Heritability Estimates under Single and Multi-Trait Animal Models in Murrah Buffaloes

A. Jain* and D. K. Sadana[1]

Dairy Cattle Breeding Division, National Dairy Research Institute, Karnal - 132001, India

ABSTRACT : First lactation records of 683 Murrah buffaloes maintained at NDRI, Karnal which were progeny of 84 sires used for comparing the heritability estimates of age at first calving, first lactation milk yield and first service period under single and multiple trait models using restricted maximum likelihood (REML) method of estimation under an individual animal model. The results indicated that the heritability estimates may vary under single and multiple trait models depending upon the magnitude of genetic and environmental correlation among the traits being considered. Therefore, a single or multiple trait model is recommended for estimation of variance components depending upon the goal of breeding programme. However, there may not be any advantage of considering a trait with zero or near zero heritability and having no or very low genetic correlation with other traits in the model. Lower heritability estimates of part lactation yield (120-day milk yield) implied that there may not be any advantage of considering this trait in place of actual 305-day milk yield, whereas, comparable heritability estimates of predicted 305-day milk yield suggested that it could be used for sire evaluation to reduce the cost of milk recording under field conditions. (*Asian-Aus. J. Anim. Sci. 2000. Vol. 13, No. 5 : 575-579*)

Key Words : Animal Model, Multi-Trait, Murrah Buffaloes, Lactation, Age at First Calving

INTRODUCTION

In an animal breeding programme, accurate heritability estimates are important not only for giving appropriate weightage to the traits being considered for improvement but also for estimation of correct breeding value of the animals. In India heritability estimates have generally been obtained using least-squares technique under single trait models whereas the heritability estimates may vary depending upon whether the model used is single or multiple trait (Lin and Lee, 1986). In addition, use of individual animal model, by utilizing all the available information, would further increase the accuracy when compared with a sire or maternal grandsire model (Dong et al., 1988). This study was undertaken to compare the heritability estimates obtained from single and multiple trait animal models. The predicted lactation yield and part lactation records were also studied to examine whether these traits could be taken in place of actual 305 days lactation yield for sire evaluation.

MATERIALS AND METHODS

First lactation records of 683 Murrah buffaloes,

progeny of 84 sires maintained at National Dairy Research Institute (NDRI), Karnal were used. The records pertained to the year of birth from 1967 to 1991 and year of calving from 1971 to 1994. Cases of culling in the middle of lactation, abortion and other pathological causes affecting the lactation were considered abnormal and hence such records were excluded from the analysis. The records with less than 500 kg of milk production or less than 100 days of lactation length were also excluded. A total of 17% records were discarded on account of these restrictions.

In view of small differences expected from year to year and to increase the class frequency, the total duration from 1967 to 1994 was classified into five periods based on year of birth (67-70, 72-76, 77-83, 84-87 and 88-91) and year of calving (71-74, 75-80, 81-86, 87-90 and 91-94). Moreover, a year was divided into four seasons viz. winter (December-March), summer (April-June), rainy (July-September) and autumn (October-November) to account for within year environmental effects. The small, unbalanced data spread over a number of years used in the present study is typical of the data generated from animal breeding programmes in India.

The traits considered were age at first calving (AFC), first lactation 305-day or less milk yield (F305MY), 305-day predicted yield (PY305), 120-day milk yield (MY120) and first service period (FSP). The predicted yield was estimated based on three test day yields taken by stratified random sampling technique using the regression equation developed by Dass (1995) for Karnal farm. The accuracy of

* Corresponding Author: A. Jain. National Bureau of Animal Genetic Resources, Karnal-132 001, India. Tel: +91-11-184-271250, Fax: +91-11-184-253654, E-mail: anand_nbagr@yahoo.com.

[1] Senior Scientist, Dairy Cattle Breeding Division.

prediction (R^2 value) was 88.2 per cent.

Statistical methodology

The general animal model used was as under:

$$y = Xb + Zu + e$$

For three traits, the model could be expressed as:

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \end{bmatrix} = \begin{bmatrix} X_1 & 0 & 0 \\ 0 & X_2 & 0 \\ 0 & 0 & X_3 \end{bmatrix} \begin{bmatrix} b1 \\ b2 \\ b3 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 & 0 \\ 0 & Z_2 & 0 \\ 0 & 0 & Z_3 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \\ u_3 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \end{bmatrix}$$

where,

y_i is the vector of observations for i^{th} trait ($i=1, 2, 3$).

b_i is the vector of fixed effects of period (1,2,..5) and season (1, 2, 3, 4) for i^{th} trait. For AFC, period and season of birth of the animal were considered, whereas for milk yield and FSP, period and season of calving were considered. Service period was also considered as a covariable to milk yield traits in some single and two trait models.

u_i is a vector of random, additive genetic effect of animal for i^{th} trait.

X_i & Z_i are design matrices for fixed and random animal effects respectively,

with $E(y)=Xb$ and variance covariance structure as given by:

$$\text{var} \begin{bmatrix} u_1 \\ u_2 \\ u_3 \\ e_1 \\ e_2 \\ e_3 \end{bmatrix} = \begin{bmatrix} A\,\sigma^2_{a1} & A\,\sigma_{a12} & A\,\sigma_{a13} & 0 & 0 & 0 \\ A\,\sigma_{a21} & A\,\sigma^2_{a2} & A\,\sigma_{a23} & 0 & 0 & 0 \\ A\,\sigma_{a31} & A\,\sigma_{a32} & A\,\sigma^2_{a3} & 0 & 0 & 0 \\ 0 & 0 & 0 & I\,\sigma^2_{e1} & I\,\sigma_{e12} & I\,\sigma_{e13} \\ 0 & 0 & 0 & I\,\sigma_{e21} & I\,\sigma^2_{e2} & I\,\sigma_{e23} \\ 0 & 0 & 0 & I\,\sigma_{e31} & I\,\sigma_{e32} & I\,\sigma^2_{e3} \end{bmatrix}$$

$$= \begin{bmatrix} A*T & 0 \\ 0 & I*E \end{bmatrix} = \begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix}$$

where,

var(u) = G
var(e) = R
cov(u, e') = 0 and
var(y) = V=ZGZ'+R

T is the matrix (3 x 3) of additive genetic variance and covariance

A is a numerator relationship matrix between animals taking all the available relationships tracing back to the foundation stock.

E is the residual (co)variance matrix, and

* represents direct product operator (Searle, 1966)

Data were analyzed using Derivative Free Restricted Maximum Likelihood (DFREML) program of Meyer (1993) which attempts to locate the maximum of the likelihood function (L) without using information from derivative of L.

Maximizing the likelihood

Maximization of the likelihood function was achieved by using Quadratic approximation method (Graser et al., 1987) for single trait models and Simplex method (Nelder and Mead, 1965) for multi-trait models. The convergence was assumed when the variance among the function values was less than 10^{-8}. After convergence, the parameter space was re-searched within a range of 40% of the values obtained at convergence in the previous run to ensure that the maximization attained was global and not local.

The standard errors of the genetic parameters for single trait models were estimated as described by Meyer (1989). In case of multiple trait models, the standard errors of the estimates were not computed in

Table 1. REML estimates of variance components - single trait models

Trait	Additive Genetic Variance	Residual Variance	Heritability Estimates
AFC	5.955	27.537	0.1778 ± 0.0722
F305MY	18249.60	152466.43	0.1069 ± 0.0683
F305MY+covFSP	15128.04	15588.80	0.1157 ± 0.0845
PY305	22074.78	125337.78	0.1497 ± 0.0699
PY305+covFSP	20716.46	98631.20	0.1736 ± 0.0902
MY120	2901.93	30947.18	0.0857 ± 0.0744
MY120+covFSP	3115.18	27884.48	0.1005 ± 0.0928
FSP	~0	12479.94	~0

Note : Number of observations for AFC, F305MY, PY305 and MY120 were 683.
Number of observations for FSP and when FSP was taken as a covariable were 502.

Table 2. REML estimates of (co)variance components - two trait models

Traits	Genetic (co)variance matrix		Residual (co)variance matrix		Parameter estimates	
AFC and F305MY						
AFC	5.972		27.527			0.0936
F305MY	-25.732	18823.16	249.705	151929.5	0.1783	0.1102
AFC and F305MY+covFSP					-0.0767	
AFC	5.980		27.503			0.0790
F305MY	-39.743	18380.51	205.317	112931.2	0.1786	0.1400
AFC and PY305					-0.1199	
AFC	5.872		27.610			0.0997
PY305	-34.993	21781.74	256.488	125559.0	0.1754	0.1478
AFC and PY305+covFSP					-0.0978	
AFC	5.95		27.53		0.1778	0.0931
PY305	-27.85	23202.05	213.43	95460.29	-0.0749	0.1955
AFC and MY120						
AFC	5.91		27.57		0.1764	0.0927
MY120	-3.80	2999.58	102.46	30846.38	-0.0286	0.0886
AFC and MY120+covFSP						
AFC	5.93		27.55		0.1771	0.0820
MY120	15.63	3422.18	67.88	27553.00	0.1097	0.1105

Note: In the 'parameter estimates' column along the diagonal are estimates of heritability, above the diagonal are phenotypic correlation estimates and below the diagonal genetic correlation estimates.
Number of observations for AFC, F305MY, PY305 and MY120 were 683.
Number of observations for Milk Yield Traits with FSP as a covariable were 514.

view of the report by Nunez-Deminguez et al. (1993) that approximation of standard errors were satisfactory for single trait models with direct genetic or direct genetic plus environmental effects whereas the approximation was very unsatisfactory in case of multiple trait models.

RESULTS AND DISCUSSION

Age at first calving (AFC)

The REML heritability estimate of AFC was 0.1778 under single trait model and ranged from 0.1754 to 0.1801 under different multiple trait models. The small change in the heritability estimates under multiple trait models was due to low genetic and phenotypic correlation of AFC with MY traits and FSP (table 2 and 3).

Milk yield traits (F305MY, PY305 and MY120)

The heritability estimate under the single trait model was 0.1069 ± 0.0683 for F305MY. The estimate of 0.1497 ± 0.0699 for PY305 was slightly higher, and 0.0857 ± 0.0744 for MY120 was slightly lower than that of F305MY. When FSP was taken as a covariable to the milk yield (MY) traits in the model, an increase in the heritability estimates was observed. This is due to the fact that some variation in milk

yield is due to the variation in service period. When service period was considered as a co-variable in the model, some of the non-genetic variation in milk yield was accounted for. Therefore, in this model, there was a decline in error variance leading to an increase in heritability estimates.

The heritability estimated under two trait (AFC & MY) models were 0.1102, 0.1478 and 0.0886 for F305MY, PY305 and MY120, respectively. The small increase in the heritability estimates under the two trait models was in agreement with the observed genetic and phenotypic correlation between these traits. However, the absolute differences between genetic and phenotypic correlation estimates were comparatively higher in the models where FSP was taken as a covariable to the MY traits (MY+covFSP, AFC). Therefore, a reasonable improvement in the heritability estimates was observed in these models as compared to the corresponding models without FSP as a covariable. The reason of this increase can partially be attributed to the fact that consideration of FSP as a covariable accounted for non-genetic variation without much affecting the genetic variation. This is evident from the reduction in the error variance of the MY traits.

The three trait model considered AFC, MY and FSP simultaneously. The heritability estimates under the

Table 3. REML estimates of (co)variance components - three trait models

Traits	Additive genetic (co)variance matrix			Residual (co)variance matrix			Parameter estimates		
AFC, F305MY, FSP									
AFC	6.04			27.50			0.1801	0.0941	0.0078
F305MY	-16.89	14378.66		241.97	156043.60		-0.0573	0.0844	0.2664
FSP	25.0E-05	37.0E-05	13.0E-05	5.04	12267.10	12442.48	0.0090	0.0003	0.0000
AFC, PY305, FSP									
AFC	5.88			27.61			0.1755	0.0990	0.0043
PY305	-48.18	19732.69		267.85	127418.60		-0.1415	0.1341	0.1539
FSP	96.0E-04	39.0E-03	0.40	2.76	6555.39	12328.54	0.0063	0.0004	0.0000
AFC, MY120, FSP									
AFC	5.98			27.51			0.1787	0.0919	0.0084
MY120	-3.04	3100.02		100.87	30757.56		-0.0223	0.0916	0.0106
FSP	18.89	152.02	68.05	-13.50	64.99	12210.04	0.9360	0.3310	0.0055

Note: In the 'parameter estimates' column along the diagonal are heritability estimates, above the diagonal are phenotypic correlation and below the diagonal are genetic correlation.
Number of observations for AFC, F305MY, PY305 and MY120 were 683.
Number of observations for Milk Yield Traits with FSP as a covariable were 514.

three trait model were 0.0844, 0.1341 and 0.0916 for F305MY, PY305 and MY120 respectively. The estimates were lower than those obtained under single- and two-trait models. This was due to the fact that the genetic correlation of milk yield traits with FSP was practically zero. The environmental association between milk yield traits and FSP was better accounted for when FSP was taken as a covariable to the milk yield traits rather than taking it as a variable. But, when FSP was taken as a major trait then there would be a dramatic increase in the dimensions of search and little is known about the shape of the likelihood surface for such multi-traits. Therefore, in case of a three trait model with small data set, the surface of convergence may be flatter as compared to a two trait model.

The results suggested that there may not be any advantage of considering a trait with zero or near zero heritability, like FSP, in the model. The two trait model considering first lactation 305-days yield with FSP as a covariable and AFC (F305MY+covFSP, AFC) was appropriate for obtaining REML heritability estimates of these traits in Murrah buffaloes. The heritability estimates of MY120 were lower than those for F305MY in all the models. This suggested that the gain due to decrease in the generation interval is likely to be offset by lower heritability estimates when part lactation milk yield (MY120) is considered in place of F305MY. However, comparable heritability estimates of PY305 suggested that predicted milk yield (PY305) could be used in place of actual milk yield (F305MY) under the field conditions for sire evaluation provided the proposition is also supported by other criteria.

First service period (FSP)

The heritability estimates of FSP were either zero or not different from zero under all the models. There was no advantage of considering FSP as a main trait in the model because the large variation in service period could be attributed to the environmental factors like variation in management practices, availability of feed and fodder etc.

The results of the present investigation indicated that the heritability estimates may vary under single and multiple trait models depending upon the magnitude of genetic and environmental correlation among the traits being considered. Therefore, a single or multiple trait model should be used for estimation of variance components depending upon the goal of breeding programme. However, there may not be any advantage of considering a trait with zero or near zero heritability and very low or no genetic correlation with other traits in the model.

ACKNOWLEDGEMENT

REFERENCES

Dass, G. 1995. Studies on prediction of lactation yield based on test day values in buffaloes. Ph. D. Dissertation. National Dairy Research Institute, Karnal, Haryana, India.

Dong, M. C., L. D. Van Vleck and G. R. Wilton. 1988. Effect of relationship on variance components with an Animal Model and REML. J. Dairy Sci. 71:3047-3052.

Graser, H. U., S. P. Smith and B. Tier. 1987. A derivative-free approach for estimating variance components in animal models by restricted maximum likelihood. J. Anim. Sci. 64:1362-1370.

Lin, C. Y. and A. J. Lee. 1986. Sequential estimation of genetic and phenotypic parameters in multiple trait mixed model analysis. J. Dairy Sci. 69:2696-2703.

Meyer, K. 1989. Restricted Maximum Likelihood to estimate variance components for animal models with several random effects using a derivative-free algorithm. Genet.

Sel. Evo. 21:317-320.

Meyer, K. 1993. Derivative Free Restricted Maximum Likelihood programme. User notes. University of New England, New South Wales, Armidale, Australia.

Nelder, J. A. and R. Mead. 1965. A simplex method for minimisation. Comp. J. 7:147-151 (Cited by Meyer, 1993).

Nunez-Dominguez, R., L. D. Van Vleck, K. G. Boldman and L. V. Cundiff. 1993. Correlation for genetic expression for growth of calves of Hereford and Angus dams using a multivariate animal model. J. Anim. Sci. 71:2330-2340.

Searle, S. R. 1966. Matrix Algebra for the Biological Sciences (Including Application in Statistics). John Wiley & Sons. Inc., NY, USA.