animal Husbandry Research Centre, Naivasha. A total of 19,313 first three lactation test- day milk yield records for 1,892 Sahiwal cattle were available for use. Data were recorded between 1978 and 2002. First TD comprised of daily yield records sampled between days 2 and 15 post partum while second TD comprised of daily yield sampled between days 16 and 31. Time interval between successive tests was approximately 30 days. Daily milk yield record was calculated as the sum of milk recorded in the morning and evening. A maximum of eight TDs were allowed due to short lactation length in *Bos indicus* cattle, usually less than 280 days, (Ilatsia *et al*,. 2007). Description of data used is given in Table 1.

Table 1. Number of records (N), means and standard deviations (SD) for milk yield in the first three lactations

Parity	AGC	YSTD	Animal	Subj		nrec	mean	sdev	min	max
1	6	100	1692	1419	MY	8385	4.4	2.3	0.5	15
					DIM	8385	94.6	70.0	2.00	235
2	8	96	1388	1148	MY	6440	5.1	2.7	0.50	15
					DIM	6440	94.6	70.4	2.00	236
3	7	86	971	786	MY	4488	5.0	2.7	0.50	17
					DIM	4488	93.7	69.8	2.00	235

Methods

Random regression model was used and LP models applied to test-day milk yield data to describe daily variation in milk yield in Sahiwal cattle. Test-day records from the first three lactations were treated as different samples from same herd. Fixed factors were Year Season of Test-Day (YSTD) and Age Class (AGC). Thirty (30) LP models were used to describe additive genetic and permanent environmental effects, in each parity. Heterogeneous residual variances were modeled considering eight residual classes as follows; 2-32, 33-63, 64-94, 95-125, 126-156, 157-187, 188-218 and 219-249.

Random Regression Equation Assuming The Same Sub-Model To Fit Fixed, Genetic And Permanent Environment Effects.

$$y_{ikl} = YSTD \; + AgC + \sum_{m=1}^{K_B} \beta_m \; x_{(m)}(t_{ik}) + \sum_{m=1}^{K_A} \alpha_{km} \, \varphi_m(t_{ik}) + \sum_{m=1}^{K_P} P_{km} \, \varphi_m(t_{ik}) + \; e_{ikl}$$

Where; y_{ikl} ith DIM milk yield for cow k

YSTD: Year Season of test-day

AgC: Age class

β_m: mth fixed regression coefficients for cow k

t_{ik}: ith DIM for cow k

$x_{(m)}$ (t_{ik}): mth covariates evaluated,

αk_m: mth additive genetic random regression coefficients for cow k,

P_{km}: mth permanent environmental random regression coefficients for cow k,

φ_m: mth polynomial evaluated

KB: order of Legendre Polynomial for fixed regression coefficients

KA and KP are respectively, the order of Legendre Polynomials for additive and permanent environmental random regression coefficients

e_{ikl}: Residual effect for milk yield

Model Comparison and Selection

Random Regression Models were compared and selected using -2logL, AIC and BIC model selection criterion. AIC and BIC are computed as follows:

AIC= -2log$L$ + 2k

Where, k is the number of free parameters in model.

BIC= -2log$L$ + k log (λ)

where k is as in AIC criteria, and, using REML, $\lambda = n - r(X)$, n being equal to number of test-day records and $r(X)$ equal to rank of systematic effects incidence matrix.

Likelihood ratio test (LRT) was used to compare different error covariance structures for each model. Significance of differences between models was obtained using a chi-square test, based on Chi-square distribution table.

Analysis of Random Regression Coefficients Covariance Matrix and Estimation of (Co)Variances

Random regression model was used to estimate (Co) variance components for test-day milk yield traits for first three lactations. First five LP orders were calculated from normalized Legendre Polynomials (Muasya et al., 2014) as follows:

$$\theta_0 = 0.7071 w^0$$

$$\theta_1 = 1.2247 w^1$$

$$\theta_2 = (-0.7906 \; w^0) + 2.3717 w^2$$

$$\theta_3 = (-2.8062 \; w^1) + 4.6771 w^3$$

$$\theta_4 = 0.7955 \; w^0 \; -7.9550 \; w^2 \; + 9.2808 \; w^4$$

Where w is the standardized DIM ranging from -1 to 1 and is derived as:

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

Where t_i is days in milk on i^{th} DIM; t_{min} is the earliest DIM, while t_{max} is the latest DIM

Estimates of daily additive genetic and permanent environmental (co)variances for each data set were obtained from estimates of covariance matrices among random regression coefficients for additive genetic and permanent environmental effects (Muasya et al., 2014).

$$\sigma^2_{ai,j} = q_i G q_i'$$

and

$$\sigma^2_{pei,j} = q_i P q_i'$$

where, $\sigma^2_{ai,j}$ and $\sigma^2_{pei,j}$ are, respectively, additive genetic and permanent environmental (Co)variances for DIM i and DIM j. q_i is the nth Legendre Polynomial associated with parameter i. G and P are covariance matrices for additive genetic and permanent environment random regression coefficients, respectively.

Heritability for daily milk yield and genetic correlation between days in milk (DIMs) were calculated as follows (Mosharraf et al., 2014);

Heritability ($h^2_{(i)}$) for i[th] DIM

$$h^2_{(i)} = \frac{\sigma^2_{\alpha(i)}}{\sigma^2_{\alpha(i)} + \sigma^2_{pe(i)} + \sigma^2_e}$$

Where, $\sigma^2_{\alpha(i)}$ is additive genetic variance for DIM *i*; $\sigma^2_{pe(i)}$is permanent environmental variances for DIM *i*; and σ^2_e is residual variance.

Genetic correlations ($r_{gi,j}$) between DIM *i* and *j*;

$$r_{gi,j} = \frac{\sigma_{ai,j}}{\sqrt{\sigma^2_{ai} \cdot \sigma^2_{aj}}}$$

where, $r_{gi,j}$ is the genetic correlation between DIM *i* and *j*, $\sigma_{ai,j}$ Covariance between *DIM i* and j, σ^2_{ai} additive genetic variance for DIM *i* and σ^2_{aj} additive genetic variance for DIM *j*.

Additive genetic variances, Permanent environmental variances and Heritability for lactation milk yield were calculated as follows (Muasya et al., 2014);

Additive genetic variance for lactation milk yield;

$$\sigma^2_{ai} = Z_{ci} K_a Z'_{ci}$$

where, σ^2_{ai} is the additive genetic variance for milk yield and Z'_{ci} is the summation of coefficients for i[th] Legendre Polynomial order (transposed). K_a is the diagonal matrix for additive genetic effect.

Permanent environmental variance for lactation milk yield;

$$\sigma^2_{pei} = Z_{ci} K_p Z'_{ci}$$

Where, σ^2_{pei} is permanent environmental variance for milk yield and K_p is the diagonal matrix for permanent environmental effect.

Heritability for lactation milk yield;

$$h^2_i = \frac{\sigma^2_{ai}}{\sigma^2_{ai} + \sigma^2_{pei} + \mathrm{K} * \sigma^2_{ec}}$$

where h^2_i is heritability for lactation milk yield, σ^2_{ai} is the additive genetic variance for lactation milk yield, σ^2_{pei} is the permanent environmental variance for milk yield, σ^2_{ec} is the residual variance for class c and *k* is the earliest DIM and for this study *k* is 2.

Estimation of Breeding Values

Solutions for random regression coefficients for each animal and LP coefficients for DIM were used to estimate breeding values (EBVs) for each animal at any point in the lactation curve. If $\hat{a}_i$ is a K_a x 1 vector of additive genetic random regression coefficients for animal i and Z_t is K_a x 1 vector of Legendre Polynomial coefficients evaluated at day t (Muasya et al., 2014);

$$\hat{a}_i = \begin{bmatrix} \hat{a}_{i\ 0} \\ \hat{a}_{i\ 1} \\ \hat{a}_{i\ 2} \\ \hat{a}_{i\ 3} \\ \hat{a}_{i\ 4} \end{bmatrix}, \qquad Zt \begin{bmatrix} \Phi_{0\ t} \\ \Phi_{1\ t} \\ \Phi_{2\ t} \\ \Phi_{3\ t} \\ \Phi_{4\ t} \end{bmatrix}$$

EBV for animal i for day t;

$$EBVT_{it} = \sum_{j=0}^{Ka-1} \hat{a}_{ij}\, \Phi_j\, (DIM_t)$$

EBV for an animal i in parities one and three was given by summation of daily EBVs from DIM 2 to DIM 235 as:

$$\begin{aligned} EBVT_i &= \sum_{t=2}^{235} (\hat{a}_{i0}\Phi_{t0} + \hat{a}_{i1}\Phi_{t1} + \hat{a}_{i2}\Phi_{t2} + \hat{a}_{i3}\Phi_{t3} + \hat{a}_{i4}\Phi_{t4}) \\ &= \left(\sum_{t=2}^{235} \Phi_{t0} \sum_{t=2}^{235} \Phi_{t1} \sum_{t=2}^{235} \Phi_{t2} \sum_{t=2}^{235} \Phi_{t3} \sum_{t=2}^{235} \Phi_{t4}\right) \hat{a}_i \\ &= Z_{c235MY}\hat{a}_i \end{aligned}$$

EBV for an animal i in parity two was given by summation of daily EBVs from DIM 2 to DIM 236 as:

$$\begin{aligned} EBVT_i &= \sum_{t=2}^{236} (\hat{a}_{i0}\Phi_{t0} + \hat{a}_{i1}\Phi_{t1} + \hat{a}_{i2}\Phi_{t2} + \hat{a}_{i3}\Phi_{t3} + \hat{a}_{i4}\Phi_{t4}) \\ &= \left(\sum_{t=2}^{236} \Phi_{t0} \sum_{t=2}^{236} \Phi_{t1} \sum_{t=2}^{236} \Phi_{t2} \sum_{t=2}^{236} \Phi_{t3} \sum_{t=2}^{236} \Phi_{t4}\right) \hat{a}_i \\ &= Z_{c235MY}\hat{a}_i \end{aligned}$$

The following parameters were calculated as follows:

EBV for milk yield;

$$t_i = Z_{ci} K_a \hat{a}_i$$

where, t_i is the EBV for milk yield for animal i, Z_{ci} is the summation of coefficients for LP orders, K_a is the diagonal matrix for animal covariance matrix and $\hat{a}_i$ is the random regression coefficients for the corresponding LP order i.

Results

Model Comparison

Model LP (5,5RV8) with 5 regression coefficients was sufficient to model both additive genetic and permanent environmental variability in milk yield in the three parities. In parity one model LP (5,5RV8) had the smallest values of -2LogML, AIC and BIC. In parity two models -2LogML and AIC values were smallest in model LP (5,5RV8) while BIC values were smallest in model LP (3,5RV8). The results for parity two were the same for parity three except that in parity three model LP (2,5RV8) had the smallest value of BIC. Across the three parities values of -2LogML, BIC and AIC, were larger in models assuming homogeneous residual variances than in corresponding models assuming heterogeneous residual variances.

The first 3 eigen values for additive genetic effect explained 99.81% (parity one), 99.57% (parity two) and 99.39 (parity three) while eigen values for permanent environmental effect explained 99.78% (parity one), 99.43% (parity two) and 99.99 % (parity three) of variation of random regression coefficients, see table 2.

Table 2. Eigen values for random effects in milk yield in parities one, two and three

Parity	1		2		3	
AG and PE Eigen values	AG %	PE %	AG %	PE %	AG %	PE %
1st	92.43	80.41	81.34	82.49	87.42	75.27
2nd	5.29	11.86	14.33	11.87	10.18	15.51
3rd	2.09	4.71	3.9	3.54	1.79	5.88
4th		2.8		1.53		3.33
Total	99.81	99.78	99.57	99.43	99.39	99.99

AG; Additive Genetic and PE; Permanent Environment

Estimates of (Co) Variances for Random Regression Coefficients

In parity one, additive genetic variances (AGVs) increased from DIM 6 to DIM 51 and then started declining towards the end of lactation. Permanent environmental variances (PEVs) decreased from DIM 2 towards the end of lactation with slight increases between (DIM 23 and DIM 44) and (DIM 227 and DIM 235).

In parity two AGVs increased from DIM 2 to DIM 27, then started declining towards the end of lactation with some slight increases between (DIM 126 and DIM 204), and (DIM 205 and DIM 236). The PEVs declined from DIM 2 to DIM 10 and started increasing from DIM 11 to DIM 45 after which the PEV decreased towards the end of lactation, with some slight increases between DIM 227 and DIM 236.

In parity three, AGVs were similar to the trend in parity one (see Figure 1a). The PEVs declined from DIM 2 towards the end of lactation with some slight increases between (DIM 25 and DIM 41), and (DIM 122 and DIM 188).

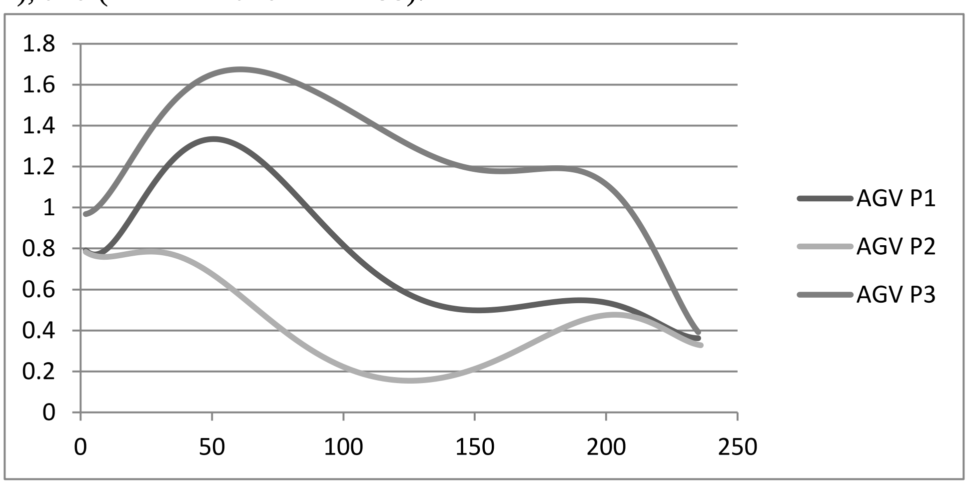

Figure 1a. Additive genetic variances

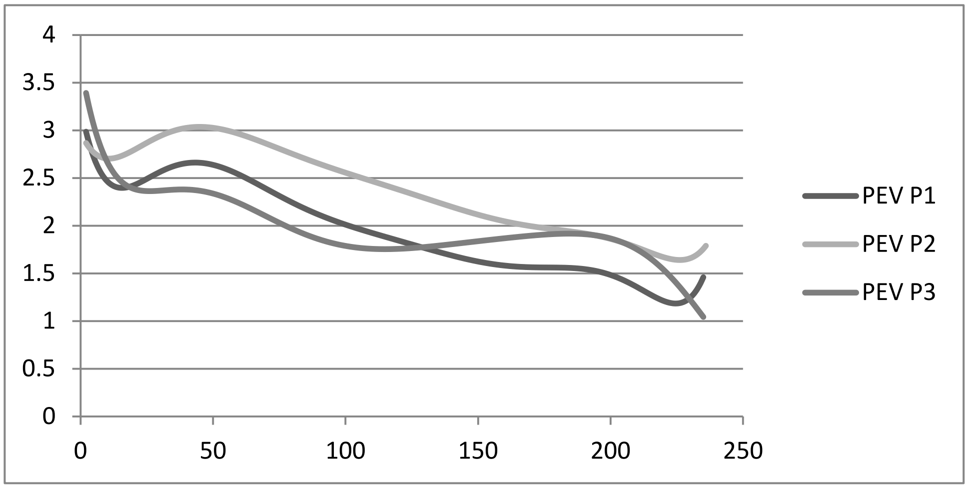

Figure 1b. Permanent environmental variances

Heritability estimates for daily milk yield ranged from 0.150 to 0.265, 0.046 to 0.169 and 0.165 to 0.378 in parities one two and three, respectively. Among the three parities heritability estimates were highest in parity three, followed by parity one with the lowest estimates in parity two.

Table 3. Average heritability for daily milk yield in 8 classes of heterogeneous residual variances

Parity	Class 1 2-32	Class 2 33-63	Class 3 64-94	Class 4 95-125	Class 5 126-156	Class 6 157-187	Class 7 188-218	Class 8 219-249
1	0.188	0.260	0.248	0.206	0.185	0.193	0.215	0.186
2	0.150	0.149	0.093	0.054	0.061	0.113	0.164	0.143
3	0.227	0.317	0.340	0.365	0.325	0.312	0.299	0.242

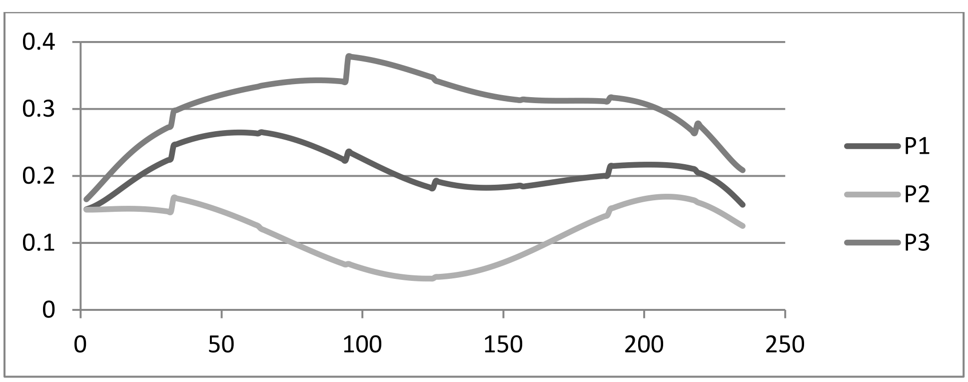

Figure 2. Heritability for daily milk yield in the three parities

Genetic correlations between daily milk yield ranged from 0.332 to 0.995, 0.129 to 0.996 and 0.092 to 0.988 in parities one, two and three, respectively. Correlations between milk yields obtained at consecutive days in milk were positive and decreased as interval between days in milk increased.

Heritability estimates for lactation milk yield was highest in parity three followed by parity one and lowest in parity two. Average heritability estimates were 0.309, 0.144 and 0.422 for parities one, two and three, respectively.

Estimates of Breeding Values

Rank correlations between sires based on EBVs in model L(5,5RV8) and lower models ranged from -0.089 to 0.222 in parity one, -0.132 to 0.295 in parity two and -0.100 to 0.177 in parity three. Product moment correlations between EBVs in model L(5,5RV8) and other models ranged from 0.790 to 0.990, 0.805 to 0.966 and 0.883 to 0.993 in parities one, two and three, respectively. Sire rank and product moment correlations were drawn from sires with at least 30 daughters, since more offspring per breeding animal allows more accurate estimation of breeding values.

Discussion

Model Comparison

Model LP(5,5RV8) with 5 additive genetic and 5 permanent environmental random regression coefficients was sufficient to model variability in milk yield, across the three parities. Models which assumed homogeneous residual variances produced worst fit, which suggests that residual variances have different behavior during lactation period. Similar results were found by Peixoto *et al.,* (2014) and Muasya *et al.,* (2014). Values of -2logL, AIC and BIC decreased from models with lower LP order of fit towards models with higher LP order of fit. These results agree with findings by de Oliveira et al., (2010). Models with same LP order for additive genetic and permanent environment had higher values of -2logL, AIC and BIC than models with same LP orders for additive genetic but different orders for permanent environment. Therefore, there was improvement of -2logL, AIC and BIC values when LP order for additive genetic effects was fixed and LP for permanent environment was modified, same results were obtained by Laureano *et al.,* (2014). The –2LogML of successively nested models were compared using LRT (P=0.05). Differences observed between hierarchical models across three parities were large enough to state that there were significant improvements when LP orders of fit increased. Number of eigen values chosen should be able to explain at least 98% of variation of random regression coefficients. First three eigen values and first four eigen values, respectively, explained over 98% of total variation of random regression coefficients for both additive genetic and permanent environmental effects.

Estimates of (Co) Variances for Random Regression Coefficients

Additive genetic variances were higher during early and mid lactation than towards end of lactations. Permanent environmental variances declined from beginning to end of lactation and could be due to better feeding during early lactation. Estimates of PEVs across three parities were higher during early than late lactation, same results were found in study by Byeong-Woo *et al.*, (2009) and Shahabodin *et al.,* (2012).

Heritability estimates for daily milk yield were lower than heritability estimates found by Ilatsia *et al.,* (2007) which ranged from 0.28 to 0.46, 0.38 to 0.52 and 0.33 to 0.52 in first, second and third lactations, respectively. Lower estimates are more accurate than higher estimates, RRM increases accuracy of genetic evaluation due to increasing volume of data per animal (Ghaderi-Zefrehei *et al.,* 2014).

Genetic correlations between milk yields obtained at consecutive days in milk were positive and decreased as interval between days in milk increased. These results agree with those of Takma and Akbas, (2007) with genetic correlation range of 0.51 to 0.99 between test-day milk yield. However, association between DIM in relation with increasing interval between days in milk was not linear in parity one and two in which there were high genetic correlations between late and early daily milk yields. Similar results were found by Ghaderi-Zefrehei *et al.,* (2014). High heritability estimates for lactation milk yield suggest that selection for lactation milk yield across three parities can be done at any stage of lactation.

Estimates of Breeding Values

High product moment correlations between EBVs in model (5,5RV8) and lower models indicate that all other models could be used to select same sets of bulls while low sire rank correlations show that there's re-ranking of sires in each model.

Conclusion

Model LP (L5, 5RV8), was sufficient to model variability in milk yield due to additive genetic and permanent environmental effects. Models which assumed homogeneous residual variances produced worst fit and therefore, heterogeneity in residual variance should be considered when modeling milk yield in Sahiwal cattle. Heritability estimates for daily milk yield across three parities were highest during early and mid lactation. Genetic correlations between daily milk yields were high and positive across three parities, implying that selection for milk yield can be done at any DIM. Heritability for lactation milk yield was highest in parity three followed by parity one and then two. Heritability tells the breeder how much confidence to place in the phenotypic performance of an animal when choosing parents of the next generation. High heritability implies a strong resemblance between parents and offspring with regard to a specific trait, while low heritability implies a low level of resemblance. High product moment correlations between EBVs in model (5,5RV8) and lower models indicate that all other models could be used to select same sets of bulls. Low sire rank correlations show that there's re-ranking of sires in each model.

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