



Estimation of variance components of milk yield and genetic evaluation of Sahiwal cattle using mixed linear models

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ABSTRACT

First lactation 305 days milk yield (FL305DMY) records (2032) on Sahiwal cows, maintained at 3 different farms in India were analyzed to estimate the impact of direct additive genetic, maternal additive genetic and cow's permanent environmental effects on milk yield and to compare sire model (BLUP) with 3 different animal models *i.e.* simple univariate model (AM I), univariate model with maternal effect and cow's permanent environmental effect (AM II) and multivariate model (AM III) of sire evaluation. The sire model of BLUP was least capable to estimate genetic differences amongst bulls. The heritability estimate for milk yield using sire model was lowest (0.141), followed by animal Models, viz. AM II (0.236), AM III (0.260) and AM I (0.292). Among animal models, lowest estimate of heritability obtained using AM II indicated for presence of significant amount of maternal additive genetic variance (26485.05 kg²) and maternal effect explained 11.1 % of total phenotypic variation in milk yield. The permanent environmental effect of cows explained 2.5 % variation of milk yield. The AM II was most effective model in terms of efficiency and accuracy over other models of sire evaluation. The rank correlations amongst the estimated breeding values of sires for FL305DMY were higher ranging from 0.898 (sire model versus AM III) to 0.991 (AM I versus AM II) indicating similarity in ranking of sires to the degree of 90 percent and above from different methods of Sahiwal sire evaluation.

Key words: Animal model, Cattle, Maternal effect, Sahiwal, Sire evaluation

The maternal effects have been defined as any influence of dam that affects the performance of its offspring beyond the effects of directly transmitted genes. Schutz *et al.* (1992) suggested that milk yield, intra-uterine environment and mothering ability in mammals are common components of maternal effect, which might both be genetically and environmentally determined. Albuquerque *et al.* (1998) suggested that maternal genetic effects were not important for yield traits in dairy cattle. But in tropical countries the impact of maternal effect may not be ignored for yield traits of zebu cattle. Although, numerous reports of maternal effects on growth traits of meat animals are available, but only few reports (Albuquerque *et al.* 1998, Edriss *et al.* 2006, Kumar *et al.* 2009) of maternal effects on yield traits of dairy cattle are available. Accordingly, the present investigation was undertaken to estimate the impact of direct additive genetic, maternal additive genetic and cow's permanent environmental effects on milk yield and to compare sire

model with three animal models in Sahiwal cattle.

MATERIALS AND METHODS

Source of data: First lactation 305 days milk yield (FL305DMY) records (2032) of Sahiwal cows, sired from 114 sires and maintained at 3 associated herds (NDRI Karnal, GLF Lucknow and CGBF, Durg) under tropical agro-climatic zone of India over a period of 39 years (1966 to 2004) were collected. Sires having 5 or more progeny were included in the study. The lactation records of animals producing less than 500 kg in lactation were considered as abnormal and were not included in the study. The climate of all 3 farms is subtropical in nature. Artificial insemination is practised at all 3 farms over selected cows with the semen of progeny tested bulls. Feeding on green fodder throughout the year was the policy of the farms but during lean period green fodder, silage and hay have been provided. At NDRI farm machine milking was practised and cows were milked thrice a day. However, at GLF Lucknow and CGBF Durg, hand milking was practiced and calves were allowed for controlled suckling of whole milk up to 60 days, prior and after the milking.

Statistical analysis: The summary of data structure is

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Table 1. Summary of data structure

Data	First lactation 305 days milk yield
Number of animals with records	2032
Number of base animals	684
Number of animals with unknown sire	481
Number of animals with unknown dam	839
Number of sires with progeny records	114
Number of dams with progeny records	1405
Number of grand-sires with progeny records	103
Number of grand-dams with progeny records	676
Mean, kg	1523.75
Standard deviation, kg	554.54
Coefficient of variation, %	36.4

presented in table 1. The seasons (4 namely winter, summer, rainy and autumn), farms (3) and periods (13 as per set of sires used in herds) of calving were used as fixed effects. The age at first calving was used as linear covariable in sire model and univariate animal model, whereas it was used as an auxiliary trait in multivariate model because of its higher estimate of heritability (0.39). Sires in all 3 methods and dams along with sires in animal models were considered as random effects.

In the present investigation, best linear unbiased production (BLUP) based sire model (SM) described by Henderson (1975) was used for estimation of variance components of FL305DMY and further it was compared with animals models. Estimation of variance components using derivative free restricted maximum likelihood algorithm as described by Meyer (1989, 1998) were;

Univariate derivative free restricted maximum likelihood animal models;

AM I (Animal model I): $Y = Xb + Za + e$

AM II (Animal model II): $Y = Xb + Za + M_m + W_p + e$

Multi-trait derivative free restricted maximum likelihood (MTDFREML);

AM III (Animal model III): $Y = Xb + Za + e$

In MTDFREML method four auxiliary traits (age at first calving, first service period, first days open and first lactation length) along with principal trait (FL305DMY) were included in multivariate model.

In animal models, Y is a vector of records; denotes the vector of fixed effects, X is the matrix that associates b with Y ; a is the vector of breeding values for direct genetic effects (both parents), Z is the matrix that associates a with Y ; m is the vector maternal genetic effects contributed by dams to records of their progeny, M is the matrix that associates m with Y ; p is the vector of permanent environmental effect, W is the matrix that associates p with Y ; and e is the vector of residuals effects, peculiar to observations that are not explained by other parts of the model. The effectiveness of different sire evaluation methods was judged by using the

criteria such as within sire variance or error variance, Log L value, coefficient of variation (%) and rank/simple product moment correlations. The sire evaluation method with lowest error variance was considered as most efficient and appropriate. The relative efficiencies of each model were calculated by dividing their error variances with the error variance of most efficient model. The most accurate method showed the highest Log L value. The coefficient of variation (CV %) of FL305DMY from different models of sire evaluation were estimated for judging the stability of sire evaluation methods (Banik and Gandhi 2006). The nearer the CV (%) of adjusted data to CV (%) of unadjusted data of first lactation 305 days milk yield, the more stable was the method. After estimation of breeding value of sires, the sires were ranked as per genetic merit. The Spearman's rank correlations and product moment correlations between breeding values of sires derived by various methods were also used to judge the effectiveness of different methods.

RESULTS AND DISCUSSION

Variance components: The variance components as well as direct and maternal heritabilities estimated by different models of sire evaluation are presented in table 2. The direct additive genetic variance was lowest (34611.27 kg²) in BLUP based sire model as compared to all the animal models based on the algorithm of DFREML. The heritability estimate obtained by sire model was lowest (0.141) as compared to all the animal models. Among 3 different animal models the simplest single trait AM I had maximum direct additive genetic variance (69474.28 kg²) and so maximum direct

Table 2. Variance components (kg²) and heritability for FL305DMY using different models of sire evaluation

	Sire model	Animal models		
	BLUP (SM)	AM I	AM II	AM III
σ_a^2	34611.27	69474.28	56607.31	61172.00
σ_m^2	—	—	26485.05	—
σ_c^2	—	—	5921.84	—
σ_e^2	211506.09	168031.49	149394.57	173650.00
σ_p^2	246117.36	237505.78	238408.78	234820.00
h_d^2	0.141	0.292±0.04	0.237±0.04	0.260
h_m^2	—	—	0.111±0.03	—
h_c^2	—	—	0.025±0.02	—
Log L	—	-13464.38	-13455.82	-42274.59
RE	0.706	0.889	1.000	0.860
CV (%)	30.21	31.98	32.04	36.39

SM, Sire model; AM, animal model; σ_a^2 , direct additive genetic variance; σ_m^2 , maternal additive genetic variance; σ_c^2 , cows (animals) permanent environmental variance; σ_e^2 , random residual variance; h_d^2 , direct heritability; h_m^2 , maternal heritability; h_c^2 , ratio of cow's permanent environmental variance to phenotypic variance; RE, relative efficiency of model with respect to AM II which had minimum error variance; Log L, log likelihood; CV (%), coefficient of variation in %.

heritability (0.29 ± 0.04). When, the maternal additive genetic effect and permanent environment effect of cows were present in AM II, the direct additive genetic variance reduced to 56607.31 kg^2 and presence of maternal additive genetic variance was significant (26485.05 kg^2); whereas the variance due to permanent environmental effect of cows was 5921.84 kg^2 . It influenced the direct estimate of heritability which reduced to 0.236 ± 0.04 and maternal heritability was 0.111 ± 0.03 . Thus maternal effect explained 11.1 % of total phenotypic variation in milk yield of Sahiwal cows. The cow's permanent environmental heritability was 0.025 ± 0.02 and explained 2.5 % variation of milk yield in Sahiwal cattle. The multi trait animal model (AM III) had no advantage over AM I because it had lower direct additive genetic variance and higher error variance than AM I. The heritability estimate obtained by sire model was lowest because of least contribution via additive genetic variance. Among all the animal models used for study the additive genetic variance was maximum in AM I because of improper partitioning of variance with lesser number of effects in the model. The direct additive genetic variance and heritability estimate reduced in the animal model with maternal effects (AM II) indicated that maternal effect inflated these estimates on higher side in AM I and AM III. So, it could be concluded that inclusion of more effects in animal model helped in proper partitioning of variance and reduction in direct heritability. Presence of significant estimate of maternal heritability may be due to strong mothering ability of cows at GLF, Lucknow and GCBF, Durg because of suckling practices being followed at these 2 farms. Albuquerque *et al.* (1998) and Edriss *et al.* (2006) reported maternal heritability as 0.008 and 0.07 for milk yield in dairy cows and a non-significant decrease in direct heritability after inclusion of maternal effect in animal models. Similar to our findings Kumar *et al.* (2009) reported 4.4 % to 7.2 % variation due to maternal effect in pooled lactation milk yield of Sahiwal cows. On contrary, Boettcher and Gibson (1996) reported about 0.5% of total phenotypic variation for first lactation milk yield ascribed due to maternal effect in Canadian Holsteins using an animal model. In agreement with present findings larger estimates of maternal effect have been described in the literature for Holsteins (Bell *et al.* 1985, Schutz *et al.* 1992). Using similar models, Huizinga *et al.* (1986) reported that cytoplasmic effects contributed 6.0 % of the phenotypic variance of milk yield

in Holstein Friesian and Dutch Friesian crossbred cows. Khattab *et al.* (2005) reported removal of additive maternal genetic effects from the animal model increased estimates for heritability of additive genetic effects by 1 % for 305 days milk and concluded the additive maternal genetic effect do not seem to make important contribution to the phenotypic variance for milk yield. Reed and Van Vleck (1987) reported lack of cytoplasmic inheritance for milk yield of temperate dairy cattle. On contrary, Wolf *et al.* (2005) reported low and negative maternal effects for milk yield of Czech dairy cows. In agreement with findings, Berry *et al.* (2008) reported a significant maternal genetic variance for 305 days milk yield in first and third lactation of dairy cattle. Finally, it was revealed that in present investigation the maternal heritability was highest than all other reports cited above. Therefore, in tropical country like India where weaning is delayed under semi-intensive management conditions, it becomes necessary to integrate out the variance of maternal effect from the variance of direct additive genetic effect. In present investigation the multitrait model (AM III) had no further advantage over simple single trait animal model (AM I) because of its lower direct additive genetic variance and higher error variance than AM I.

Sire evaluation: The average breeding values of sires estimated by different models are presented in Table 3. The average breeding value of sires for FL305DMY was 1581.80 kg using sire model (SM). The range of breeding value was minimum (921.92 kg) because of lowest CV (30.21%) of adjusted records of FL305DMY. The simplest animal model of sire evaluation (AM I) had average breeding value of 1523.78 kg and the breeding value ranged from 2063.26 kg to 667.42 kg. The range of breeding value was highest (1395.84) in AM I. Under AM II, the average breeding value was 1523.78 kg (Table 3). The breeding value ranged from 2003.97 kg to 831.58 kg with a difference of 1172.39 kg (table 3). The range of breeding value in AM III was 1249.33 kg with maximum breeding value of 2051.10 kg (34.60% above the average breeding value) and minimum breeding value of 801.77 kg (47.38% below the average breeding value). The average breeding value of Sahiwal bulls for FL305DMY was highest (1581.80 kg) using BLUP method of sire evaluation whereas it was lowest (1523.78 kg) in all 3 animals. On contrary, using BLUP method of sire evaluation comparatively lower estimates of breeding values were

Table 3. Average breeding values (BV) estimates of sires for FL305DMY by different methods

Sire evaluation methods	Average BV (kg)	Number of sires above average BV	Number of sires below average BV	Maximum BV (kg)	Minimum BV (kg)	Range of BV (kg)
BLUP (SM)	1581.80	60 (52.63)	54 (47.37)	2023.62 (27.94)	1101.70 (30.35)	921.92
AM I	1523.78	56 (49.12)	58 (50.88)	2063.26 (35.40)	667.42 (56.19)	1395.84
AM II	1523.78	58(50.87)	56 (49.13)	2003.97 (31.51)	831.58 (45.42)	1172.39
AM III	1523.78	55 (48.24)	59 (51.76)	2051.10 (34.60)	801.77 (47.38)	1249.33

Figures in the parentheses indicate the percentage.

reported by Pundir *et al.* (2004) and Banik and Gandhi (2006) in Sahiwal sires. However, Banik and Gandhi (2006) reported a close estimate (1503.99 kg) of breeding value in Sahiwal sires using DFREML method of sire evaluation. The highest range of estimated breeding values for Sahiwal sires in AM I indicated that this model differentiated genetically amongst bulls to the largest extent as compared to other methods. The lowest range of breeding values using sire model (BLUP) indicated that this method was least capable to estimate genetic differences amongst bulls as compared to other animal models and thus there was scope for underestimation of breeding values for some of the superior sires and vice versa. Thus, using AM II having an optimum range of EBVs, an optimum number of sires were having estimated breeding values 20 % (four sires) above the average breeding value and thus leaving least scope for underestimation or overestimation of breeding values; whereas in same case these numbers were too low (one sire) in SM and on higher side (six sires in each) in other two animal models (AM I and AM III).

Comparison of sire evaluation models: The AM II had minimum error variance and therefore, it was considered to be most efficient followed by AM I, AM III and BLUP based SM, respectively. The relative efficiencies of sire model, AM I and AM III were 70.6 %, 88.9 % and 86.0 %, respectively, as compared to AM II (Table 2). In agreement with our report Sahana and Gurnani (1999), Mukherjee (2005) and Banik and Gandhi (2006) reported that DFREML was more efficient compared to least squares method and BLUP method of sire evaluation. The proximity of adjusted CV (%) with unadjusted data CV (34.40%) was lowest in AM III with the adjusted CV of 36.39%, followed by AM II (32.04%), AM I (31.95%) and SM (30.23%). Thus, alteration of adjusted CV (%) with unadjusted CV (%) was minimum in AM III (1.99 %) followed by AM II (2.36 %), AM I (2.45 %) and SM (4.17 %). Although AM III was found to be most stable because of least alteration of adjusted CV (%) with unadjusted CV (%) but other animal models were very close to it in terms of their stability where alteration percent ranged from 1.99 % in AM III to maximum 2.45 % in AM I. Whereas, the sire model was least stable because of highest alteration (4.17 %) of adjusted CV (%) with unadjusted CV (%) and these finding was in agreement of the reports of Gandhi and Gurnani (1991). On the contrary, Banik and Gandhi (2006) reported SM was more stable than AM I and least squares methods of sire evaluation in Sahiwal cattle. Accuracy of different animal models were judged on the basis of log L value. Animal models with higher Log L values were supposed to be more accurate. AM I and AM II had similar Log L values revealed almost similar accuracy whereas the lowest Log L value was in AM III indicated that AM III was least accurate. The rank and product moment correlations among breeding values of sires estimated from different models of sire evaluation were statistically significant

Table 4. Rank correlations (above diagonal) and product moment correlations (below diagonal) among different methods of sire evaluation on the basis of FL305DMY yield

Sire evaluation methods	BLUP (SM)	AM I	AM II	AM III
BLUP (SM)	1.00	0.925**	0.936**	0.898**
AM I	0.895**	1.00	0.991**	0.967**
AM II	0.908**	0.993**	1.00	0.957**
AM III	0.881**	0.981**	0.972**	1.00

**Significant at 1% level.

($P < 0.01$) and very high (Table 4). However, the rank and simple correlations of sire model with all animal models were comparatively lower than those correlations among animal models. The present finding was in agreement with Banik and Gandhi (2006), reported lower rank and simple correlations between SM (BLUP) and AM I in Sahiwal cattle evaluated on the basis of FL305DMY. Similar to present findings, Sahana and Gurnani (1999), Mukherjee (2005) and Banik and Gandhi (2006) also reported high rank correlations between DFREML, least squares method and BLUP methods and suggested that these methods were more or less similar in ranking of dairy sires for FL305DMY.

Thus it was concluded that the impact of maternal inheritance on milk production can't be ignored in tropical country like India. The direct maternal variance had a significant influence on partitioning of total phenotypic variance of milk yield. So it is necessary to incorporate the maternal effect during genetic evaluation of Sahiwal cattle population for getting better and reliable result. The sire model could not be as good as any of the animal model for an efficient, accurate and stable genetic evaluation of dairy cattle. Among animal models, the model with maternal effect (AM II) could be advocated for efficient, accurate and fairly stable genetic evaluation of Sahiwal cattle for proper discrimination amongst sires.

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