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Estimation of direct and maternal (co)variance components for lactation traits in Jersey crossbred cattle at an organized farm

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ABSTRACT

Genetic parameters and (co)variance components were estimated for 305 days milk yield (305DMY), total milk yield (TMY), lactation length (LL) and peak yield (PY) in an organized herd of Jersey crossbred cattle. Restricted maximum likelihood (REML) fitting an animal model and ignoring or including maternal genetic or permanent environmental effects was used for carrying out analyses. Six different animal models were fitted for all traits. The best model was chosen after testing the improvement of log-likelihood values. Direct heritability estimates were 0.55, 0.50, 0.25 and 0.41 for 305DMY, TMY, LL and PY, respectively. Maternal genetic effects contributed 9 and 17% of the total variance for 305DMY and PY, respectively. Results suggest that maternal additive effect was important for 305 days milk yield and peak yield whereas permanent environmental maternal effects did not contribute to the total phenotypic variance of the considered traits in our study. Moderate to high direct heritability estimates varying from 0.25 to 0.55 for all considered lactation traits in this study suggests that there is adequate scope of improvement for these traits through selection under the prevailing management conditions. Further, for 305 days milk yield and peak yield maternal heritability was found to be imperative indicating that for improving these traits through selection both direct additive as well as maternal genetic effect must be taken into consideration.

Key words: Animal Model, Jersey crossbred cattle, Lactation traits, Maternal effects, Variance components

Accuracy of identifying genetically superior animals is most important for obtaining actual genetic improvement in a breeding programme. The primary goal of animal breeder is to maximize rate of genetic improvement through selection. In a dairy enterprise, this implies maximizing genetic improvement of milk production of animals. The population of crossbred cattle in India is 39.73 million (19th All India Livestock Census, 2012) which is 20.18% of total cattle population in the country. Crossbred cattle play a major role in the Indian economy through milk production as it contributes 40.43 million tonnes (26%) to total milk production in the country. In India, selection for milk yield in crossbred cattle is generally based on the lactation performance records. So, proper evaluation of lactation traits is needed in order to estimate genetic parameters precisely which will further help in selection of superior animals.

The existence of maternal lineage and its effects on yield in dairy cattle has been confirmed by several workers (Huizinga *et al*. 1986, Schutz *et al*. 1992, Boettcher *et al*. 1996). The term maternal effect implies an influence of the mother on her offspring other than through the genes she transmits to offspring. Maternal performance variations between females may arise from either genetic or environmental sources. The environmental effect of the dam is referred to as maternal influence and it may be because of several factors like cytoplasm of the egg, intra-uterine environment or post-natal environment as milk production and/or mothering ability. Maternal effects are especially important in early life but also may have carry-over effects later in life. According to Bell *et al*. (1985), maternal lineage accounted for 2% variation in milk yield whereas Huizinga *et al*. (1986) reported 6% variation in milk yield due to maternal lineage. Hence, for formulation of an optimum breeding programme in dairy cattle a better understanding of the reasons of genetic variation in maternal effects and the relationship between direct genetic and maternal genetic effects is of paramount importance. Nasholm and Danell (1994) observed that when maternal genetic effects were ignored during computation of genetic estimates it leads to upward biased heritability estimates and hence in turn reduced realized selection efficiency. Similar findings were reported by Meyer (1992) and Rumph *et al*. (2002) on ignorance of maternal effects. Consequently, errors and bias in estimation of genetic parameters can lead to sub-optimal selection decisions resulting in slow genetic progress (Hazel

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et al. 1994). Thus, for assessing the impact of maternal lineage on genetic evaluations, particularly in crossbred dairy cattle, it is crucial to accurately estimate the effect of maternal lineage. Hence, present study was undertaken with the objective to estimate variance and (co)variance components due to direct genetic effects, maternal genetic effects and maternal permanent environmental effects for lactation traits, viz. 305 days milk yield (305DMY), total milk yield (TMY), lactation length (LL) and peak yield (PY) in Jersey crossbred cattle.

MATERIALS AND METHODS

Data: Data used in the present study were obtained from the records maintained on Jersey crossbred cattle at Eastern Regional Station of ICAR- National Dairy Research Institute, Kalyani, West Bengal (India). The farm is situated in the lower Gangetic basin of West Bengal, with an average altitude of 9.75 meters above the mean sea level on 22.59' N latitude and 88.29' E longitude. The prevalent climatic condition is hot humid. The average annual maximum and minimum temperature is 31°C and 20°C, respectively. The maximum and minimum humidity is 91% and 58%, respectively with average1250 mm of annual rainfall. The months of July to October (83%) are having maximum precipitation. Thus, it is obvious that cattle maintained here get exposed to wide range of changes in temperature and humidity. In 1964, Eastern Regional Station of ICAR-NDRI was started in Calcutta. A herd of Red Sindhi cows, called LAL GORU's FARM in Bengali, was started in the same year at Milk Colony of Haringhata farm of Nadia, West Bengal, which was later shifted to Kalyani. Some Tharparkar and Jersey × Tharparkar cows were transferred from Karnal, Haryana to ERS-NDRI, Kalyani in 1972 onwards. Initially, crosses of Holstein Friesian with Tharparkar, Jersey with Red Sindhi and Jersey with Tharparkar were evolved at this station. Further, a three breed combination were also evolved by crossing Jersey × Tharparkar with Holstein Friesian × Tharparkar with a genetic combination of 3/8 Holstein Friesian, 3/8 Jersey and 2/8 Tharparkar. Three breed crosses didn't show any advantage over the Jersey × Tharparkar half-bred and Jersey crosses were significantly better than Friesian crosses as evident by earlier experiments. Pedigree of each animal was traced back for deducing its genetic group. Liquid semen was used for breeding of animals at this station earlier but in 1982, artificial insemination was started at this station with frozen semen procured from ICAR-NDRI, Karnal and Kerala Milk Marketing Board. Currently, semen of ½ Jersey × ½ Red Sindhi bulls is being used for insemination of cows in the herd. Loose housing system was followed for keeping cattle and free movement as well as sufficient exercise was provided to the animals. Standardized ration comprised of concentrate and *ad libitum* green fodder was provided to the lactating animals in order to meet their nutritional requirements. Maintenance diet included concentrate @1.5 kg/day and additional concentrate @1.0 kg for every 2.5 liters of milk produced above 5.0 litres daily yield to meet the extra energy requirements was provided.

Data on lactation traits [viz. 305 days milk yield (305DMY), total milk yield (TMY), lactation length (LL) and peak yield (PY)] of Jersey crossbred cattle maintained over a period of 34 years (1981–2014) were utilized for this study. Number of records analyzed for animal model and least-squares analysis are presented in Table 1 and 2, respectively.

Statistical analyses: Estimates of (co)variance components and heritabilities for various lactation traits were estimated by fitting a series of univariate animal models using a derivative free REML algorithm (Meyer 2000). Maternal genetic or permanent environmental effects were considered by including appropriate random effects into the model of analysis. Data were first analyzed by least-squares analysis of variance (Harvey 1990) to identify the significant fixed effects to be included in the model to estimate genetic parameters by animal model. The variance of function values (-2 log L) in the Simplex less than 10^{-8} was assumed as a criteria for the convergence of REML solutions. As a part of the DFREML program (Meyer 2000), standard errors were calculated for the estimated parameters. Following six univariate animal models were fitted to estimate (co)variance components for each trait:

$y = Xb + Z_a a + e$
$y = Xb + Z_a a + Z_c c + e$
$y = Xb + Z_a a + Z_m m + e$ with Cov (a, m) = 0
$y = Xb + Z_a a + Z_m m + e$ with Cov (a, m) = $A\sigma_{am}$
$y = Xb + Z_a a + Z_m m + Z_c c + e$with Cov (a, m) = 0
$y = Xb + Z_a a + Z_m m + Z_c c + e$with Cov (a, m) = $A\sigma_{am}$

where y is a n ×1 vector of observations for each trait; b, a, m, c and e are vectors of fixed effects, direct additive genetic effects, maternal additive genetic effects, permanent environmental effects of dam and the residual effects, respectively; X, Z_a, Z_m, $Z_c$are the incidence matrices of fixed effects, direct additive genetic effects, maternal genetic effects and permanent environmental effect of the dam; A depicts numerator relationship matrix between animals; and σ_{am} is the covariance between additive direct and maternal genetic effects. The (co)variance structure for the model was:

$V(a) = A\sigma_a^2$, $V(m) = A\sigma_m^2$, $V(c) = Ip\sigma_c^2$, $V(e) = I_R\sigma_e^2$ and $Cov(a, m) = A\sigma_{am}$

where I_P and I_R are identity matrices with orders equal to the number of dams and the number of progeny, respectively and σ^2_a, σ^2_m, σ^2_c and σ^2_e are direct additive genetic variance, maternal additive genetic variance, maternal permanent environmental variance, and residual variance, respectively. Estimates of heritability (h^2), maternal heritability (m^2) and permanent maternal environmental effects (c^2) were calculated as ratios of estimates of, and, respectively, to the phenotypic variance (σ^2_p). The direct-maternal correlation (r_{am}) was computed as the ratio of the estimates of direct-maternal covariance (σ_{am}) to the product of the square roots of estimates of and σ^2_a and σ^2_m.

Log-likelihood ratio tests having χ^2 distribution with degrees of freedom equal to the difference between the numbers of parameters for the 2 models were used to choose the most appropriate model for each trait (Meyer 1992). The statistics of the likelihood ratio (LR_{ij}) test for sequentially reduced models (Rao 1973) was:

$$LR_{ij} = -2 \log_e (L_j/L_i) = 2 \log_e L_i - 2 \log_e L_j$$

where L_i is the maximum likelihood for the complete model (with the maternal effect) and L_j is the maximum likelihood for the reduced model (without the maternal effect). Significance was tested at $P<0.05$ by comparing differences in log-likelihoods to values for a chi-square distribution.

RESULTS AND DISCUSSION

Number of observations, phenotypic means, standard deviations and coefficients of variations for different lactation traits are presented in Table 1. Coefficients of variation for all considered traits ranged from 28.93–44.05%. Overall least-squares means for 305DMY, TMY and PY were 2309.30, 2663.08 and 12.49 kg, respectively with an overall average lactation length of 363.93 days. Means and coefficients of variations for different traits in the present study were within the range of estimates obtained by other workers in different cattle breeds and their crosses (Ahmad *et al*. 2003, Saha *et al*. 2010, Mandal *et al*. 2013, Krishantan and Sinniah 2014, Ratwan *et al*. 2016a). Period of calving, season of calving, parity of animals and genetic group of animals had significant effect on majority of traits in this study. Effects of different environmental factors on considered lactation traits were in accordance with the findings of Saha *et al*. (2010), Mandal *et al*. (2013), Japheth *et al*. (2015) and Ratwan *et al*. (2016a, 2016b).

Estimates of (co)variance components and genetic parameters for 305 days milk yield of crossbred cattle along with log-likelihoods values for each analysis under the six different models are presented in Table 3. Estimates of heritability for 305 days milk yield depending on the model used ranged from 0.42 to 0.55. For this trait, ignoring maternal effects (Model 1) yielded higher estimates of σ^2_a and h^2 than other models except models 4 and 6. Fitting a permanent environmental maternal effect (Model 2) markedly increased the log-likelihood value over that for Model 1 (Table 3), indicating a significant maternal effect accounting for 7% of the total variance in this trait while correspondingly reducing the heritability estimate from 0.50 to 0.42. Fitting a maternal genetic (Model 3) rather than permanent environmental effect also resulted in an increase in log-likelihood over Model 1 but the resulting likelihood was very similar to that of Model 2. The estimate of maternal heritability from Model 3 was 8%, with a corresponding decrease in the estimate of direct heritability to 42%. Fitting a non-zero covariance (r_{am}) along with a maternal genetic effect (Model 4) resulted in large negative (–0.67) direct-maternal covariance estimates for this trait and also gave significant improvement in likelihood compared to Model 3. Fitting both genetic and environmental components of the dam effect (Model 5) resulted in a significantly better fit compared to model 4 but no improvement in log-likelihood values than models 2 and 3. Allowing for a direct-maternal covariance in Model 6 yielded large negative estimate of r_{am}, and accounted for 15% of total variance but did not produce a significant improvement in likelihood compared to Model 5. The estimated value for direct and maternal heritability for 305 days milk yield was 0.55 and 0.09 under the best fitted model in the present study (Table 4). Similar findings for the contribution of maternal genetic (m^2) effects to total phenotypic variance in 305 days milk yield were reported by Edriss *et al*. (2006) in Iranian Holstein cattle. However, Lee and Han (2004) observed the lower estimates of direct heritability (0.25) and maternal (m^2) effect (4.5%) for this trait in Holstein cattle than the present findings. Khattab *et al*. (2005) also reported only 1% contribution of maternal genetic effects (m^2) to the total phenotypic variance. The present study revealed that there is no contribution of permanent maternal (c^2) effect to the total phenotypic variance of 305 days milk yield under the best model. However, Ojango and Pollot (2001) and Khattab *et al*. (2005) reported 5 and 13% contribution of permanent environment (c^2) effect on 305 days milk yield, respectively in HF cattle. Amimo *et al*. (2007) reported direct heritability as 0.12 and 26% contribution of permanent maternal (c^2) effect to 305 days milk yield in Ayrshire cattle in Kenya. Using DFREML, Banik and Gandhi (2010) observed direct heritability estimates for first lactation 305 days milk yield as 0.22 in Sahiwal cattle.

Table 1. Characteristics of data structure for lactation traits in Jersey crossbred cattle

Items/Traits	305DMY (kg)	TMY (kg)	LL (days)	PY (kg)
No. of records	1170	1160	1160	1240
No. of animals	493	488	487	505
No. of sires with progeny record	59	59	59	59
No. of dams with progeny record	218	216	216	226
Progeny per sire	19.71	19.56	19.56	20.92
Progeny per dam	5.31	5.31	5.32	5.45
Mean	2303.47	2678.35	369.78	12.34
Standard deviation	803.43	1179.69	128.75	3.57
CV (%)	34.88	44.05	34.82	28.93
Period of data	1981–2014	1981–2014	1981–2014	1981–2014

305DMY, 305 days milk yield; TMY, Total milk yield; LL, Lactation length; PY, Peak yield.

Results for (co)variance components and genetic parameters of total milk yield together with the maximum log-likelihoods values for each analysis is summarized in Table 3. Depending on model used, estimates of direct heritability for total milk yield varied from 0.47 to 0.56 in different models. Model 1, which ignored maternal effects, overestimated direct additive genetic effects compared with models 2, 3 and 5. Introducing either a permanent

Table 2. Least-square means along with standard errors of different lactation traits in Jersey crossbred cattle

Effects/Traits	305DMY	TMY	LL	PY
Overall mean	2309.30±29.71 (1214)	2663.08±42.86 (1214)	363.93±4.58 (1214)	12.49±0.12 (1296)
Period of calving	**	**	**	*
PD1 (1981–1985)	2212.79±104.41^{bc} (67)	2711.68±150.63^{a} (67)	396.26±16.10^{a} (67)	11.63±0.45^{c} (64)
PD2 (1986–1990)	2405.98±71.74^{ab} (137)	2824.27±103.50^{a} (137)	359.65±11.06^{ab} (137)	12.24±0.30^{bc} (146)
PD3 (1991–1995)	2461.59±62.10^{a} (161)	2900.63±89.60^{a} (161)	392.49±9.58^{a} (161)	12.84±0.26^{ab} (171)
PD4 (1996–2000)	2497.93±56.16^{a} (222)	2950.67±81.01^{a} (222)	384.94±8.66^{a} (222)	13.01±0.23^{a} (235)
PD5 (2001–2005)	2473.13±55.69^{a} (209)	2802.78±80.34^{a} (209)	361.76±8.59^{a} (209)	12.87±0.23^{ab} (217)
PD6 (2006–2010)	2133.10±52.48^{c} (254)	2334.46±75.71^{b} (254)	338.04±8.09^{bc} (254)	12.50±0.22^{abc} (270)
PD7 (2011–2014)	1980.57±60.85^{c} (164)	2117.08±87.78^{b} (164)	314.39±9.38^{c} (164)	12.30±0.24^{bc} (193)
Season of calving	**	**	NS	**
S1 (Winter)	2481.22±43.53^{a} (395)	2851.41±62.80^{a} (395)	369.12±6.71 (395)	13.17±0.18^{a} (413)
S2 (Summer)	2271.40±43.54^{b} (406)	2648.70±62.81^{b} (406)	367.39±6.71 (406)	12.65±0.18^{b} (442)
S3 (Rainy)	2175.28±41.14^{b} (413)	2489.12±59.35^{b} (413)	355.27±6.34 (413)	11.63±0.17^{c} (441)
Parity of animals	**	NS	**	**
P 1	2083.58±43.77^{b} (339)	2544.52±63.14 (339)	390.16±6.75^{a} (339)	10.72±0.18^{b} (356)
P 2	2271.28±47.92^{a} (271)	2618.66±69.13 (271)	367.91±7.39^{b} (271)	12.52±0.20^{a} (286)
P 3	2382.26±56.06^{a} (194)	2710.92±80.88 (194)	365.48±8.64^{b} (194)	12.81±0.23^{a} (210)
P 4	2402.15±67.76^{a} (131)	2710.61±97.75 (131)	354.95±10.45^{b} (131)	12.97±0.28^{a} (143)
P 5	2424.11±79.23^{a} (97)	2720.19±114.30 (97)	354.98±12.21^{b} (97)	13.14±0.33^{a} (105)
P 6	2342.26±91.91^{a} (70)	2755.37±132.59 (70)	372.98±14.17^{ab} (70)	12.65±0.38^{a} (75)
P 7 (> 6 all lactations)	2259.45±75.83^{a} (112)	2581.29±109.40 (112)	341.07±11.69^{b} (112)	12.59±0.31^{a} (121)
Genetic group of animals	**	**	NS	**
GG1 (1/2 J ×½ RS)	2656.04±79.57^{a} (96)	3071.60±114.80^{a} (96)	370.56±12.27 (96)	13.54±0.34^{a} (98)
GG2 (1/2 J × ½ T)	2583.95±47.21^{a} (281)	2984.70±68.10^{a} (281)	361.54±7.28 (281)	13.81±0.20^{a} (291)
GG3[1/2 J × ¼ (HF/BS) × ¼ (Sahiwal/RS)]	2374.12±96.34^{b} (70)	2784.41±138.99^{ab} (70)	388.38±14.86 (70)	12.97±0.40^{ab} (76)
GG 4[1/2 J × 1/4 T × ¼ (RS/Desi)]	2273.25±66.00^{bc} (153)	2658.23±95.21^{bcd} (153)	359.70±10.18 (153)	12.52±0.27^{b} (165)
GG 5 (50% J)	2118.07±61.26^{cd} (173)	2422.95±88.38^{cd} (173)	350.17±9.45 (173)	11.77±0.26^{cd} (185)
GG 6 (½ J Misc. group)	2138.15±91.56^{bcd} (76)	2366.80±132.09^{cd} (76)	335.77±14.12 (76)	11.60±0.38^{cd} (82)
GG 7 (<50% J)	2305.22±70.62^{b} (124)	2684.04±101.88^{bc} (124)	375.59±10.89 (124)	12.42±0.29^{bc} (134)
GG 8 (>50% to 62.5% J)	2311.11±65.09^{b} (163)	2651.79±93.91^{bcd} (163)	364.93±10.04 (163)	12.30±0.27^{bcd} (178)
GG 9 (>62.5% J)	2023.79±92.72^{d} (78)	2343.20±133.76^{d} (78)	368.76±14.30 (78)	11.42±0.38^{d} (87)

Figures in parenthesis depict number of observations; **Significant at 1% level of significance; *Significant at 5% level of significance; NS, Non-Significant; Means with different superscripts differ significantly ($P<0.05$) from each other.

environmental maternal effect (model 2) or a maternal additive effect (model 3) decreased the estimate of additive heritability in the tune of 6% and 2%, respectively. Models 2 and 3 yielded estimates of c^2 and m^2 that explained only 3% and 1% of phenotypic variance, respectively. Model 5, which included both additive maternal and maternal permanent environmental effects, was similar to models 2 and 3 and did not significantly improve goodness of fit. Hence, the estimates of c^2 and m^2 from model 5 were almost similar with the models 2 and 3. Models 4 and 6 which included the direct maternal additive covariance, yielded similar estimates of direct heritability and maternal additive effect and did not produce significant improvement in likelihood values as compared to other models. The estimates of the direct maternal additive correlation ranged from -0.76 to -0.81. Estimates of (co)variance components and genetic parameters for lactation length along with log-likelihoods values for each analysis under the six different models are presented in the Table 3. Model 1, where maternal effects were ignored, heritability was biased upward for this trait as compared to other models. Introducing permanent environmental effects associated with the dam (Model 2) explained only 4% of total phenotypic variance and the reduction in direct heritability was 20% in comparison with Model 1 but fitting a c^2 effect didn't increase the likelihood significantly over that for a simple animal model. Model 3, which included maternal genetic effects in place of permanent environmental maternal effects, identified maternal effect contributing 6% of total variation and also yielded further reduction in estimates of h^2 relative to Model 1. Fitting a non-zero covariance (r_{am}) along with a maternal genetic effect (Model 4) resulted a significant maternal effect of 0.14 along with the negative direct-maternal covariance estimate (-0.52) for this trait but gave no significant improvement in likelihood compared to Model 3. Model 5 attempted to disentangle genetic and environmental components of the dam effect. Estimates of m^2 from Model 5 were similar to the estimates of model 3 but much smaller than those obtained from Model 4. Addition of a direct-maternal covariance in Model 6 yielded negative estimate (-0.52) of r_{am}, but inclusion of the covariance component did not improve goodness of fit

Table 3. Estimates of (co)variance components and genetic parameters for 305 Days milk yield (kg^2), total milk yield (kg^2), lactation length (days^2) and peak yield (kg^2) in Jersey crossbred cattle

Traits	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
305 days milk yield						
σ^2_n	307123.69	250357.10	255452.16	315209.40	249722.27	315731.18
σ^2_m	–	–	48475.66	53976.26	0.05	53971.59
σ_{am}	–	–	–	-87822.63	–	–87962.74
σ^2_c	–	41786.64	–	–	41961.80	45.40
σ^2_e	300495.77	298688.40	299895.86	295591.14	298784.17	295482.55
σ^2_p	607619.46	590832.14	603823.69	576954.16	590468.29	577267.98
h^2	0.50	0.42	0.42	0.55	0.42	0.55
m^2	–	–	0.08	0.09	0.00	0.09
c_{am}	–	–	–	–0.15	–	–0.15
r_{am}	–	–	–	–0.67	–	–0.67
c^2	–	0.07	–	–	0.07	0.00
Log L	–7903.51	–7900.74	–7901.94	–7898.16	–7900.74	–7898.16
Total milk yield						
σ^2_n	691339.83	643890.97	675767.11	753570.82	644125.06	750433.50
σ^2_m	–	–	14698.71	36392.97	5.69	28105.35
σ_{am}	–	–	–	–121851.36	–	–117311.99
σ^2_c	–	35235.25	–	–	35528.05	5994.24
σ^2_e	683199.02	682016.13	683078.98	675380.36	681870.55	675516.21
σ^2_p	1374538.85	1361142.35	1373544.80	1343492.76	1361529.35	1342737.31
h^2	0.50	0.47	0.49	0.56	0.47	0.56
m^2	–	–	0.01	0.03	0.00	0.02
c_{am}	–	–	–	–0.09	–	–0.09
r_{am}	–	–	–	–0.76	–	–0.81
c^2	–	0.03	–	–	0.03	0.01
Log L	–8287.76	–8287.40	–8287.73	–8286.16	–8287.40	–8286.16
Lactation length						
σ^2_n	4008.15	3185.32	2796.10	3007.10	2804.60	3004.85
σ^2_m	–	–	970.42	2201.01	795.47	2207.40
σ_{am}	–	–	–	–1333.97	–	–1336.42
σ^2_c	–	669.04	–	–	172.03	0.15
σ^2_e	11923.31	11907.36	12008.16	11821.83	11987.14	11821.11
σ^2_p	15931.46	15761.71	15774.68	15695.98	15759.25	15697.10
h^2	0.25	0.20	0.18	0.19	0.18	0.19
m^2	–	–	0.06	0.14	0.05	0.14
c_{am}	–	–	–	–0.09	–	–0.09
r_{am}	–	–	–	–0.52	–	–0.52
c^2	–	0.04	–	–	0.01	0.00
Log L	–5950.34	–5949.85	–5949.68	–5948.68	–5949.66	–5948.68
Peak yield						
σ^2_n	5.19	4.07	3.74	4.49	3.75	4.49
σ^2_m	–	–	1.34	1.82	0.83	1.81
σ_{am}	–	–	–	–1.63	–	–1.62
σ^2_c	–	0.84	–	–	0.40	0.00
σ^2_e	6.39	6.34	6.37	6.27	6.36	6.27
σ^2_p	11.58	11.26	11.45	10.95	11.33	10.95
h^2	0.45	0.36	0.33	0.41	0.33	0.41
m^2	–	–	0.12	0.17	0.07	0.17
c_{am}	–	–	–	–0.15	–	–0.15
r_{am}	–	–	–	–0.57	–	–0.57
c^2	–	0.07	–	–	0.04	0.00
Log L	–1971.20	–1967.37	–1966.99	–1962.30	–1966.69	–1962.30

σ^2_a, σ^2_m , σ^2_c, σ^2_e and σ^2_p are additive direct, maternal direct genetic, maternal permanent environmental, residual variance and phenotypic variance, respectively; h^2 is heritability; m^2 is maternal heritability (σ^2_m/ σ^2_p); r_{am} is the additive direct-maternal genetic correlation; χ^2= σ^2_c/ σ^2_p and Log L is the log likelihood expressed as a deviation from the model with highest likelihood.

Table 4. Estimated parameters and their standard errors from the best model for each trait

Trait	Model	h^2	m^2	c^2	σ^2_n	σ^2_m	σ^2_c	σ^2_e	σ^2_p
305 DMY	4	0.55	0.09	–	315209.40	53976.26	–	295591.14	576954.16
TMY	1	0.50(0.04)	–	–	691339.83	–	–	683199.02	1374538.85
LL	1	0.25(0.05)	–	–	4008.15	–	–	11923.31	15931.46
PY	4	0.41	0.17	–	4.49	1.82	–	6.27	10.95

when compared with model 5. Direct heritabilities estimate for total milk yield and lactation length of crossbred cattle were 0.50 and 0.25, respectively under best model in the present data set (Table 4). No maternal effects either genetic or/and permanent environment (c^2) effects was observed on these traits in this study. The direct heritabilities estimate for total milk yield and lactation length in the present study were in agreement with other published values reported for different cattle breeds and its crosses (Filho *et al.* 2006, Haile *et al.* 2009, Saha *et al.* 2010). However, Ojango and Pollot (2001) and Boujenane (2002) reported permanent maternal (c^2) effect as 0.03 and 0.05 for lactation length and total milk yield, respectively in HF cattle. As compared to the present study, Ojango and Pollot (2001) in HF cattle and Al-Samarai *et al.* (2015) in HF cattle reported very low direct heritability estimates for lactation length. Using animal model, Banik and Gandhi (2010) estimated the direct heritability for first lactation milk yield and first lactation length as 0.102 and 0.089, respectively in Sahiwal cattle. Gorbani *et al.* (2011) reported that direct additive (h^2) effect for milk yield as 0.24 in Iranian Brown Swiss crossbred cattle.

(Co) variance components and genetic parameters for peak yield along with log-likelihoods values for each analysis are presented in the Table 3. The direct heritability estimates for peak yield ranged from 0.33 to 0.45 in different models. Ignoring maternal effects (Model 1) produced higher estimates of σ^2_a and h^2 than other models. Inclusion of either a permanent environmental maternal effect (model 2) or a maternal additive effect (model 3) produced a significant improvement in likelihood compared with model 1. In Model 2, a significant maternal effect accounting for 7% of the total variance was identified with corresponding reduction of heritability estimate from 0.45 to 0.36. Fitting a maternal genetic (Model 3) yielded a significant estimate of maternal heritability of 12%, with a corresponding decrease in the estimate of direct heritability to 27%. Further, the inclusion of both additive and permanent environmental maternal effects in model 5 did not significantly improve the likelihood compared with either model 2 or model 3. Inclusion of the direct maternal covariance in models 4 and 6 yielded estimates for ranged from -1.62 to -1.63 with corresponding estimates of r_{am} of -0.57, and also produced significant improvements in likelihoods as compared to models 2 and 3. Estimate of direct heritability (0.41) for peak yield in the present study (Table 4) was well comparable with the findings of other studies (Deshpande and Bonde 1981, Deb *et al.* 2008) on different cattle breeds/crosses. Rekaya *et al.* (2000), Dhaka *et al.* (2002) and Lakshmi *et al.* (2010) reported lower estimates of direct heritability ranging from 0.16–0.29 in different cattle breeds as compared to the present findings. Maternal genetic component (m^2) was found to be an important component while estimating heritability for peak yield and contributed 17% to the total phenotypic variance for this trait (Table 4). High heritability estimates for peak yield suggests that there is ample scope of improvement through selection for this trait. Generally, in dairy cattle, calves do not nurse by their dams, so additive maternal effects in the present study would be caused by intrauterine environment. The estimates of maternal heritabilities for 305 days milk yield and peak yield were low to moderate in nature, i.e., 0.09 and 0.17, respectively in this study, may be due to combined effects of additive genetic effect of dam and cytoplasmic inheritance as it is difficult to separate the effect of additive genetic maternal differences from the effect of cytoplasmic differences as stated by Brumby (1960).

In conclusion, the findings of the present study confirmed the importance of implementing the correct model for estimation of (co)variance components and genetic parameters for lactation traits of Jersey crossbred cattle. Ignorance of maternal effects leads to overestimation of the heritability for 305 days milk yield and peak yield of animals. Maternal heritability was important for 305 days milk yield and peak yield in this study. Hence, both direct additive and maternal genetic effect must be taken into consideration for improving these traits through selection.

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