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RESEARCH ARTICLE

Estimation of direct and maternal covariance of production efficiency traits in Murrah buffalo

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Abstract: The study employed data collected from 662 Murrah buffaloes meticulously documented over a 24-year period (1996-2019). The data were sourced from historical pedigree records maintained at the buffalo farm of the Department of Livestock Production and Management (LPM) at Lala Lajpat Rai University of Veterinary and Animal Sciences in Hisar. The average values under univariate animal model for production efficiency traits *viz.* MCI and MSC were 4.84 kg/day and 1.33 kg/day, respectively. Six univariate animal models were utilized to compute (co)variance components and heritabilities for traits related to first lactation production efficiency. Among these models, Model 1 was identified as the most suitable for calculating milk yield per day of calving interval (MCI), while Model 2 proved optimal for milk yield per day of age at second calving (MSC). Maternal effects were observed to influence MSC (ranging from 0.09 to 0.22). The heritability estimates for the production efficiency traits, namely MCI and MSC, were 0.35±0.12 and 0.15±0.09, respectively. The breeding values for production efficiency traits ranged from 0.46 kg/day for MCI to 0.63 kg/day for MSC. A significant and positive genetic correlation between additive and maternal effects was identified, ranging from 0.41 to 0.98. This suggests a consistent and strong interaction between genetic factors inherited from the dam. Rank correlation of breeding values across all six models ranged from 0.71 (non-significant) to 1.00 for MCI and MSC. MCI exhibited positive genetic and phenotypic trends, showing annual increases of 0.009±0.005 kg/day and 0.148±0.018 kg/day, respectively. In contrast, MSC displayed a very low negative genetic trend (-0.001±0.001 kg/day), while a positive phenotypic trend was observed at 0.047±0.006 kg/day per year. These trends indicate that both selection and management practices are concurrently contributing to the improvement of production efficiency traits.

Keywords: Production efficiency traits; Univariate animal model; Maternal effects; Spearman's rank correlation; Genetic trends and phenotypic trends

Introduction

India holds the top position globally in milk production, boasting the largest buffalo population featuring premier breeds such as Murrah, Nili-Ravi, Bhadawari, and Surti. The Murrah buffalo, particularly, serves as the focal point of the dairy industry and is utilized as an improving breed not only in India but also in several other countries, as indicated by NBAGR (2006). Indigenous and non-descript buffaloes contribute significantly, accounting for 45% of India's total milk production, reaching 89 million tonnes (DAHD, 2022-23). A linear animal model incorporates both direct and maternal genetic effects, featuring covariance between them, along with a maternal permanent environmental effect. Additive maternal effects, as defined by Schutz et al. (1992), encompass any influence from a dam on its offspring, excluding the effects of directly transmitted genes affecting the offspring's performance. Maternal effects comprise additive genetic maternal effects and environmental maternal effects. The maternal environment primarily encompasses factors like the mother's milk yield, mothering ability, and the uterine environment. The maternal genotype influences the phenotypic expression of the offspring through its genotype for maternal effects and its direct additive genes for growth. Exclusion to consider maternal genetic effects in the statistical model results in biased upward heritability estimates and diminished realized efficiency of selection compared to expectations, as demonstrated by Rashidi et al. (2008), Jafaroghliet al. (2010), Eskandarinasabet al. (2010), and Prakash et al. (2012).

Genetic and phenotypic trends indicates the improvement in overall productivity over an entire year or period, depends upon the time taken into account. Annual rate of change in productive and reproductive traits reveal the quantitative appraisal and genetic gain per year. Keeping the environmental trends aside, we can measure the change in performance of the population for

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an economic trait per year or period, can estimate the phenotypic and genetic trends. The genetic and phenotypic trends were estimated by regressing breeding value and phenotypic value of the trait on year of the birth of the bull/animal, respectively. Several researchers (Yadav et al. (1983), Sahana and Sadana (1998), Chakraborty et al. (2010), Singh et al. (2011) and Chakraborty and Dhaka (2012) reported genetic and phenotypic trends in various traits in Murrah buffaloes.The present study is conducted to know the impact of additive and maternal influences on production efficiency traits and to determinethe progress through phenotypic and genetic trends is necessary to assess the effectiveness of selection within a population over time.

Materials and Methods

Source of data

The research dataset includes information from 662 Murrah buffaloes meticulously recorded over a span of 24 years (1996-2019). These invaluable data, pertaining to crucial production efficiency traits, were sourced from historical pedigree-sheets maintained at the buffalo farm within the Department of Livestock Production and Management (LPM) at LalaLajpat Rai University of Veterinary and Animal Sciences, Hisar. The research site, Hisar, is characterized by a semi-arid, sub-tropical climate and is geographically situated at 29° 10' N latitude, 75° 40' E longitude, with an altitude of 215.2 meters.

Traits under study

The production efficiency traits under this study included were milk yield per day of calving interval (MCI) and milk yield per day of age at second calving (MSC) of first lactation. Milk yield per day of calving interval was calculated by dividing total lactation milk by calving interval. Milk yield per day of age at second calving was the daily outcome of milk yield up to the second calving. It was calculated by dividing the total lactation milk yield by total age in days up to second calving. Buffaloes with lactation periods shorter than 150 days or yielding less than 500 kg of milk were excluded, as were those flagged as outliers based on abnormal records such as abortion, mastitis, and chronic illnesses. The study's herd maintained a male to female ratio of 1:50.

Statistical analyses

Estimations of (co)variance components and heritabilities for various traits were computed using a set of univariate animal models. The analysis utilized the average information restricted maximum likelihood (AIREML) algorithm implemented with WOMBAT software (Meyer,2007). The primary focus was on first lactation production efficiency traits. To estimate maternal (co)variance components, six distinct models were applied. Each trait underwent a univariate analysis in which variance and (co)variance components were estimated. The models considered or excluded maternal components, providing a comprehensive exploration of the trait characteristics.

Model 1: $y = X\hat{a} + Z_1a + e$

Model 2: $y = X\hat{a} + Z_1a + Z_2m + e$ **with** $\mathrm{Cov}(a, m) = 0$

Model 3: $y = X\hat{a} + Z_1a + Z_2m + e$ **with** $\mathrm{Cov}(a, m) = A\sigma_{am}$

Model 4: $y = X\hat{a} + Z_1a + Z_3c + e$

Model 5: $y = X\hat{a} + Z_1a + Z_2m + Z_3c + e$ **with** $\mathrm{Cov}(a, m) = 0$

Model 6: $y = X\hat{a} + Z_1a + Z_2m + Z_3c + e$ **with** $\mathrm{Cov}(a, m) = A\sigma_{am}$

Where, $y = n \times 1$ vector of observations for each trait; X = Incidence matrix that relates data to the unknown vector of fixed effects $\hat{a}$; Z_1 = Incidence matrix that relates unknown vector of direct (a) breeding values, to y; Z_2 = Incidence matrix that relates unknown vector of maternal (m) breeding values, to y; Z_3 = Incidence matrix that relates unknown additional random vector of permanent maternal environmental effects (c) to y; e = Unknown vector that contains random residuals due to environmental effects; A = Numerator relationship matrix; $\acute{o}_{am}$ = Covariance between direct and maternal additive genetic effects.

Heritability (h^2) was obtained in all the models; however, maternal heritability (m^2) was estimated in Model 2, 3, 5 and 6. Maternal permanent environmental (c^2) was evaluated in Model 4, 5 and 6 whereas correlations between direct and maternal additive genetic (r_{am}) components were obtained under Model 3 and 6.

Assumptions of the model were:

$V(a) = A\sigma^2_a$, $V(m) = A\sigma^2_m$, $V(c) = I\sigma^2_c$, and $V(e) = I\sigma^2_e$

Where, I = Identity matrix, σ^2_a = Direct additive genetic variance, σ^2_m = Maternal additive genetic variance, σ^2_c = permanent environmental variance, σ^2_e = Residual variance

Estimated (co) variance components were used to obtain,

$(h^2=\sigma^2_a/\sigma^2_p)$ = Heritability

$(m^2=\sigma^2_m/\sigma^2_p)$ = Maternal heritability

$(c^2=\sigma^2_c/\sigma^2_p)$ = common environmental variance as a proportion of phenotypic variance

$[r_{am} = (\sigma_{am}/{”}\sigma^2_a \times \sigma^2_m)]$ = Direct-maternal genetic correlation

$(h^2_t=(\sigma^2_a+0.5\sigma^2_m+1.5\sigma_{am})/\sigma^2_p)$ = Total heritability (Willham,1980)

$(t_m = (1/4)\, h^2 \pm m^2 \pm c^2 \pm r_{am}\, m^{2}{”}h^2)$ = Maternal effect across year repeatability for dam performance (Willham, 1972)

Identification of optimum model for different traits-

The model possessing the highest log-likelihood, deemed the 'best' model, underwent a comparison with every other model using the AIC criteria. The goal was to identify the simplest model whose log-likelihood did not significantly differ from that of the 'best' model. The comparison among all models was executed through the likelihood ratio test (LRT). The statistical measure for the likelihood ratio test (LR_{ij}) for sequentially reduced models (Rao, 1973) is as follows:

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

Where,

L_i = Maximum likelihood for the complete model (with the maternal effect);

L_j = Maximum likelihood for the reduced model (without the maternal effect).

An effect was considered to have a significant impact if its inclusion resulted in a noteworthy increase in log-likelihood compared to a model that omitted it. Statistical significance, determined at $P<0.05$, involved assessing differences in log-likelihood values. This comparison was conducted against a Chi-square distribution with degrees of freedom equal to the variance in the number of (co)variance components fitted for the two models.Spearman's rank correlation and Pearson correlation of the estimated breeding values for first lactation production efficiency traits were computed using IBM SPSS Statistics version 23.

Estimation of Genetic and Phenotypic Trends:

Estimation of Genetic Trends

The genetic trends of different traits were estimated by taking regression of weighted average of sire's estimated breeding value (WAEBV) for each year on year. The WAEBV for the kth year was calculated as follows:

$$\mathbf{\Sigma n_{ik} S_i / n_{.k}}$$

Where,

n_{ik} = number of daughters of sire i (i =1,2,3,4………………..n) in year k

S_i = estimated breeding value of sire i.

$n_{.k}$ = total no. of daughters of n sires in year k.

Estimation of Phenotypic Trends

Phenotypic trends for each trait were estimated as linear regression of performance of population on year.The standard error for of linear regression required for estimating phenotypic and genetic trends was estimated using formula given by Falconer (1991).

$$\text{S.E. (b)} = \sqrt{} \; [\{1 / (N-2)\} \{(\sigma^2_x / \sigma^2_y) - b^2\}]$$

Where,

N = number of period observations of x and y,

$\sigma^2_{y=}$ variance of y,

$\sigma^2_{x=}$ variance of x and

b = regression coefficient of y on x.

Results and Discussion

The average values under univariate animal model using WOMBAT software for production efficiency traits *viz.* MCI and MSC were 4.84 kg/day and 1.33 kg/day, respectively (Table 1). Average value of MCI were close to the findings of Godara (2003), Chakraborty et al. (2010) and Patil et al. (2018) but lower values were reported by Kumar et al. (2000) and Suresh et al. (2004), however, higher estimates ranging from 13.7 to 26.4 kg/day were obtained by Arbel et al. (2001) and Zambianchi et al. (1997) in Holstein cows. The heritability estimates of the production efficiency traits *viz.* MCI and MSC were 0.35±0.12 and 0.15±0.09, respectively. MCI and MSC were found moderate and low heritable respectively; which were in accordance with the findings of Chakraborty et al. (2010b) and Patil et al. (2018). The range of breeding values of production efficiency traits was 0.46 kg/day for MCI and 0.63 kg/day for MSC.

The analysis of variance components and genetic parameters for milk yield per day of calving interval (MCI) revealed varying estimates under different models (Table 2). In Model 1, the additive genetic variance (σ^2_a) was estimated at 1.50, which remained consistent in Models 2 and 3. However, Model 4 showed a slight increase to 1.53, and this remain persisted in Models 5 and 6. The maternal genetic variance (σ^2_m) ranged from 1.43 to 1.80 across the models, indicating some variability. The heritability

Table 1: Sum model values for production efficiency traits

Particulars	MCI	MSC
No. of animal IDs in data file	662	662
No of sires	169	169
No of sires with records & progeny in data	120	120
No of dams with progeny in data	105	105
Mean	4.84	1.33
Standard Deviation	1.51	0.59
Minimum	0.1	0.2
Maximum	9.52	4.83

(h^2) exhibited fluctuations from 0.26 to 0.41, suggesting that genetic factors contribute moderately to the variation in MCI which were in accordance with the findings of Chakraborty et al. (2010) and Patil et al. (2018) in Murrah buffaloes and Zambianchi et al. (1997) in Holstein cows. The proportion of the variance attributed to the common environment (c^2) ranged from 0.21 to 0.32, indicating a notable environmental influence. High and positive genetic correlation between the additive effect and materanl effect varied from 0.41 to 0.67, suggesting that there is a consistent and strong interaction between the genetic factors inherited from the dam. The range of genetic correlations observed across models highlights the importance of considering both additive and maternal genetic effects in breeding programs aimed at improving milk production in the given population. The estimates of the permanent environment variance (σ^2_p) ranged from 3.77 to 5.81, indicating substantial overall variability in Milk yield. The log-likelihood values varied among models, with Model 1 showing a significant difference compared to other models, as denoted by the double asterisks (**). Scanty information was available on the use of different animal model on MCI and MSC. The observation in these estimates provide insights into the genetic and environmental factors influencing milk yield per day of calving interval.

Based on loglihood value, model 3 outcame as appropriate model for MSC but there was no significant difference reported between the model 2 and model 3. Therefore, model 2 was taken to be the best model. This model constituted direct additive and maternal components the direct additive and maternal variance were 0.12 and 0.14, respectively. And the direct additive and maternal heritability for this model were 0.08 and 0.19, respectively. This model had lowest heritability among different models, ranged from 0.07 to 0.15 (Table 3). The additive genetic variance (σ^2_a) ranged from 0.08 to 0.15 across models, with Model 4 exhibiting the highest estimate. Maternal genetic variance (σ^2_m) varied between 0.10 and 0.17, reaching its peak in Model 5. The

Table 2: Estimates of co(variance) components and genetic parameters for Milk yield per day of calving interval

Trait	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_a	1.50	1.50	1.41	1.53	1.53	1.53
σ^2_m		1.80	1.52		1.63	1.43
σ_{am}			0.98			0.61
σ^2_c				1.22	1.22	1.22
σ^2_e	0.98	0.50	0.61	1.02	1.02	1.02
σ^2_p	3.99	3.81	5.64	3.77	5.40	5.81
h^2	0.35	0.39	0.30	0.41	0.28	0.26
m^2		0.47	0.35		0.30	0.25
r_{am}			0.67			0.41
c^2				0.32	0.23	0.21
h^2_t	0.38	0.63	0.65	0.41	0.43	0.54
t_m	0.09	0.57	0.64	0.43	0.59	0.63
Log-L	-681.00**	-760.20	-769.16	-742.87	-696.69	-692.26

** denotes significant difference among LRT value

Table 3: Estimates of co(variance) components and genetic parameters for Milk yield per day at age of second calving

Trait	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_a	0.11	0.12	0.11	0.15	0.11	0.08
σ^2_m		0.14	0.12		0.17	0.10
σ_{am}			0.01			0.12
σ^2_c				0.11	0.10	0.10
σ^2_e	0.21	0.18	0.18	0.20	0.18	0.18
σ^2_p	0.27	0.25	0.34	0.26	0.28	0.35
h^2	0.15	0.08	0.09	0.14	0.07	0.08
m^2		0.19	0.09		0.22	0.12
r_{am}			0.98			0.98
c^2				0.04	0.004	0.004
h^2_t	0.39	0.76	0.53	0.58	0.68	0.89
t_m	0.04	0.22	0.21	0.08	0.24	0.24
Log-L	213.63	217.51**	218.55	213.74	217.08	218.17

**denotes significant difference among LRT value

Table 4: Rank correlations coefficient of entire six models of production efficiency traits

	Production Efficiency Traits					
MCI	1	2	3	4	5	6
1	1	0.71	0.71	0.86*	0.86*	0.86*
2	0.71	1	1.00**	0.86*	0.93**	0.90**
3	0.71	1.00**	1	0.86*	0.93**	0.84**
4	0.86*	0.86*	0.86*	1	1.00**	1.00**
5	0.86*	0.93**	0.93**	1.00**	1	0.98**
6	0.86*	0.90**	0.84**	1.00**	0.98**	1
MSC						
	1	2	3	4	5	6
1	1	0.71	0.86*	1.00**	0.71	0.71
2	0.71	1	0.95**	0.71	0.98**	0.98**
3	0.86*	0.95**	1	0.86*	0.90**	0.98**
4	1.00**	0.71	0.86*	1	0.78*	0.78*
5	0.71	0.98**	0.90**	0.78*	1	0.97**
6	0.71	0.98**	0.98**	0.78*	0.97**	1

Where *P<0.05, **P<0.01

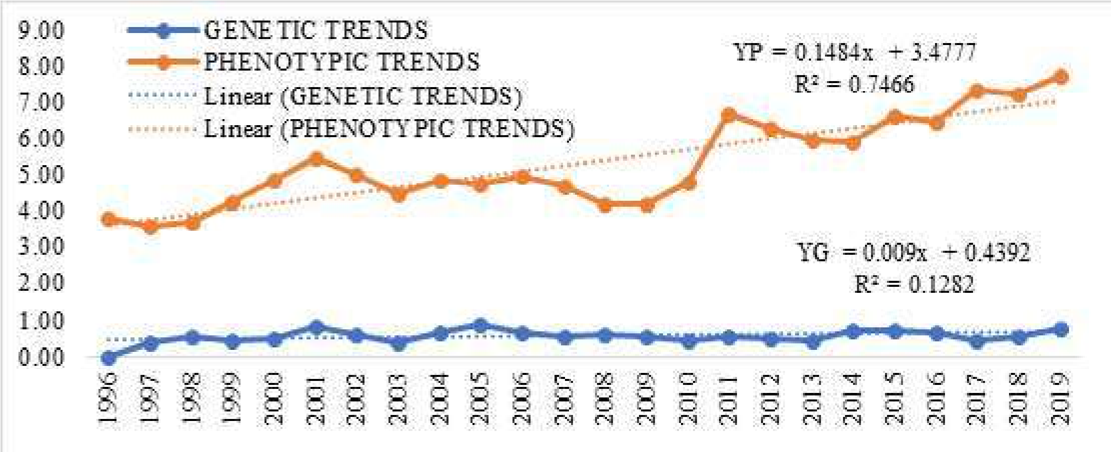
Table 5: Genetic and phenotypic correlation of performance traits using Bi-variant animal model

Traits	MCI	MSC
MCI	-	0.51**±0.19
MSC	0.73±0.05	-

Table 6: Year wise genetic and phenotypic trends of production efficiency traits

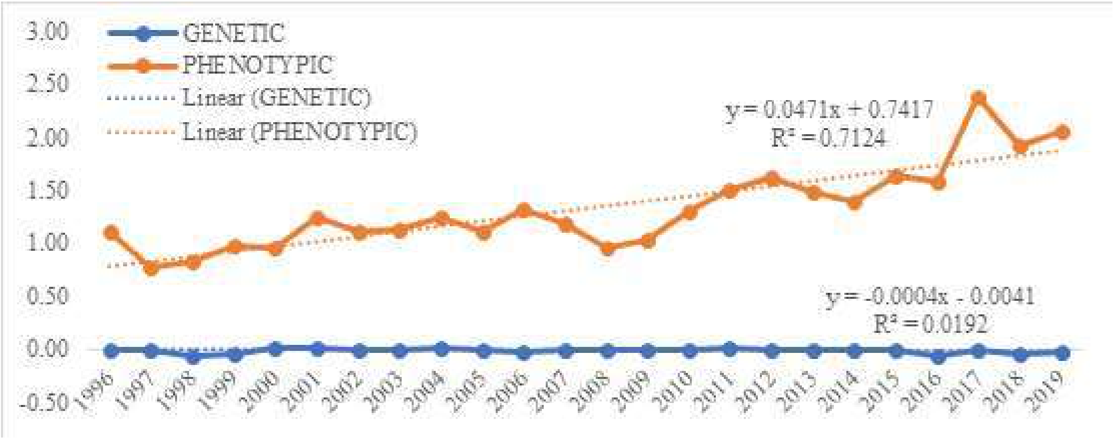
Traits	Genetic trends (Y_G)	Phenotypic trends (Y_P)	$R^2_{G(\%)}$	$R^2_{P(\%)}$
MCI (kg/day)	0.009±0.005	0.148**±0.018	13	75
MSC (kg/day)	-0.0004±0.000	0.047**±0.006	2	71

Fig. 1 Genetic and phenotypic trends of MCI



heritability (h^2) fluctuated between 0.07 and 0.15, showcasing the range of genetic influence on MSC, these estimates were comparable with Chakraborty et al. (2010) and Patil et al. (2018). Noteworthy was the consistently high genetic correlation (r_{am}) of 0.98 between additive and maternal effects across all models. Environmental components, such as the common environment (c^2), ranged from 0.004 to 0.04, indicating a subtle environmental contribution. Evaluating the significance of model fit, Model 2 emerged as the most suitable, with a log-likelihood value of 217.51. Importantly, the difference between the maximum log-likelihood value and Model 2's value was not statistically significant,

Fig. 2 Genetic and phenotypic trends of MSC



affirming the adequacy of Model 2 in capturing the underlying genetic architecture of milk yield per day at the age of the second calving. Rank correlations coefficient of the breeding values of all the 6 models used for each trait has been shown in Table 4 for production efficiency traits. The lowest and highest values of rank correlation of breeding values of all six models were ranged from 0.71 (non-significant) to 1.00 for MCI and MSC. The genetic correlation between MCI and MSC using bi-variate analysis was 0.73±0.05 and phenotypic correlation was 0.51±0.19 which was highly significant at $p<0.01$ (Table 5). Similar to the findings of Kandasamy et al. (1991), Chakraborty et al. (2010) and Patil et al. (2018).

Year wise genetic and phenotypic trends of production efficiency traits is shown in table 6. Positive genetic and highly significant ($p<0.01$) phenotypic trends were shown by MCI, as 0.009±0.005 kg/day and 0.148±0.018 kg/day annually. This indicated that selection as well as management practices going on hand in hand to raise the production efficiency traits. MSC had very low negative genetic trend (-0.001±0.001 kg/day) which was non-significant while positive and highly significant ($p<0.01$) phenotypic trend was shown by MSC as 0.047±0.006 kg/day per year, indicated the decrease in variability in this trait along the years. In contrast to this, Chakraborty and Dhaka (2012) reported negative genetic and phenotypic trends for MCI and MSC and Sahana and Sadana (1998) found negative genetic trend for MCI. However, Sharma and Singh (1992) reported positive genetic trends for MCI in Murrah buffalo. Similar to present study, Sahana and Sadana (1998) and Singh et al. (2003) reported positive phenotypic trends in Murrah buffaloes and Karan Swiss cattle.

Conclusion

The positive trends indicated the improvement in production efficiency traits over the years which pointed towards the better selection strategy, nutrition and management practices being followed at the farm.

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