



Impact of additive direct and maternal heritability on production efficiency traits in Jersey crossbred cattle

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ABSTRACT

Variance components, direct and maternal heritability were estimated for milk production efficiency traits namely, milk yield per day of lactation length (MY/LL) and milk yield per day of calving interval (MY/CI) in Jersey crossbreds maintained at Eastern Regional Station of ICAR-National Dairy Research Institute, West Bengal (India). Data analyses were done using restricted maximum likelihood (REML) method with six alternative animal models (direct and including or excluding maternal associated effects). The best model was chosen after testing the improvement of the log-likelihood values and it revealed direct heritability estimates as 0.47 and 0.25 for MY/LL and MY/CI traits, respectively. Maternal heritability (0.14) was found to be important for MY/LL trait and permanent environmental maternal effect contributed 12% to the total phenotypic variance of the MY/CI. Direct heritability estimates were high (0.47) for MY/LL and moderate for MY/CI (0.25) trait suggesting that there is ample scope of improvement through selection for milk production efficiency traits in Jersey crossbred maintained at organized herds.

Key words: Heritability, Jersey crossbred, Maternal effects, Milk production efficiency traits

In India, selection of crossbred dairy cattle is predominantly based on their standard lactation milk yield. However, besides lactation milk yield, it is important to develop certain additional criteria for selection based on milk production efficiency traits. The milk yield expressed in terms of milk yield per day of lactation length (MY/LL) and milk yield per day of calving interval (MY/CI) are considered good measures of milk production efficiency traits in dairy animals.

Several studies have confirmed the existence of maternal lineage and its effects on yield in dairy cattle (Huizinga *et al.* 1986, Schutz *et al.* 1992, Boettcher *et al.* 1996). Bell *et al.* (1985) reported that maternal lineage account for 2% variation in milk yield. However, Huizinga *et al.* (1986) reported 6% variation in milk yield due to maternal lineage. Therefore, better understanding of the reasons of genetic variation in maternal effects and the relationship between direct genetic and maternal genetic effects is of utmost importance for formulation of an optimum breeding programme in dairy cattle. Nasholm and Danell (1994)

observed the upward biased heritability estimates and reduced realized selection efficiency, when maternal genetic effects were not taken into consideration during computation of genetic estimates. Meyer (1992) and Rumph *et al.* (2002) also reported and confirmed that ignorance of maternal effects yield an upward estimate of direct heritability. Thus, such a sub-optimal selection decisions arising from errors and bias in estimation of genetic parameters can result in slow genetic progress (Hazel *et al.* 1994). Therefore, it is imperative to accurately estimate the effects of maternal lineage for assessing the impact of their effects on genetic evaluations, particularly in crossbred dairy cattle. Hence, the present study was conducted to estimate variance and (co)variance components due to direct genetic effects, maternal genetic effects and maternal permanent environmental effects for production efficiency traits viz. milk yield per day of lactation length (MY/LL) and milk yield per day of calving interval (MY/CI) in Jersey crossbred cattle.

MATERIALS AND METHODS

Data: The present study was carried out on Jersey crossbred cattle maintained at the Eastern Regional Station of ICAR- National Dairy Research Institute, Kalyani, West Bengal (India). The farm is located 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 climatic condition is hot humid. The average annual maximum temperature is 31°C and the

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minimum temperature is 20°C. The maximum humidity is 91% and minimum humidity is 58%. The annual rainfall is around 1250 mm. The maximum precipitation is between July to October (83%). The Eastern Regional Station of ICAR-NDRI was set up in 1964 in Calcutta. In the same year, a herd of Red Sindhi (RS) cows, called LAL GORU's Farm in Bengali, was started at the Milk Colony of Haringhata farm of Nadia, West Bengal, which was later shifted to Kalyani. In 1972 onwards, some Tharparkar and Jersey × Tharparkar cows were transferred from Karnal, Haryana to ERS-NDRI, Kalyani. Subsequently, crosses of Holstein Friesian with Tharparkar, Jersey with Red Sindhi and Jersey with Tharparkar were evolved in the initial stage at this station. Further, a three breed combination by crossing with Jersey × Tharparkar with Holstein Friesian × Tharparkar with a genetic combination of 3/8 Holstein Friesian, 3/8 Jersey and 2/8 Tharparkar were also evolved. Earlier experiments revealed that Jersey crosses were significantly better than Friesian crosses and 3-breed crosses didn't show any advantage over the Jersey × Tharparkar half-bred. The genetic group of each animal was deduced after back tracing of pedigree of animal. Presently, semen of ½ Jersey × ½ Red Sindhi bulls is being used for insemination of cows in the herd. The cattle were kept under loose housing system. The nutritional requirements of the lactating animals were met through a standardized ration of concentrate and *ad lib.* green fodder. Concentrate @1.5 kg/day was provided as maintenance diet and additional concentrate @1.0 kg for every 2.5 liters of milk produced above 5.0 liters daily yield to meet their extra energy requirements.

The traits included for this study were milk yield per day of lactation length (MY/LL) and milk yield per day of calving interval (MY/CI). Data sets comprise of 34 years (1981–2014) and 28 years (1986–2013), respectively for both the traits were studied. The number of records considered for MY/LL and MY/CI were 1160 and 681 pertaining to 489 and 352 animals, respectively. Numbers of sires with progeny records were 59 and 34 whereas numbers of dams with progeny records were 216 and 159, respectively. Correspondingly, progeny per sire and progeny per dam for MY/LL was 19.58 and 5.31 whilst in case of MY/CI number of progeny per sire and dam were 19.88 and 4.21, respectively for both the traits.

Statistical analysis: (Co) variance components were estimated by restricted maximum likelihood (REML) using a derivative-free algorithm fitting an animal model (DFREML, Meyer 2000). For identification of the fixed effects to be included in the model, data were first analyzed by least-squares analysis of variance (Harvey 1990). The fixed effect of period of calving, season of calving, parity of animal and genetic group of animal were included in the statistical model. Only significant effects were included in the animal model. Convergence of the REML solutions was assumed when the variance of function values ($-2 \log L$) in the Simplex was less than 10^{-8} . Analyses were restarted for several other rounds of iterations using results from the

previous round as starting values to ensure that a global maximum was reached. When estimates did not change, convergence was confirmed. Depending on the model, the log-likelihood function was maximized with respect to the direct and maternal additive variances, the permanent environmental variance of the dam and the genetic covariance between direct and maternal genetic effects. Standard errors were calculated for the estimated parameters as a part of the DFREML program (Meyer 2000).

Univariate animal models were fitted to estimate (co)variance components for each trait. The following six models were used:

$$y = Xb + Z_a a + e, \quad \dots(1)$$

$$y = Xb + Z_a a + Z_c c + e, \quad \dots(2)$$

$$y = Xb + Z_a a + Z_m m + e \text{ with Cov}(a, m) = 0, \quad \dots(3)$$

$$y = Xb + Z_a a + Z_m m + e \text{ with Cov}(a, m) = A\sigma_{am}, \quad \dots(4)$$

$$y = Xb + Z_a a + Z_m m + Z_c c + e \text{ with Cov}(a, m) = 0, \quad \dots(5)$$

$$y = Xb + Z_a a + Z_m m + Z_c c + e \text{ with Cov}(a, m) = A\sigma_{am} \quad \dots(6)$$

where y is a $n \times 1$ 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 is the 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:

$$V(a) = A\sigma_a^2, \quad V(m) = A\sigma_m^2, \quad V(c) = I_p\sigma_c^2, \quad V(e) = I_r\sigma_e^2$$

and $\text{Cov}(a, m) = A\sigma_{am}$

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_a^2 , σ_m^2 , σ_c^2 , and σ_e^2 are direct additive genetic variance, maternal additive genetic variance, maternal permanent environmental variance, and residual variance, respectively. Estimates of additive direct heritability (h^2), maternal heritability (m^2) and permanent maternal environmental effects (c^2) were calculated as ratios of estimates of σ_a^2 , σ_m^2 and σ_c^2 , respectively, to the phenotypic variance (σ_p^2). 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 σ_a^2 and σ_m^2 .

The most appropriate model for each trait was chosen by using log-likelihood ratio tests (Meyer 1992). An effect was considered to have a significant influence when its inclusion caused a significant increase in log-likelihood, compared with a model in which it was ignored. The model which includes one or more random effects was compared with most comprehensive model (which includes all random effects, here model 6) for selection/choosing of best fitted model and if the log likelihood value of any model having one or more random effect didn't differ significantly from the log-likelihood value of the most comprehensive model (here model 6) then the model having one or more random effects should be considered as the most appropriate/best

Table 1. Characteristics of data structure for milk production efficiency traits of crossbred cattle

Item/Trait	MY/LL (kg/day)	MY/CI (kg/day)
No. of records	1160	681
No. of animals	489	352
No. of sires with progeny record	59	34
No. of dams with progeny record	216	159
Progeny per sire	19.58	19.88
Progeny per dam	5.31	4.21
Mean	7.23	6.11
Standard deviation	2.17	2.01
C. V. (%)	30.01	32.90
Period of data	1981–2014	1986–2013

MY/LL, milk yield per day of lactation length; MY/CI, milk yield per day of calving interval.

fitted model for that particular trait. Significance was tested at $P < 0.05$ by comparing differences in log-likelihoods to values for a chi-square distribution with degrees of freedom equal to the difference in the number of (co)variance components fitted for the two models.

RESULTS AND DISCUSSION

Number of observations, phenotypic means, standard deviations and coefficients of variations for different lactation traits are presented in Table 1. The overall least-squares means for MY/LL and MY/CI were 7.33 ± 0.08 and 6.08 ± 0.08 kg/day, respectively. In the present study, period of calving, season of calving, parity of animals and genetic group of animals had highly significant ($P < 0.01$) effect on both TMY/LL and TMY/CI (Table 2). The overall least-squares means for MY/LL and MY/CI were comparable with other studies in crossbred cattle (Saha *et al.* 2010, Verma and Thakur 2013, Ratwan *et al.* 2016, 2017). Environmental factors like period of calving, season of calving, parity of animal and genetic group of animal had shown significant effect on MY/LL and MY/CI as reported by several workers (Singh *et al.* 2005, Lakshmi *et al.* 2010, Japheth *et al.* 2015, Ratwan *et al.* 2017).

Estimates of (co)variance components and genetic parameters for MY/LL along with log-likelihoods values for each analysis under the six different models are presented in the Table 3. Depending on the model used, there was variation in the estimates of direct additive heritability for milk yield per day of lactation length. Model 1, which ignored all sources of maternal effects, produced higher estimates of σ_a^2 than other models. Fitting a permanent environmental maternal effect (Model 2) explained 9%, of total phenotypic variance and the corresponding reduction in direct heritability was 24% in comparison with Model 1. Model 3, which included only direct and maternal additive effects, yielded a maternal effect contributing 11% for this trait but resulted similar estimate of h^2 relative to Model 2. Fitting a non-zero covariance (σ_{am}) along with a maternal genetic effect (Model 4) resulted in higher estimates of h^2 and m^2 as

Table 2. Least-squares means along with standard errors of different milk production efficiency traits in crossbred cattle

Effect/Trait	MY/LL	MY/CI
Overall mean	7.33 ± 0.08 (1203)	6.08 ± 0.08 (932)
<i>Period of calving**</i>		
PD1 (1981–1985)	6.81 ± 0.27^b (67)	5.16 ± 0.28^{bc} (60)
PD2 (1986–1990)	7.74 ± 0.19^a (135)	6.85 ± 0.21^a (103)
PD3 (1991–1995)	7.60 ± 0.16^a (159)	6.62 ± 0.17^a (131)
PD4 (1996–2000)	7.70 ± 0.15^a (220)	6.82 ± 0.16^a (169)
PD5 (2001–2005)	7.78 ± 0.15^a (207)	6.59 ± 0.16^a (160)
PD6 (2006–2010)	6.94 ± 0.14^b (251)	5.50 ± 0.14^b (209)
PD7 (2011–2014)	6.74 ± 0.16^b (164)	5.03 ± 0.19^c (100)
<i>Season of calving**</i>		
S1 (Winter)	7.77 ± 0.11^a (393)	6.42 ± 0.12^a (311)
S2 (Summer)	7.19 ± 0.11^b (405)	5.83 ± 0.12^b (307)
S3 (Rainy)	7.03 ± 0.11^b (405)	5.99 ± 0.12^b (314)
<i>Parity of animals**</i>		
P1	6.50 ± 0.12^c (336)	5.41 ± 0.12^b (282)
P2	7.13 ± 0.13^b (268)	5.92 ± 0.13^a (211)
P3	7.39 ± 0.15^{ab} (192)	6.18 ± 0.16^a (144)
P4	7.72 ± 0.18^a (130)	6.37 ± 0.19^a (105)
P5	7.75 ± 0.21^a (96)	6.23 ± 0.21^a (75)
P6	7.41 ± 0.24^{ab} (70)	6.20 ± 0.28^a (46)
P7 (> 6 all lactations)	7.42 ± 0.20^{ab} (111)	6.27 ± 0.24^a (69)
<i>Genetic group of animals**</i>		
GG1 (1/2 J \times 1/2 RS)	8.18 ± 0.21^a (94)	7.00 ± 0.21^a (77)
GG2 (1/2 J \times 1/2 T)	8.26 ± 0.12^a (280)	6.84 ± 0.13^a (234)
GG3 [1/2 J \times 1/4 (HF/BS) \times 1/4 (Sahiwal/RS)]	7.37 ± 0.26^b (69)	6.05 ± 0.27^b (56)
GG4 [1/2 J \times 1/4 T \times 1/4 (RS/Desi)]	7.26 ± 0.17^b (153)	6.10 ± 0.19^b (118)
GG5 (50% J)	6.84 ± 0.16^{bc} (171)	5.80 ± 0.17^b (127)
GG6 (1/2 J Misc. group)	7.10 ± 0.24^{bc} (74)	5.91 ± 0.27^b (53)
GG7 (<50% J)	7.14 ± 0.19^b (124)	5.94 ± 0.20^b (93)
GG8 (>50% to 62.5% J)	7.36 ± 0.17^b (162)	6.05 ± 0.19^b (114)
GG9 (>62.5% J)	6.46 ± 0.25^c (76)	5.04 ± 0.26^c (60)

Figures in parenthesis represent number of observations. **Significant at <1% level of significance.

observed in Model 3 with the corresponding estimate of r_{am} of -0.68 . In Model 5, which attempted to disentangle genetic and environmental components of the dam effects, the estimates of m^2 were much smaller than those of Model 3, and there was no significant improvement in likelihood compared to Model 3. Allowing a direct-maternal genetic covariance (σ_{am}) in Model 6 yielded estimates of r_{am} of -0.68 for this trait, and the resulting likelihood gave a significant improvement compared to Model 5. Heritability estimate of 0.47 for MY/LL as revealed by best suited model in our study (Table 3) was well consistent with the findings of Singh and Gurnani (2004) in Karan Swiss and Karan Fries (HF crossbred) cattle, Singh *et al.* (2005) in different Jersey and HF crossbred cattle and Haile *et al.* (2009) in Ethiopian Boran cattle \times HF. On contrary, lower heritability estimates for this trait was reported by Haile *et al.* (2009) in Ethiopian Boran cattle (0.13) and Saha *et al.* (2010) in Karan Fries cattle (0.38). Maternal heritability for milk yield

Table 3. Estimates of (co)variance components and genetic parameters for milk yield per day of lactation length and milk yield per day of calving interval in Jersey crossbred cattle

Trait	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
<i>MY/LL</i>						
σ_a^2	1.89	1.39	1.43	1.82	1.38	1.82
σ_m^2	-	-	0.44	0.56	0.03	0.56
σ_{am}	-	-	-	-0.69	-	-0.69
σ_c^2	-	0.37	-	-	0.36	0.00
σ_e^2	2.25	2.23	2.25	2.21	2.23	2.21
σ_p^2	4.14	4.00	4.11	3.89	4.00	3.89
h^2	0.46	0.35	0.35	0.47	0.34	0.47
m^2	-	-	0.11	0.14	0.01	0.14
c_{am}	-	-	-	-0.18	-	-0.18
r_{am}	-	-	-	-0.68	-	-0.68
c^2	-	0.09	-	-	0.09	0.00
Log L	-1269.56	-1265.56	-1267.04	-1261.11	-1265.56	-1261.11
<i>MY/CI</i>						
σ_a^2	1.10	0.73	0.72	0.97	0.72	0.92
σ_m^2	-	-	0.39	0.53	0.02	0.39
σ_{am}	-	-	-	-0.40	-	-0.33
σ_c^2	-	0.35	-	-	0.34	0.10
σ_e^2	1.92	1.88	1.90	1.86	1.88	1.86
σ_p^2	3.02	2.96	3.01	2.95	2.96	2.95
h^2	0.37	0.25 (0.07)	0.24	0.33	0.24	0.31
m^2	-	-	0.13	0.18	0.01	0.13
c_{am}	-	-	-	-0.14	-	-0.11
r_{am}	-	-	-	-0.56	-	-0.55
c^2	-	0.12 (0.06)	-	-	0.12	0.04
Log L	-682.59	-679.53	-680.94	-678.52	-679.53	-678.44

σ_a^2 , σ_m^2 , σ_c^2 , σ_e^2 and σ_p^2 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_m^2/σ_p^2); r_{am} is the additive direct-maternal genetic correlation; $c^2 = \sigma_c^2/\sigma_p^2$ and Log L is the log likelihood expressed as a deviation from the model with highest likelihood. Parameter values with bold font for particular model for each trait depicted the best model.

per day of lactation length was 0.14 in the present study. Generally, in dairy cattle, dams do not nurse their calves, so additive maternal effects in the present study would be caused by intrauterine environment. Maternal genetic effects, 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).

(Co) variance components and genetic parameter estimates for MY/CI are presented in Table 3. Estimates of direct heritability ranged from 0.24 to 0.37, depending on the model used. Ignoring maternal effects (Model 1) produced higher estimates of σ_a^2 and h^2 as compared to other models. Addition of a permanent environmental maternal effect (model 2) led to a reduction in additive direct heritability of 32% compared with model 1, and this effect accounted for 12% of phenotypic variance. Model 3, which included only direct and maternal additive effects, yielded an estimate of m^2 that explained 13% of phenotypic variance and caused a reduction of direct heritability of 35% as compared to model 1. Fitting a non-zero covariance (σ_{am}) along with a maternal genetic effect (Model 4) resulted in higher estimates of h^2 and m^2 as observed in Model 3 with

the corresponding estimate of r_{am} of -0.56. Model 5 attempted independent estimation of m^2 and c^2 , but the estimate of m^2 converged to 0.00, indicating no additive maternal variance for this trait in these data set. Adding σ_{am} in model 6 increased the estimate of the direct heritability but there was no significant improvement in likelihood compared with model 5. In this model, 13% of phenotypic variance was attributed to maternal genetic effects, 4% was associated with permanent environmental effects of the dam, and the negative estimate of σ_{am} accounted for 11.2% of the variance with a corresponding estimate of r_{am} of -0.55. The most suitable model revealed moderate heritability estimates (0.25) for MY/CI as shown in Table 3. Permanent maternal environment component was found to be important for MY/CI and constituted 12% of the total phenotypic variance in the present study. The permanent environmental effect (0.12) due to dam for milk yield per day of calving interval in this study could be an indication of the large influence of environment on milk production of animals. Deb *et al.* (2008) found similar heritability estimate for MY/CI in Bangladesh Livestock Research Institute Cattle Breed-1 as reported in the present study. Higher heritability estimate as compared to our findings were reported by several workers (Singh and

Gurnani 2004, Saha *et al.* 2010) for MY/CI in crossbred cattle. The moderate heritability estimate for MY/CI in the present study suggests that there is chance of improvement through selection for this trait.

In conclusion, present study revealed significant effect of genetic and non-genetic factors on milk production efficiency traits and moderate to high heritability estimate for MY/CI and MY/LL, respectively. This suggests that there is ample scope of improvement through selection using both traits under the prevalent management conditions. From the present study it is revealed that the maternal heritability (m^2) was important for MY/LL trait, while permanent maternal effect (c^2) due to dam was important for MY/CI trait. Thus, the results suggest that both direct and permanent environmental maternal effects are important and should be estimated and taken into consideration for analyzing and evaluating the milk production efficiency traits in Jersey crossbred cattle. Results from this study will further augment in formulating breeding strategy.

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